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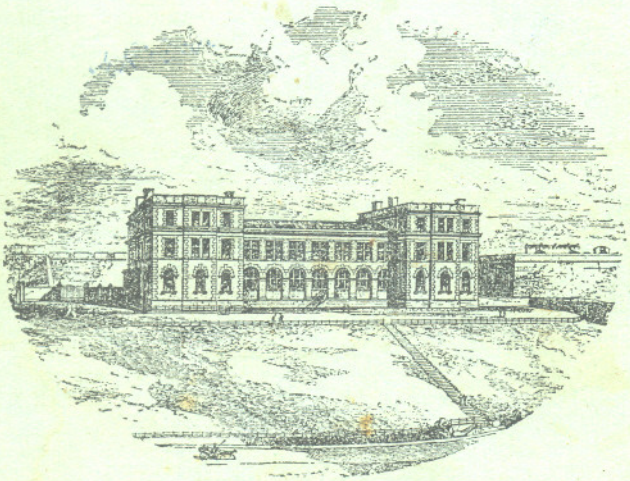

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The Relation of the Plankton to some Chemical and Physical Factors in the Clyde Sea Area.

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With 9 Figures in the Text and 10 Plates.

CONTENTS

THE changes in the plankton and their relationship to the chemical and physical factors has long been a subject of inquiry, and an impetus has recently been given to this work by the development of more accurate methods of estimation of some of the factors by various workers on both the biological and chemical sides (Lohmann (**18**), McClendon (**19**), Atkins (**1**, **2**, **3**, **4**, **5**), etc.). Only in isolated cases, however, has more than a general relationship been made out, and this work was undertaken with the object of correlating as closely as possible the changes in the plankton with the changes in some of the chemical and physical factors.

Plant and animal life is abundant in the Clyde Sea Area, and it was thought that the changes occurring would be more marked and so more easily studied than in the open sea. In 1924 a series of three cruises was made round the whole area, and in 1925 this number was increased to five and further chemical estimations were made. In 1926 it was felt that more frequent observations would lead to more valuable results, and Loch Strivan was visited weekly for the greater part of the year.

Description of Clyde Sea Area.

The area has been described in detail by Mill (**20**), and a summary of his description is given below (Text Fig. 1).

The Kintyre peninsula, which forms the western boundary of the area, is separated from Ireland by the North Channel, eleven miles across. The southern boundary of the area stretches from the Mull of Kintyre to Galloway, a distance of twenty-three miles. On the south it is divided from the Irish Sea by the Great Plateau, which has an average depth of 24 fathoms, this deepening northward to the Arran Basin. The islands of Arran, Inchmarnock, Bute, and the Cumbraes divide this into a number of narrow sounds, continued to the north as a series of lochs or fjords. The north-west is prolonged into Loch Fyne, which curves off to the north-east, and the north-east into Loch Long. This is joined on the east by the shallow estuary of the Clyde, the only important river entering the area.

The most important physical divisions, for details of which the monograph by Mill should be consulted, are shown on the sketch map. The Arran Basin, into which the Great Plateau descends, is shaped like the Greek letter λ, the western branch of the Arran Basin forming the short leg and the Central and Eastern Basins the long leg, which reaches as far north as the Otter Spit. The maximum depth is about 107 fathoms, which is also the maximum for the area.

The Dunoon Basin is a straight trough (54 fathoms maximum depth), which runs up Loch Long as far as its junction with Loch Goil. The estuary, which joins it at the middle point, shoals off rapidly, the navigable channel being maintained by dredging. On the north the estuary is joined by the Gareloch, which has a maximum depth of 21 fathoms. Loch Long is a continuation to the north of the Dunoon Basin with a maximum depth of 35 fathoms, and Loch Goil, with a maximum depth of 47 fathoms, joins it on the west.

Loch Strivan, which runs almost due north and south, has a maximum depth of 42 fathoms ; the Kyles of Bute and Loch Ridun are shallower, the maximum depth being 23 fathoms. Loch Fyne is divided into two basins, the Gortans Basin and the Upper Loch Fyne Basin, the former with a maximum depth of 36 fathoms and the latter with a maximum depth of 80 fathoms.

The different lochs are separated from the more open water by " thresholds " or bars, these being more marked in some lochs than in others. Loch Strivan is an apparent exception, unless the shallow plateau between it and the Dunoon Basin be counted as such.

As regards the effect of the river, Mill says : " The Clyde Sea Area has no more intimate physical relation with the river after which it is

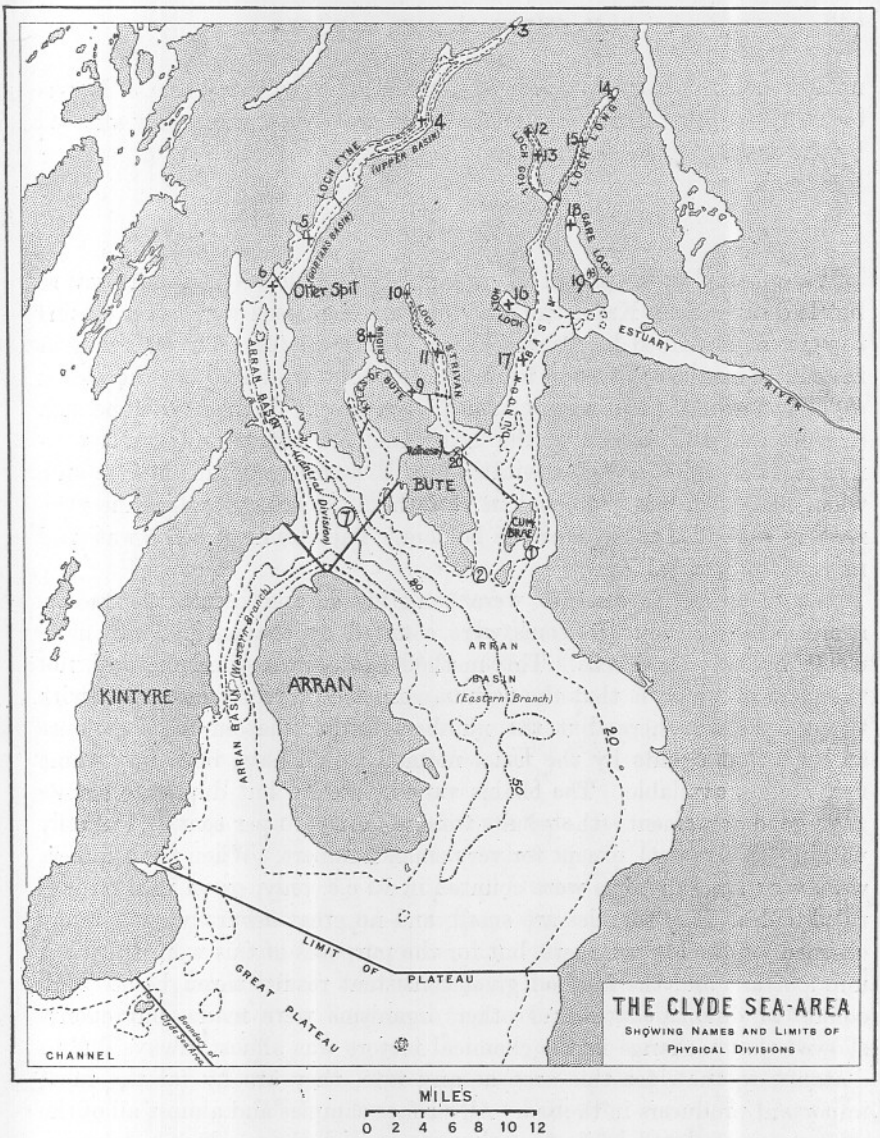

FIG. 1.—Depth contours are shown for – – – – 20 fm., –.–.– 50 fm., ... 80 fm. Stations worked are shown by crosses and numbers.

	Depth in fm.		Depth in fm.
No. 1. Keppel	—	No. 11. Clapochlar	40
No. 2. Garroch Head	60	No. 12. Loch Goil Head	27
No. 3. Cuill	15	No. 13. Stuckbeg	40
No. 4. Strachur	75	No. 14. Arrochar	10
No. 5. Gortans	30	No. 15. Thornbank	35
No. 6. Otter	30	No. 16. Holy Loch	10
No. 7. Inchmarnock	88	No. 17. Gantock	55
No. 8. Loch Ridun	10	No. 18. Gareloch Head	10
No. 9. Strone Cotes	20	No. 19. Clynder	23
No. 10. Loch Strivan Head	12	No. 20. Meteorological Station.	

named than the North Sea has with the Thames or the Rhine." In the lochs, on the other hand, the surface layers are often considerably affected by the drainage from the hills.

Methods.

Water samples were taken at various depths with the insulating water-bottle described by Knudsen (**16**). The tow-nets used were (*a*) a closing tow-net as described by Ostenfeld and Jespersen (**25**), but with canvas instead of open mesh in the top part of the net (mesh 200 to the inch); (*b*) open tow-nets (diameter of mouth 18 inches) of 30 meshes to the inch (coarse) and 120 meshes to the inch (fine). A coarse and a fine tow-netting were always taken within 1 or 2 fathoms of the surface and, when the depth was greater than 15 fathoms, a coarse and a fine tow-netting were also taken near the bottom. The closing tow-net was used mainly for vertical hauls.

The water-bottle samples were centrifuged, and counts in 20 c.c. samples were made. Diatoms were counted by chains, and not, as is usual, by individual cells. This method has certain disadvantages, not the least of which is that the results cannot be directly compared with those from elsewhere, but the numbers during diatom maxima were so large that counts by the usual method would have been impossible in the time available. The chains vary in length, but duplicate counts gave good agreements (the results were within ± 10 per cent and usually within ± 5 per cent), except for very small numbers. When the numbers were very large diatoms were counted in 10 c.c. only, or on part only of ruled slides. The samples are small, and no great accuracy is therefore claimed for the low numbers, but for the purposes of this work these are unimportant and the method gives consistent results throughout. Full counts of dinoflagellates and other organisms were made, but events showed that a change in the chemical factors was almost always due to diatoms, so that, for this area at any rate, they are by far the most important producers in the sea. All surface samples and almost all of the others were counted while fresh in order to see the small naked forms, but a few from the deeper layers in 1924 and 1925 and two from Loch Strivan in 1926 were preserved in formalin.

Quantitative estimations of the tow-nettings were not attempted. The speed of drift varied so much with the wind and tide that they were not always comparable among themselves, and, in addition, so much passes through the meshes of the nets that water samples are a more reliable guide for the microplankton. Several times during the year results from tow-nettings and water samples were completely at variance, because, of two diatoms present, one was much larger than the other,

and so, though really unimportant, was retained in much greater numbers in the tow-net than the other smaller form.

In the curves which follow, diatom numbers are drawn on the logarithmic scale. This is necessary because of the enormous variation, but it leads to an inevitable difficulty in reading them. The numbers quoted in the text always refer to the number of diatom chains (or other organisms) present in a 20-c.c. water sample.

The water samples were transferred at once to oxygen bottles and Winchesters, the temperature being taken by a standard thermometer and read to ·01° C.

Salinity was determined by titration of the chloride and dissolved oxygen by Winkler's titration method.

The pH value was read by McClendon's (**19**) method, the three indicators, phenol red, cresol red, and thymol blue, being used and values read to ·01 pH. The comparison tubes were renewed on several occasions, either because a fresh dilution of the dye proved necessary or because one or more of the tubes showed a change. In the early cruises 30 c.c. tubes were used, but from 1925 10 c.c. tubes were used, as it was found as easy to read these. Corrections were not made for the change in salinity in the upper layers, since dilution was due to the addition of water whose pH value and buffer effects were not known. The results will thus be liable to error in cases when the salinity change is marked, but, as will be seen, this effect is very small compared to the other changes encountered.

Phosphates were estimated by Atkins' modification of the Denigès method (**4**) in 1925 and 1926, and silicates by his modification of Diénert and Wandenbulcke's method in 1926 (**2**, **5**).

Nitrates were determined by Harvey's (**10**) method in 1926 and nitrites by Orr's (**23**) modification of Buch's method.

During the early part of the work estimations of the organic matter by Lenormand's (**17**) method were made. This was given up for two reasons : (*a*) there was an unknown amount of organic material, including diatoms, in suspension ; (*b*) the tint of the test solution was not the same as that of the standard, a difficulty which has since been overcome. The results obtained proved of little value in relating the different factors.

The curves for oxygen saturation were obtained from Fox's (**7**) table and those of S_t by Knudsen's (**15**) tables.

The meteorological data were obtained from Mr. Davidson through the courtesy of Sir John Reid, to both of whom our thanks are due. The meteorological station (see Fig. 1) is situated on Bute to the south of Loch Strivan. The daily records of hours of sunshine were kindly given by the Rothesay Town Council.

Wind force is given on the Beaufort scale, and the graph (Plate I,

Fig. 2) has been formed by taking the N. and S. components of the wind each day. As the loch lies almost due north and south these are the important directions. This, however, is only an approximation, as winds which vary a little from these directions tend to draw up or down the loch. With easterly or westerly winds there are variable gusts in the loch, but no steady wind.

The Effect of Streams.

Since inshore waters are richer in plankton than the open sea it is to be expected that the inflow from streams is at least partly the cause of this. It was necessary for this reason to examine the streams in the area. A general division can be made into the polluted and unpolluted streams. The polluted streams are those which have a town or village on their banks, and include the Clyde itself and the larger streams in Ayrshire. The unpolluted streams are those at the heads of lochs. The former are rich in dissolved phosphate and silicate, and certainly contain important quantities of dissolved nitrogen compounds, though no analyses of these were made. The rivers in the lochs, on the other hand, are rich in dissolved silicates (averaging about 4 mg. per litre), though the value varies considerably, and poor in dissolved phosphate (varying from zero to 20 mg. per cubic metre). There are a few exceptions to this in the lochs, but in all cases when phosphate is higher than this there is evidence of pollution. The small quantity of phosphate in the streams at Loch Strivan head is shown clearly by Plate VIII, Fig. 14, where phosphate values are low on three occasions (June 21st, August 19th, October 4th), when diatoms (Plate VIII, Fig. 15) are low in numbers and salinity (Plate VI, Fig. 10) exceptionally low.

Several analyses of the nitrates in the streams were made, and in all cases high results were obtained, but this is probably due in part to the presence of ferric iron in solution. The slopes of the lochs consist of mica schists and contain considerable quantities of magnetite, from which iron may possibly be derived. The variation in silicate results from the rapid change in the volume of the streams after a shower of rain. The slopes of the lochs are generally very steep, especially in Loch Strivan, and rain-water drains off rapidly. Organic matter in the streams was high compared with the sea. In polluted streams it was very high, and in the unpolluted streams varied from 4 to 6 mg. per litre.

Loch Strivan, 1926.

The work on Loch Strivan was carried out in greater detail than that on the rest of the area, and the results obtained proved useful for the understanding of conditions found in previous years. It will therefore

be convenient to take it first. The loch, which was visited weekly from the end of January till the end of November, was chosen for the work because of its peculiar advantages. It is close to the Marine Station and can be reached in 2–3 hours, its sheltered position makes it possible to work there in any weather and a good harbour lies near. It is the only loch with no village on its shores, and so there is no risk of contamination. The ratio of water-surface : land-drainage area : total area is 1 : 3·11 : 4·11. This means that rainfall has less effect than in any other loch except the Gareloch, which is unsuitable, because it is affected by the River Clyde. Two small streams enter at the head, while during rain innumerable burns form on the steep slopes. The total area of the loch is five square miles (Text Fig. 1, north of dotted line). Two stations were worked, one at the head of the loch in the narrow part, and one off Clapochlar Point (see Text Fig. 1). The positions varied somewhat due to drifting of the boat ; the depths worked in were about 14 fathoms at Loch Strivan head, and about 30 fathoms at Clapochlar. At both stations the bottom sample was taken at 1 fathom above the bottom.

The changes during the year followed much the same course at both stations ; but Loch Strivan head, on account of its position and depth, is subject to greater fluctuations in salinity and is more easily affected by mixing due to wind. Clapochlar is more stable and more reliable, and the descriptions which follow refer to it, although they are generally true for Loch Strivan head also.

Horizontal curves showing the course of events throughout the year have been drawn for total diatoms (Plate I, Fig. 1 ; Plate IX, Fig. 16), diatom species at the surface (Plate II, Fig. 3), wind (Plate I, Fig. 2), air temperature (Plate X, Fig. 18), sea temperature (Plate V, Fig. 9 ; Plate VI, Fig. 11), salinity (Plate VI, Fig. 10 ; Plate X, Fig. 19), S_t (Plate VII, Fig. 12), pH value (Plate II, Fig. 4), dissolved oxygen saturation (Plate III, Fig. 5 ; Plate VII, Fig. 13), and phosphate (Plate III, Fig. 6 ; Plate VIII, Fig. 14). Plates I–V should be consulted in reading the following descriptions :—

January 29th–March 17th. Up till March 17th vertical mixing was going on in the loch, the temperature falling from bottom to surface. There were considerable fluctuations in the salinity of the surface layer, which was generally low, while the deeper layers did not vary much. The pH value also was lowest at the surface, while the values in the deeper layers were much the same and kept at about pH 8·00. The dissolved oxygen saturation values generally rose towards the surface, which is not to be expected since vertical mixing was still going on. There were irregularities in the curves, the values at some depths being unexpectedly low. The cause is uncertain, but it is suggestive that herring were unusually abundant and were being fished in the loch. Phosphate values

varied between 40 and 50 mg. per cubic metre. During this time diatoms were very scarce.

March 23rd. The diatoms were not counted on March 17th, but on the 23rd (Plate IV, Fig. 7, and Table I) there were already 8,000 at the surface and 450 at 5 fathoms. Probably they had been present at the surface only, the week before. These samples contained almost nothing but *Skeletonema costatum*, which was the predominant species during the spring maximum. Other diatom species were present, but were negligible in numbers. The temperature still fell to the surface, but the surface layer was slightly supersaturated with oxygen, and the pH value had risen and the phosphate fallen a little. The other layers were unaffected.

TABLE I. March 23rd.

Depth in fm.	Temperature in °C.	Salinity. ‰	pH value.	% saturation of O_2.	Phosphate mg. per c/m.	Diatom chains in 20 c.c.
0	6·66	28·83	8·05	106·5	38	8,020
5	7·09	32·05	8·03	95·7	47	448
10	7·00	33·50	8·00	91·5	46	34
20	7·07	34·08	7·99	84·0	46	—
33	7·06	33·98	7·99	82·8	46	—

On *April 2nd* (Plate IV, Fig. 7, and Table II) the diatoms were still richest at the surface (24,000), but they were also rich at 5 and 10 fathoms. The loch was homothermic and mixed from top to bottom, and there was a general rise in pH and oxygen values from top to bottom (the 5-fathom layer was slightly supersaturated with oxygen), and a fall in phosphate in all layers. Mixing had evidently distributed the photosynthetic changes throughout the water.

TABLE II. April 2nd.

Depth in fm.	Temperature in °C.	Salinity. ‰	pH value.	% saturation of O_2.	Phosphate mg. per c/m.	Diatom chains in 20 c.c.
0	6·98	33·42	8·06	97·3	32	24,200
5	6·94	33·51	8·05	103·1	32	14,920
10	6·97	33·70	8·04	94·2	35	11,600
20	7·00	34·46	8·04	93·7	41	78
33	7·10	34·63	8·03	92·5	39	—

On *April 7th* (Plate IV, Fig. 7, and Table III) diatoms had reached their maximum for the year (33,000) at 5 fathoms, while the surface numbers had fallen off considerably, and the 10-fathom numbers were still increasing. A sudden rise in air temperature caused a rise in the temperature of the surface layer. The temperature there was now higher than

that of the deeper layers, and remained so till the autumn. This rise stopped vertical mixing due to temperature, and was followed by a differentiation of the loch. The pH value showed a sharp rise at the surface and a slight one at 5 fathoms. The surface layer was highly supersaturated with oxygen (139 per cent), and the 5-fathom layer slightly so. The phosphate at the surface showed an abrupt fall to its minimum value for this increase (12 mg. per cubic metre) and a smaller fall at 5 fathoms.

TABLE III. April 7th.

Depth in fm.	Temperature in °C.	Salinity. °/₀₀	pH value.	% saturation of O_2.	Phosphate mg. per c/m.	Diatom chains in 20 c.c.
0	8·68	32·06	8·36	138·6	12	10,200
5	7·10	33·57	8·07	104·2	25	33,000
10	6·94	33·76	8·04	97·5	47	13,500
20	7·02	34·65	8·02	91·4	50	903
30	7·12	34·97	8·03	93·2	41	131

On *April 13th* (Plate IV, Fig. 7, and Table IV) the diatoms had decreased at both surface and 5 fathoms, while the 10-fathom layer had reached its maximum (15,000). Diatoms were rich also to the bottom of the loch. The temperature had risen slightly; the pH value at the surface had reached its maximum for the spring increase (pH 8·38), and had risen considerably at 5 fathoms, and slightly at 10 fathoms and 20 fathoms. The dissolved oxygen saturation had fallen a little at the surface, but had risen to its maximum for 5 fathoms (117 per cent). The phosphate remained steady at the surface, showed a further fall at 5 fathoms and a pronounced fall at 10 fathoms.

TABLE IV. April 13th.

Depth in fm.	Temperature in °C.	Salinity. °/₀₀	pH value.	% saturation of O_2.	Phosphate mg. per c/m.	Diatom chains in 20 c.c.
0	8·32	32·38	8·38	135·0	15	2,036
5	7·53	33·55	8·22	116·5	17	3,617
10	7·00	33·89	8·09	95·5	31	15,000
20	7·05	34·53	8·08	90·6	40	9,210
33	7·09	34·75	8·05	89·7	43	9,270

On *April 20th* (Plate IV, Fig. 7, and Table V) diatoms had almost disappeared, rising to a few hundreds only in the deeper layers. The pH value had fallen considerably at the surface and slightly at 5 fathoms while at 10 fathoms it had risen slightly. The dissolved oxygen saturation value showed a considerable fall at both surface and 5 fathoms.

At 10 fathoms it had risen, and this layer was supersaturated (101 per cent) for the only time during the year. The 20-fathom value showed a slight fall. The phosphate values remained much the same at the surface and 5 fathoms, below which the change was small.

TABLE V. April 20th.

Depth in fm.	Temperature in °C.	Salinity. °/₀₀	pH value.	% saturation of O_2.	Phosphate mg. per c/m.	Diatom chains in 20 c.c.
0	7·63	33·43	8·20	105·9	16	27
5	7·63	33·41	8·20	105·1	19	—
10	7·32	33·69	8·14	101·2	23	86
20	7·04	34·33	8·02	86·7	37	274
30	7·09	34·59	8·02	81·3	44	325

This marks the end of the spring diatom increase. It is obvious that there is a close connection between the number of diatoms present and the changes in the sea-water. The diatoms begin to increase at the surface and spread downwards, the numbers decreasing in the surface layer when its phosphate content has fallen to a low value, and at 5 fathoms when this in turn has lost most of its phosphate. In the 10-fathom layer the changes are not so marked, and the phosphate is not used up to the same extent. Below this the diatoms are very rich, but only for a short time, and the changes are slight and irregular. The high numbers may be due to diatoms which are falling from the surface layers to the bottom, and are not photosynthesizing. Changes in pH, oxygen, and phosphate values correspond to diatom numbers, but there is sometimes an apparent lag between the appearance of diatoms and the changes in any particular layer. It seems doubtful whether this really occurs, and probably if the loch were visited every day a better correlation would be found.

April 27th–May 18th. A small second wave of Skeletonema now appeared at the surface, and reached its maximum (2,500) at 5 fathoms a week later. It had at the same time spread to the bottom. The following week, May 11th, a second and larger wave of Skeletonema appeared at surface and 5 fathoms, reaching a value of 9,000. The high number at the 5 fathoms this week may be partly due to the remains of the first wave, but from the behaviour of Skeletonema as a rule this does not seem probable. During these waves the pH and dissolved oxygen saturation values followed the course of the diatoms exactly at the surface and at 5 fathoms. At 10 fathoms there was a corresponding rise in dissolved oxygen saturation, but not in pH value. The surface phosphate value remained low all this time, but there was, on 27th April, a steep rise in

the value of the 5- and 10-fathom layers, which was probably due to mixing with the deeper water. After this the values in these layers followed the course of the diatoms.

May 18th–June 4th. On May 18th the number of diatoms was almost the same from top to bottom, and a few hundred *Chætoceros cinctum* were present in the surface layers. The following week, however, Skeletonema numbers had fallen very low and about 1,000 Chætoceros were present at surface, 5 fathoms and 10 fathoms. On June 4th Chætoceros had its maximum of 2,500, but was present only at the surface.

In spite of its small numbers Chætoceros had a remarkably large effect on pH, dissolved oxygen saturation, and phosphate values at all three depths, the 10-fathom effect being delayed (cf. p. 846). The surface and 5-fathom layers were completely denuded of phosphate on 25th May. On June 4th dissolved oxygen saturation and pH values were falling and phosphate was being regenerated at 5 fathoms, at which depth there were only a few diatoms.

During this period there was in the deeper layers a gradual fall in dissolved oxygen saturation and pH value, and a gradual rise in phosphate, which continued till the autumn turnover.

June 10th–July 14th. Diatoms were now very scarce until the 29th June (Plate I, Fig. 1 ; Plate II, Fig. 3), when there was a sudden appearance of 3,000 at the surface. The following week this rich layer was found at 10 fathoms, while at the surface and at 5 fathoms diatoms were scarce, although presumably they had been numerous at 5 fathoms during the week. The diatoms were mixed, *Cerataulina bergoni, Skeletonema costatum,* and *Chætoceros* spp. forming the majority. On July 14th diatoms had disappeared again. While diatoms were few there was a fall in pH and dissolved oxygen saturation values, the latter actually falling below 100 per cent at the surface on June 22nd. Phosphate was being regenerated. With the appearance of the diatoms the pH and dissolved oxygen saturation values rose and phosphate fell at the surface, while the 5- and 10-fathom layers were affected in succeeding weeks. The two weeks following the 29th June were marked at the surface by a further rise in pH and dissolved oxygen saturation value and a fall in phosphate, although there were no diatoms to account for it. The deep layers were unaffected, and were steadily becoming richer in phosphate and lower in pH value and oxygen saturation.

July 21st–September 28th. The end of July marks the beginning of another series of diatom increases which lasted till the middle of September. It began on July 21st (Text Fig. 2 and Table VI) with a few hundred *Nitzschia seriata* present in the surface and 5-fathom layers. The following week (Text Fig. 3 and Table VII) the numbers at both depths had increased to thousands, and on August 3rd (Text Fig. 4 and Table VIII)

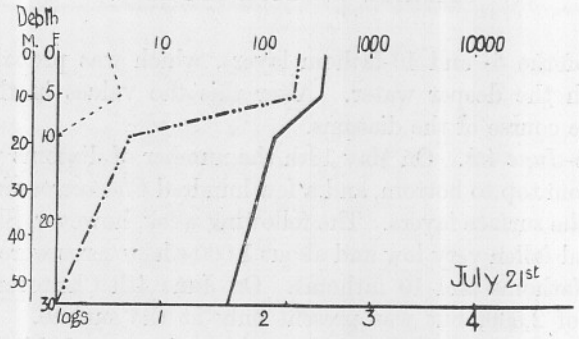

FIG. 2.

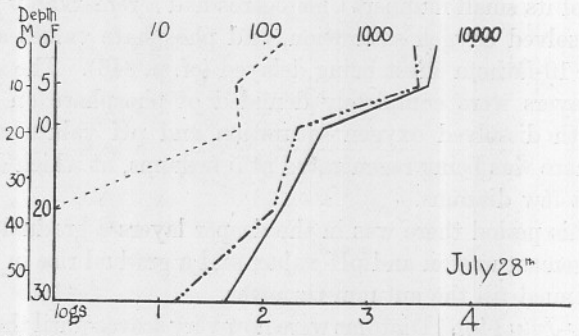

FIG. 3.

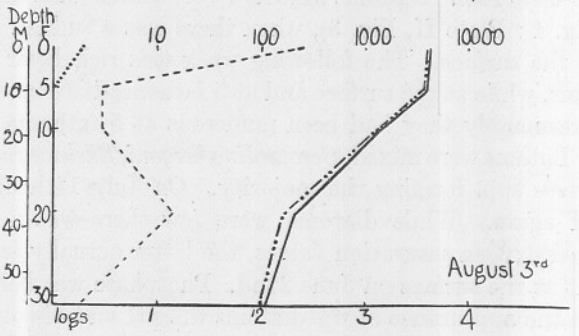

FIG. 4.

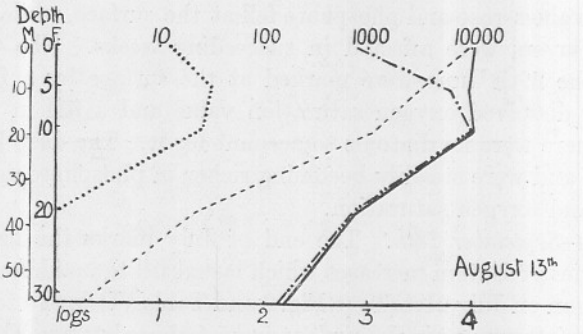

FIG. 5.

FIGS. 2–5.—Clapochlar, 1926. Distribution of diatoms.
——— total diatoms. —. .—. . *Nitzschia seriata*, – – – *Leptocylindricus danicus*, ... *Eucampia zoodiacus*.

there was a further small rise in both layers, while the numbers at 10 fathoms had increased to more than 1,000. This week there were also 300 *Leptocylindricus danicus* at the surface. On August 13th (Text Fig. 5, Table IX) both species of diatom had increased, and there were about

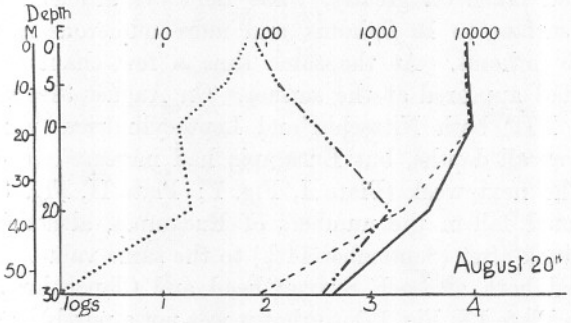

FIG. 6.

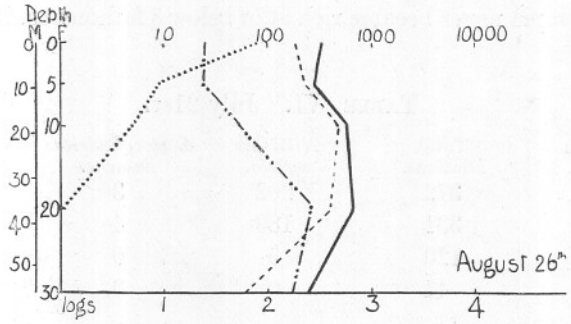

FIG. 7.

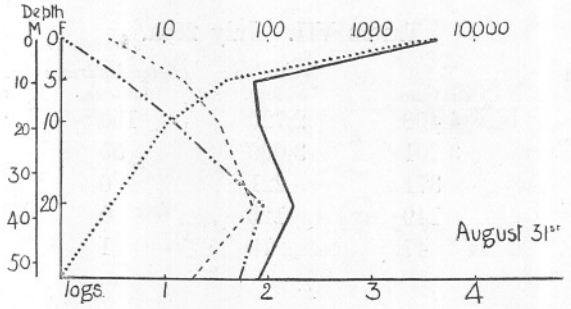

FIG. 8.

FIGS. 6–8.—Clapochlar, 1926. Distribution of diatoms.
——— total diatoms, —.—.— *Nitzschia seriata*, – – – – *Leptocylindricus danicus*, ... *Eucampia zoodiacus*.

10,000 present at the surface, 5 and 10 fathoms. The surface sample contained practically nothing but Leptocylindricus, the 5-fathom sample a mixture of Nitzschia and Leptocylindricus, and the 10 fathom and samples below mainly Nitzschia. Nitzschia had left the surface, and

had begun to sink into the deeper layers, having its maximum at 10 fathoms, while Leptocylindricus was still richest at the surface. The following week (Text Fig. 6 and Table X) marked a further stage in this process. Nitzschia was now richest at 20 fathoms, though its numbers had fallen off greatly, while Leptocylindricus was uniformly rich from surface to 10 fathoms, and more numerous than Nitzschia even at 20 fathoms. At the same time a few chains of *Eucampia zoodiacus* had appeared at the surface. On August 31st (Text Fig. 8, and Table XII) both Nitzschia and Leptocylindricus were negligible in number at all depths, but Eucampia had increased to 4,000 at the surface. The next week (Plate I, Fig. 1; Plate II, Fig. 3) there was an unexpected fall in the numbers of Eucampia, although they rose again the week after (September 14th) to the same value. This curious fall occurred both at Loch Strivan head and Clapochlar and also at Keppel (see Plate IX, Fig. 17), so that it was not a purely local phenomenon. Eucampia never became rich at or below 5 fathoms and disappeared after this.

TABLE VI. July 21st.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	372	202	3	0
5	331	180	4	0
10	120	5	0	0
30	44	0	0	0

TABLE VII. July 28th.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	4,468	2,720	150	0
5	3,701	3,000	55	1
10	371	221	6	0
20	149	123	0	0
31	47	15	1	0

TABLE VIII. August 3rd.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	4,339	4,000	254	2
5	3,970	3,900	3	0
10	1,337	1,312	3	0
20	203	171	14	0
31	111	100	2	0

TABLE IX. August 13th.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	10,459	800	9,600	12
5	9,633	6,300	3,200	31
10	10,511	10,100	1,216	25
20	781	700	23	0
31	160	152	2	0

TABLE X. August 20th.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	8,256	80	8,100	65
5	8,377	128	8,200	40
10	9,229	296	8,900	14
20	3,550	1,500	2,000	18
30	451	338	87	1

TABLE XI. August 26th.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	323	25	181	81
5	283	24	227	9
10	561	53	474	5
20	665	255	385	1
30	247	169	60	0

TABLE XII. August 31st.

Depth in fm.	Total Diatoms.	*Nitzschia seriata.*	*Leptocylindricus danicus.*	*Eucampia zoodiacus.*
0	4,371	0	3	4,200
5	74	4	15	40
10	83	13	34	11
20	179	89	70	3
29	81	54	19	0

The agreement between the different factors and the diatoms was not so well shown during the early part of this period, the effect of Nitzschia and Leptocylindricus being small and that of Eucampia very large. There is no obvious relation to temperature, though in the surface layers this remained high. pH value kept high and the surface layer supersaturated with oxygen till Nitzschia reached its maximum, when there was a further increase. The high pH value was maintained during the

maximum of Leptocylindricus and phosphate fell definitely. There was a fall in pH value and dissolved oxygen saturation and a rise in phosphate in the week when diatoms were low between the Leptocylindricus and Eucampia increases, but when this last diatom appeared in numbers the pH value and dissolved oxygen saturation rose almost as high as during the spring maximum and phosphate was completely utilised.

The following week there was an unexpected rise in pH value, which had reached its maximum for the year (pH 8·46), although diatoms had decreased and oxygen saturation had fallen considerably. It looks as if oxygen were more sensitive to change than pH value. Meanwhile, phosphate had remained at zero. At 5 fathoms there was the same general agreement shown with the first two diatoms; the pH value remained high, the oxygen saturation rose and phosphate fell. Eucampia, as might be expected from its small numbers, shows no effect at or below 5 fathoms.

At 10 and 20 fathoms there were some peculiarities. The sharp peaks at these depths on the 20th August correspond to peaks in the temperature curves. This was a day on which a south-west wind of force 5 was blowing, and was by far the roughest day on which the loch was worked. Wind is a cause of mixing and, as these peaks show on all the curves, it seems probable that they are related to this rather than to photosynthesis alone.

This diatom-rich period confirms the fact, observed first in spring, that a diatom increase appears first at the surface and then at successive depths. It is also remarkable because the diatoms composing it come, not together, but successively, each appearing as the previous one has left the surface and sunk to deeper layers.

Judging from numbers alone one would have supposed that the Nitzschia and Leptocylindricus increases formed the autumn maximum, but when pH, dissolved oxygen, and phosphate values are taken into account it is seen that Eucampia, although lowest in number, has an effect comparable only to that of the spring increase.

October 5th–December 2nd. This was the last diatom maximum. On October 5th there was a very small increase of *Rhizosolenia setigera* to nearly 500 in the surface layer only, but the species had disappeared the following week. pH and dissolved oxygen saturation values at the surface rose, and phosphate fell to correspond, but no effect was shown in deeper layers. There was on this day a small rise both in air and sea-surface temperatures, and part of the phosphate fall may be due to the exceptionally low salinity.

On October 12th and 19th the surface temperature fell sharply, and by November 3rd the temperature gradient was reversed and the warmest water was at the bottom. On this date the bottom temperature reached

its maximum for the year (11·91° C.), and thereafter began to fall. On October 27th in the bottom layer there was a rise in the pH value and dissolved oxygen content and a fall in phosphate, which became still more marked the next week. On November 3rd the other curves also indicate a general mixing.

During these weeks *Skeletonema costatum* appeared at the surface again, but only in small numbers (100–300). A few were present at 5 fathoms, but the numbers in depths below this never rose above 120. Occasional chains of Skeletonema were met with during the summer, most often in deep-water samples, so it is possible that the slight autumnal rise was due to spores brought up from the bottom by vertical mixing.

Plate II, Fig. 3 shows those diatoms which formed an important increase, but there were, of course, many other species present. The most important was *Chætoceros sociale*, which occurred from July till the beginning of October with a maximum of 1,500 on August 2nd at Loch Strivan head. Thalassiosira (*T. nordenskioldii* and *T. gravida* were the commonest species) is peculiar in that it comes along with Skeletonema, and their numbers during the spring maximum rise and fall together. On May 24th, however, when Skeletonema had almost disappeared, the number of Thalassiosira still rose, and it had its maximum (1,400) at Loch Strivan head, 11 fathoms, that week.

In autumn two species of diatom became abundant in the tow-nettings, although their numbers in the water samples were negligible. These were *Melosira* sp., common from September 20–28th, and *Chætoceros didymum*, common from September 22nd till the end of November (with a maximum number of 82 in the water samples).

A comparison of the results obtained at Clapochlar with those at the head of the loch show that there is a general agreement between them (see Plate VIII, Fig. 15; Plate IX, Fig. 16). The same diatom increases occurred, and the maxima were generally in the same week. The air temperature (Plate X, Fig. 18) and loch temperature at the head (Plate V, Fig. 9) were somewhat more closely related than at Clapochlar (Plate VI, Fig. 11). pH, dissolved oxygen saturation, and phosphate values agreed except for the third wave of Skeletonema, which had no effect at the head. When the salinity is low the surface pH and phosphate values are affected by it, the latter being reduced to a low value three times when there were no diatoms to account for it (see Plate VIII, Fig. 14).

The occurrence of dinoflagellates throughout the year is irregular, and they were never numerous except in the surface layer. They appeared and disappeared suddenly, and did not always occur at both stations in the same week, while numbers were higher at Loch Strivan head than at Clapochlar. They caused no noticeable change in pH, dissolved

oxygen, or phosphate values. A comparison of salinity (Plate VI, Fig. 10 ; Plate X, Fig. 19), temperature (Plate V, Fig. 9 ; Plate VI, Fig. 11), and dinoflagellates (Plate V, Fig. 8) shows that an increase in dinoflagellates generally coincides with low salinity and a rise in temperature, although there are a few cases in which it is related to low salinity alone or high temperature alone. This agreement is more marked at Loch Strivan head, and as the salinity there is always lower this may explain their greater abundance.

The commonest forms during these increases were the small photosynthetic peridinians. *Peridinium triquetra* was the most abundant of these, but very often the theca had been discarded, and only a naked brown spore was visible, so that it was impossible to identify the species. *P. triquetra* had its maximum (823) at Loch Strivan head on October 5th. *Minuscula bipes* was abundant (213) on April 6th at Strivan head, and *Diplopsalis* spp. at both stations (231 at Loch Strivan head, 99 at Clapochlar) on August 30th and 31st.

The larger species of Peridinium and Ceratium were naturally more abundant in the tow-nettings than in the water samples. Peridinium was common from April onwards, first in the surface nets and later, in November, in the deep nets. Ceratium appeared in numbers in the end of July, and remained abundant till December with a maximum of *C. longipes* in July and of *C. tripos* in early September and again in November.

Animal life was not abundant in the early part of the year except for rotifers, which were numerous during most of March and April and again in July. Occasional swarms of copepod nauplii and polychæte larvæ were met with during the early months, but the former did not become really abundant till the end of June, along with other planktonic larvæ.

The small copepods, *Acartia clausii*, *Pseudocalanus elongatus*, and *Oithona similis* all occur, being commonest in the deep layers during the summer and autumn. *Calanus finmarchicus* is the most important copepod. It was common in deep water from May onwards, although catches were rather irregular. Calanus seems to occur in swarms near the bottom of the loch, and the tow-nets probably did not always fish at the right depth and so missed them, even when they were present. The same may be said of adult euphausids, which were occasionally caught in numbers from September 20th. As a rule *Calanus* is very common at the surface during May and June, but in 1926 it did not appear there.

During June and part of July the large medusæ, *Aurelia aurita* and *Cyanea capillata*, were seen in the loch, sometimes in considerable numbers, especially in calm weather. After the middle of July they were not seen, but the stinging threads of Cyanea were still met with on

hauling up ropes from deep water. After September no traces of these were found.

It was noteworthy that in the deeper layers pH value and dissolved oxygen saturation fell while phosphate rose from May onwards. The loch had become stable, the thermal gradient to the surface being marked, so that any addition of phosphate to the deeper layers would be cumulative, while a continuous utilisation of this salt in the surface layer kept it at a more or less constant low value. It is probable that this is to be attributed partly to respiration and excretion, and partly to the gradual breaking down of organic material such as dead plants and animals.

The curves for temperature, pH and phosphate values and dissolved oxygen were very peculiar after October 20th. There was not only mixing, but also a change of the water in the loch. A layer with relatively high pH and dissolved oxygen values and lower phosphate was introduced at the bottom and spread upwards. Below the surface the temperature was variable, the highest value being found one week at 20 fathoms and later at 5 fathoms. Phosphate, which had accumulated in the loch up till now, was suddenly reduced in quantity, and reached approximately its spring value once more.

Analyses for silicates were made in the surface and bottom samples on most occasions. The silicate content will obviously depend to a considerable extent on the salinity (see p. 842). In spite of this, however, during the spring increases there was a distinct lowering of the silicate at Clapochlar, though this did not show at the head where the river enters. It is extremely improbable that silicates are of importance as a limiting factor in Loch Strivan. Nitrates were estimated in all the samples on most occasions, but very little change was found, and this is probably due to the presence of iron in addition to the traces of nitrites. Nitrites in the loch throughout the year showed no obvious relation to the phytoplankton. During the late spring and in summer and part of autumn the results were of the same nature as those described in 1925 ; that is, higher values were obtained in the deep waters. At the surface the values were generally low during this period. In winter small quantities were found throughout on most occasions. The results are probably associated with the oxygen saturation values, which are low in the deep water, and the occurrence in the surface layer may possibly be due to mixing.

1925 *and* 1924.

1925. In 1925 five cruises were made over the whole area, in January–February, April, June, August, and October. Eighteen stations were worked each time, one at the head and one in the deepest part of each

loch, and several in the more open parts of the firth. The positions were the same as those worked by Mill (**20**) in his survey of the Clyde sea area, and are shown in Text Fig. 1 (p. 839).

January–February cruise. In January and February diatoms were very scarce over all the area. Calanus was present in deep water and sometimes at the surface, while nauplii and other planktonic larvæ were occasionally abundant. During this cruise typical winter conditions were met with ; pH values were much the same from top to bottom, though often there was a slight fall towards the surface due to dilution ; dissolved oxygen and phosphate values were similar, the oxygen remaining slightly higher at the surface. Exceptions to this were found in Loch Goil, and, though less marked, in the deep water in Upper Loch Fyne. Loch Goil had hardly undergone any mixing, and was still high in phosphate and low in dissolved oxygen and pH values in the deep water. This is probably due to the sheltered position of this loch, its depth (47 fathoms) and its shallow threshold (14 fathoms).

April cruise. The April cruise was begun by a visit to the Garroch Head station on April 3rd, immediately after the spring increase of Skeletonema and Thalassiosira had started at Keppel. It was found that diatoms were present there, richest at the surface (over 10,000) and gradually decreasing in the deeper water, while the pH value was high throughout with a slight rise in the surface layer ; down to 10 fathoms the water was super-saturated with oxygen, and the phosphate values were low throughout with a slight gradient to the surface.

In Loch Fyne the next week, the fact that pH and oxygen values were fairly high throughout and phosphate comparatively low, leads one to suspect that a diatom increase had already passed and that its changes had been distributed throughout all layers by vertical mixing. Diatom numbers were very low, but increased in the deeper layers, especially at Strachur, a condition usually found only after a diatom increase.

In the rest of the area much the same conditions were found ; that is, either a diatom increase was going on or had occurred. Where diatoms were abundant there was generally oxygen supersaturation and high pH and low phosphate values at the surface, while in the deeper layers the changes were similar but less marked. The depths at which changes had occurred agreed with the depths which diatoms had reached.

On several occasions there were marked irregularities in the pH value, though neither phosphate nor dissolved oxygen values showed corresponding changes. At first it was thought that this might be due to contamination, as it was found at the Gantock Station. Later in the cruise, however, it was met with in Loch Fyne and at Strone Cotes in the Kyles of Bute. Every precaution was taken to prevent accidental contamination and

the determinations were repeated several times. Only on a few occasions after this was the same phenomenon met with.

Calanus was present in deep water and sometimes at the surface, and occasional swarms of nauplii and other planktonic larvæ were met with.

June cruise. During the June cruises a diatom increase was going on over most of the area. In Loch Fyne and in the Dunoon Basin and the lochs connected with it Skeletonema and Thalassiosira were very abundant. In most cases the surface layers were supersaturated with oxygen, the pH values high and the phosphate low, and the curves for these generally agreed with the number and position of diatoms. Gareloch head was an exception to this, and here, in spite of a high diatom content, phosphate was high and dissolved oxygen low.

Loch Strivan and the Kyles were visited last, and here, although there were evidences of an increase having passed (there were nearly 3,000 Skeletonema and Thalassiosira at 20 fathoms at Clapochlar), diatoms generally were poor and the predominant species in the surface layers was *Chætoceros breve.*

Garroch Head station was worked both at the beginning and the end of the cruise, and while Skeletonema predominated at the beginning, *C. breve* did so at the end.

The most interesting feature of the June cruises was the occurrence of " water bloom " in Loch Long, caused by *Peridinium triquetra.* When the loch was reached on June 17th patches of brownish water were seen near the head, but we were informed that they had first been noticed a mile or so further down and had drifted up. The Arrochar Station was worked as usual, and in addition several samples were taken from the coloured patches. In the various surface samples the numbers of *P. triquetra* varied from 32,000–56,000, and diatoms were extremely scarce. At 3 fathoms, however, *P. triquetra* had fallen to about 800 and diatoms had increased to 23,000. At 5 fathoms *P. triquetra* were still fewer, and diatoms had fallen again to 750, while both were still fewer in the bottom sample.

The surface samples were supersaturated with oxygen and the pH values were very high but variable (pH 8·37–8·51), while the phosphate was low at both surface and 5 fathoms. As often occurred in Loch Strivan in 1926, this peridinian increase coincided with low salinity and high temperature in the surface sample.

During the cruise copepods were still numerous, but decreased in numbers towards the end of the month, while at Loch Strivan head and in Loch Ridun thousands of large *Aurelia aurita* were present.

August cruise. The next cruise was begun in the end of July when *Chætoceros sociale* was abundant both at Garroch Head and Keppel.

This species was the predominating form throughout the area except in Loch Fyne, where it was completely absent. There was generally a gradient to the surface shown in pH, phosphate and oxygen saturation values, the effect being less marked at 5 and 10 fathoms and only slight at and below 20 fathoms. Occasional abrupt changes in pH value, like those found in April, were encountered. pH values were often very high (over pH 8·30), and the water supersaturated with oxygen even at 5 fathoms. An increase of *C. sociale* was found in some of the lochs (Gareloch, Holy Loch, Loch Ridun), and here the agreement between the diatoms and the chemical factors was fairly good. In the rest of the area, however, numbers were very low and the agreement was not apparent. The results suggest that a diatom increase had just been missed. If this is so, the species was probably *C. sociale* everywhere except in Loch Fyne.

In the enclosed lochs (Loch Long, Loch Goil, and Loch Strivan) dissolved oxygen and pH values were very low and phosphate high in the deep layers (cf. Loch Strivan, 1926), but in the more open stations and in Loch Fyne this was not found.

Copepods remained numerous in the deep layers generally, and ctenophores (chiefly *Bolina infundibulum*) were common at most stations.

October cruise. During the October cruise Thalassiosira was the most important diatom. A small increase was in progress throughout the area, and was richest in Loch Long where the number of diatoms rose to 2,700. The effect on pH, dissolved oxygen and phosphate values was slight even where the diatoms were most numerous.

This month marked a return to winter conditions. The autumn overturn was not complete, although in most cases there was a slight temperature fall to the surface. pH and dissolved oxygen had fallen from their previous high values and in many cases pH value was lowest at the surface. Phosphate values in the upper layers continued lower than in the deep water, but were not so low as in summer. In very deep water in the open (e.g. Inchmarnock, 60 mg. per cubic metre at 80 fathoms), and in the sheltered lochs, values were very high. In Loch Goil there were 95 mg. per cubic metre, and it was high also in Loch Strivan. There was, however, only a slight rise to the bottom in Loch Long and Loch Fyne. Accompanying these very high phosphate values in Loch Goil and Loch Strivan there were low pH values and very little dissolved oxygen, this reaching a very low value in Loch Goil (1·90 c.c. per litre). Animal life was not very abundant, but there were occasional large hauls of Calanus from deep water. By December at the Garroch Head complete vertical mixing had taken place and diatoms were negligible in numbers.

1924. In 1924 more stations were worked and so each cruise took

longer, and conditions in one part of the area might differ considerably from those in another during the same cruise.

In January and up till the end of March diatoms were very scarce generally, but Calanus was common in most places and swarms of nauplii and lamellibranch larvæ were often encountered. Loch Fyne proved the most interesting part of the area, for the spring increase had begun there in the first few days of March, and Skeletonema and Thalassiosira were numerous in the water samples. They got richer towards the head of the loch, and there were more than 3,000 in the surface layer at Cuill. Outside Loch Fyne, in the Arran Basin and at Keppel, diatoms were scarce until the 1st April, when there was a sudden great increase. This wave of Skeletonema and Thalassiosira was found also in the Dunoon Basin and Gareloch and probably took place in all the lochs, although these were not visited at this time.

Diatoms were scarce again during April and May, while the tow-nettings were characterised by a great abundance of copepods, especially Calanus, both at the surface and in deep water, but most numerous at the surface. In the end of May, Skeletonema appeared again both at Keppel and in the Dunoon Basin, and was very rich in Loch Fyne.

During August and September an increase of *Chætoceros sociale* was going on in the Dunoon Basin and the lochs connected with it and in places, especially at the heads of the lochs, reached very high numbers. At this time, however, there were very few diatoms in Loch Fyne. *C. sociale* was present in the tow-nets as far up as the Gortans Basin, but was completely absent to the north of this. Copepods were now less common and were found chiefly in deep water.

In the end of September and October, Skeletonema and Thalassiosira appeared again, the latter being more numerous, and there was a small increase of these diatoms all over the area. The largest number of diatoms this year was invariably found at the heads of the lochs, but this was not found in 1925 or 1926.

At first the pH value alone was used as a criterion of biological changes in the water, while later organic matter, and in the last cruise dissolved oxygen and phosphate values, were also estimated. Until April the pH values were almost identical from the top to the bottom except at the heads of the lochs and in Loch Fyne and the Gareloch (very low values were met with in the latter, less than pH 7·45). After April there was generally a gradient from 20 fathoms to the surface with a slight rise even in the deepest layers. Throughout, agreement between the number of diatoms present in water samples and the pH value was rather sporadic, except in the case of very high pH values. In many cases no relation appeared to exist. The chief point of interest encountered was that the Gareloch, in spite of low salinity and very low pH values in winter, had

the highest pH value (pH 8·50) during the increase of *Chætoceros sociale* in August. The low salinity here and at the heads of lochs seems to favour peridinians, which were often abundant.

Dissolved organic matter, which in the open was generally between 1 and 2 mg. per litre, increased towards the heads of the lochs, and in the Gareloch reached over 4 mg. per litre at its highest. An examination of the rivers showed that it was present there in larger quantities.

In October the low pH and dissolved oxygen values and the high phosphate values described in detail for 1926 were met with in Loch Long, Loch Goil, and Loch Strivan, while in the upper layers the pH value was again approaching its normal winter values.

Annual Changes in the Plankton.

During these years tow-nettings and water samples were taken twice weekly off Keppel, and some conclusions can be drawn as to the usual course of events (Plate IX, Fig. 17).

There is a well-marked spring diatom maximum which starts at the end of March or the beginning of April. This consists of Skeletonema and Thalassiosira in varying proportions, but with Skeletonema usually predominant. This increase is followed by one or more secondary waves of the same diatoms, which then die away till the autumn. In September or October they increase again, but this autumn maximum varies greatly in amount, probably depending on summer conditions. In 1923 it was large and early (mid-September), and in 1926 small and late. Thalassiosira was as important as Skeletonema in every year but 1926.

Besides these there is a summer diatom maximum. In 1923 it came in July, and consisted of *Rhizosolenia fragillima*, but in the other years it was in August. *Chætoceros sociale* was the predominant form in 1924 and 1925, but in 1926, as has already been described, three species became numerous one after the other.

The larger dinoflagellates (e.g. Ceratium and some species of Peridinium) have their maximum usually in August, but the distribution of the naked forms and of some of the photosynthetic peridinians (e.g. *P. triquetra*, *Glenodinium trochoideum*) is less regular, and may depend on external conditions such as temperature and salinity.

In May and June, and sometimes in April, Calanus usually becomes abundant in the surface waters, and tow-nettings from deep water are then less rich than those from the surface. This involves a complete change of habit, for during the rest of the year, except at night, rich hauls are taken only from deep water. In 1926 they never became numerous at the surface, but in 1923, 1924, and 1925 they did, and the phenomenon has been observed elsewhere (Herdman, **12**).

The changes occurring at Keppel are, on the whole, the same as the changes in the rest of the Clyde area, Loch Fyne being the only exception. The lochs, however, show a certain independence. In 1926 the spring increase began in Loch Strivan a day or two before any rise in numbers took place at Keppel, and this was the case also with the increase of Eucampia. Leptocylindricus was much more numerous in Loch Strivan than it ever was at Keppel. Some species, too, seem to be almost restricted to one loch, e.g. *Tintinnus steenstrupii* is very rare, and the copepod *Euchæta norvegica* is rare, outside of Loch Fyne. In 1926 *Dinophysis hastata* was recorded first and became common in Loch Strivan, while it only appeared in small numbers later at Keppel.

Loch Fyne shows the greatest divergences from the rest of the area. It appears to have an earlier spring maximum (this was only found in 1924, but the results from the April cruise in 1925 indicated that it had taken place in that year too), and *Chætoceros sociale* hardly appeared there although abundant in the rest of the area.

DISCUSSION.

A comparison of the diatom curves with those for pH value, dissolved oxygen saturation and phosphate content shows a striking agreement in the surface layer (see Plate II, Figs. 3 and 4 ; Plate III, Figs. 5 and 6). An agreement though less marked is shown at 5 fathoms, still less at 10 fathoms, and only slightly at 20 fathoms. When, however, the curves are carefully followed it becomes apparent that this agreement is not close when numbers of diatoms alone are considered. For example, Chætoceros and Eucampia had an effect which would not be expected on the basis of numbers alone. The highest pH value for the year was reached during the increase of the latter diatom, which only attained a maximum number of about 4,000 chains in 20 c.c. Nitzschia and Leptocylindricus, on the other hand, had a comparatively small effect in spite of their larger numbers. Another point of apparent disagreement in the curves is the delay in reaching a maximum value in the case of pH or dissolved oxygen saturation value, or a minimum in the case of phosphate when compared with diatom numbers. From this point of view still more frequent visits to the loch would have been interesting, and it is to be expected that a comparison every one or two days would have eliminated this apparent lag. Naturally all changes in number of diatoms and other factors are minimal, since in the course of a week (the usual interval between visits) it is quite possible for important changes to occur. There are two points on the curves, however, which require further mention. The first is the high surface pH value on July 14th. This is two weeks after the date of maximum number of diatoms for this

increase, and it is possibly related to the temperature, which reached its maximum for the year on that date. The other is the high pH value on September 7th. While this might be due to the apparent lag described above, it is surprising that oxygen saturation value does not agree with it. The number of diatoms had fallen considerably, and the phosphate remained at zero. It is probable that in the surface layer dissolved oxygen saturation tends to approach 100 per cent more readily than pH value tends to fall. This will depend on the state of the sea, e.g. a choppy day would reduce supersaturation rapidly. At 5 fathoms, and to a less degree at 10 fathoms, the same changes take place a week later than at the surface. This is in accordance with the sinking of the diatoms during an increase. The changes were slight at 20 fathoms, and may have been due there (and perhaps in a less degree at 10 and 5 fathoms also) to mixing with the upper layers. As this was the case in other years also, it is likely that a depth between 10 and 20 fathoms is the limit for photosynthesis in the area.

Although sunlight is necessary for photosynthesis, too much of it is injurious. It has been found that diatom cultures grow best away from direct sunlight, and experiments at Millport have shown that, of two series of bottles of diatom culture at the same temperature, one placed in full sunlight and the other in the shade, the second will produce oxygen while the first will not and may even use it up. Even in the sea, it is possible that in summer the actual surface layer is not the optimum position for diatoms. During the increase of Nitzschia and Leptocylindricus the diatom cells in the surface sample looked pale and unhealthy with the chromatophores contracted, whereas the cells from 5 fathoms and deeper layers were perfectly normal. The same has been observed by Schimper (Karsten, 1905, **14**). In spite of this, however, photosynthesis, as measured by the change in pH, oxygen and phosphate values, was always most active at the surface. In early September, Eucampia became very rich in the surface layer, and was present in smaller numbers at 5 fathoms, but not below this. It is possible that at this time the decreasing light was limiting its development below the surface, and the same may be said of Rhizosolenia and Skeletonema.

At Plymouth (**6**) and Port Erin (**11**) the date of the spring maximum has been shown to depend largely on the amount of sunshine in the early part of the year. Conditions in this area are different. Text Fig. 9 shows the monthly averages of hours of sunshine for the years investigated, and it will be seen that the spring maximum (taken as the date on which there were 500 diatom chains in 20 c.c.) comes at almost the same date each year and actually latest in the year with most early sunshine, 1924 (see also Plate IX, Fig. 17). In Loch Fyne in that year it began nearly a month earlier than at Keppel, so it appears that in this area the amount

of sunlight is not the factor which starts off the spring increase. A measurement of the total amount of incident light and not only sunshine would be a more reliable guide. A comparison may perhaps be drawn between the growth of a diatom culture in the laboratory in winter and the early diatom increase in the enclosed waters here.

The spring increase is almost certainly not a direct effect of temperature rise, as is shown by Plate II, Fig. 3, and Plate VI, Fig. 11, and this has already been suggested by other workers. It was well under way before temperature rose.

A comparison of the number of diatoms found in the area with the numbers found in the open sea shows a very great difference. The

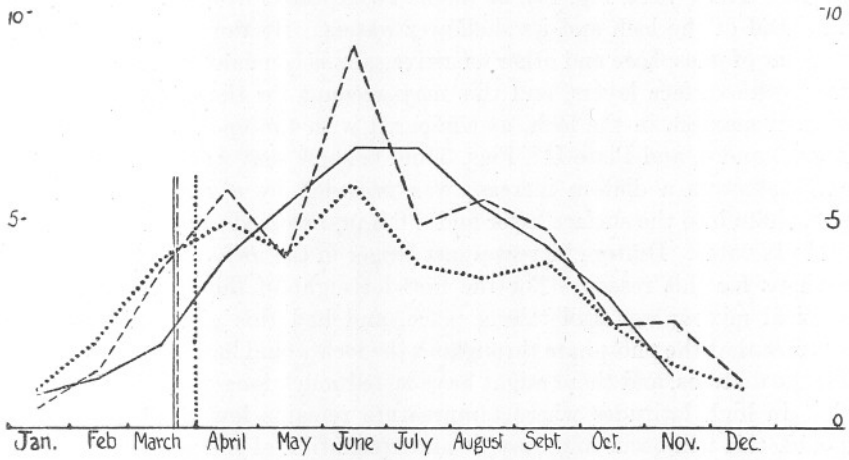

FIG. 9.—Mean monthly sunshine in .... 1924, — — — 1925, —— 1926. The vertical lines show the date of the spring diatom increase in the different years.

numbers here are very much greater, and are comparable to those found by Lohmann (**18**) at Kiel, although an exact comparison is not possible since they were not counted in the same way. Results for pH value and dissolved oxygen saturation bring out this difference clearly. The winter values for phosphate are not very different from those for the open sea, but mixing renders this salt available for plant growth much more readily than there.

Vertical mixing due to temperature gradient is not so important in the area, for the winter rains affect the salinity at the surface (see Plate VI, Fig. 10 ; Plate VII, Fig. 12 ; Plate X, Fig. 19), and the density is not the same throughout. On the other hand, the effect of wind and tide is much more marked. Tide may cause mixing in the manner described by Huntsman (**13**), while the important effect of wind for Loch Strivan among other lochs has been shown by Murray (**21**).

When the temperature curve for 1926 is compared with those for pH, dissolved oxygen saturation and phosphate values (Plate VI, Fig. 11; Plate II, Fig. 4; Plate III, Figs. 5 and 6), it is found that the dips in the curves occur on the same date in all. When it is compared with the diatom curve, however, it is found that except in a few cases (*Chætoceros cinctum* in May and Corataulina in July) the increase in diatoms does not coincide with a rise in temperature. The similarity is probably to be explained by the fact that a certain amount of mixing had been going on. The curves for different depths have approached one another, i.e. the values have been more evenly distributed throughout. This mixing is more marked at Loch Strivan head than at Clapochlar (see Plate V, Fig. 9; Plate VIII, Fig. 14), as might be expected from its situation at the head of the loch and its shallower waters. By this means a certain amount of phosphate and other nutritive salts is constantly being brought up to the surface layers, and this may account for the more numerous diatom maxima in the loch, as compared with the open sea. Plate II, Figs. 3 and 4, and Plate III, Figs. 5 and 6, show that with the exception of Chætoceros a diatom increase was preceded by a reintroduction of phosphate into the surface layer and a fall in dissolved oxygen saturation and pH value. Diatom increases last longer in the lochs than at Keppel, perhaps for this reason. For the first fortnight of the spring increase, vertical mixing was still taking place, and had this gone on it seems possible that the phosphate throughout the loch would have been available for the diatoms, and these might have lasted much longer. It is probable that in high latitudes where temperature remains low the whole year round, this will occur and may be an explanation of the greater richness of the phytoplankton there.

It has been suggested by Pearsall (**26**) that the heavy rainfall in spring and autumn increases the amount of nutritive salts brought into the sea by rivers and is sufficient to cause an increase in diatoms. On p. 842 it has been shown that little phosphate is introduced by the rivers, although silicates, and possibly other compounds, are rich. When the rainfall curve for 1926 was compared with those for salinity and for diatoms in Loch Strivan it was found that while salinity and rainfall are related, there was no relation between rainfall or salinity and diatom increases. Occasionally when the surface water was discoloured and the salinity very low (as on August 19th at Loch Strivan head) diatoms were exceedingly scarce in this layer and small photosynthetic dinoflagellates abundant. The absence of diatoms may be due simply to the fact that a layer of low salinity has been added at the top and the diatom rich layer is therefore found at a greater depth than before, a depth which may not have been sampled. Since, as a rule, samples were only taken at surface, 5, 10, 20 and 30 fathoms,

it is of course always possible that a layer rich in diatoms or other organisms may have been missed entirely, but from the consistent results and their agreement with the chemical factors this does not seem probable (see also p. 857).

One observation which has been made frequently during 1926 is that a diatom increase begins in the surface layer and spreads downwards, decreasing at the surface as it does so. This was first observed by Lohmann (**18**) at Kiel, and was inferred by Gran (**8**) from the conditions found in the north European waters. Exceptions to this rule are found in the increases of *Chætoceros cinctum* and Eucampia, although as stated above the latter may be due to autumnal light conditions. This spreading downwards is seen most clearly in the spring maximum, where it seemed to depend on the amount of phosphate present. The spring increase lasted the longest time, and in increases after this the diatoms spread downwards more rapidly. This agrees with the consistently low phosphate values in the surface during the summer. The higher temperature too may increase the rate of metabolism of the diatoms, and so cause the change to occur more rapidly. It may also be due, as Gran has suggested, to the lower viscosity of the water then. In August and September, however, the sinking is probably not due to low phosphate value, for as soon as one diatom had decreased in the surface layer another appeared there. It would seem either that each diatom depends on minute amounts of a substance, the particular substance varying with each species of diatom, or else that there is an internal factor which is not yet known. The first alternative is suggested by Overton's (**24**) analyses of some closely related species of Fucus, which had marked differences in chemical composition in spite of their growing side by side. On the other hand, Nathansohn (**22**) suggests the possibility that phytoplankton may excrete some substance into the water which is injurious to itself.

Gran and Gaarder (**9**), working in the Kristiania fjord, attributed sudden changes in the phytoplankton there to the meteorological conditions prevailing at the time. The fjord runs north and south, and with a north wind the surface layers were blown out and replaced by warmer and more saline water from below. A south wind, on the other hand, carried in the diatom-rich surface layers of the sea outside with a consequent welling out of deep water from the fjord. This action caused a great increase of diatoms at the end of March, which sank rapidly into deep water, owing to the continuous southerly wind. Such an explanation does not apply to the changes in Loch Strivan. Plate I, Fig. 2, gives the north and south components of the wind in 1926, and it will be seen that before and at the beginning of the spring maximum there were northerly, i.e. outgoing winds, and although the wind changed to southerly on April 1st this had no obvious effect on the diatoms. As they were

already rich at 5 and 10 fathoms on this date it is obvious that the sinking was not due to wind action. During the rest of the year no connection can be found between wind direction and the appearance of diatoms.

The hope that this work might give some clue to the cause of the changing species of diatom during the year was not fulfilled. Chætoceros seemed to have a greater power of utilising phosphate than Skeletonema, a power apparently shared only by Eucampia, but this is not borne out by the June cruise of 1925 in Loch Fyne, where an increase of Skeletonema reduced the phosphate to zero on one occasion.

With regard to the effects of animal life and regeneration of phosphate, precise results are not available since the tow-nettings were not quantitative. The curves show that where animal life is rich, dissolved oxygen saturation and pH value are low and phosphate high, though this is probably due in part to the breaking down of dead organisms.

The total phosphate in solution just before the autumn mixing in Loch Strivan was definitely higher than before the spring diatom increase, and the same phenomenon apparently also occurs in Loch Long and Loch Goil. Each of them seems to form a reservoir of phosphate in its deep waters till the autumn mixing takes place, when the phosphate is distributed and spring values again attained by a change of the water. How the additional phosphate is acquired is not known. This phenomenon does not occur in the more open water of the area where conditions are much more like those described by Atkins (**4**) for the English Channel.

The writers wish to express their thanks to Mr. Elmhirst, Superintendent, and members of the Staff, for their help throughout.

SUMMARY.

1. Simultaneous observations are recorded of some biological, physical, and chemical changes in the Clyde Sea Area in 1924, 1925, and 1926.

2. A close relation between diatom increases and changes in pH value, dissolved oxygen saturation and dissolved phosphate has been found.

3. It appears that the more numerous diatom increases in Loch Strivan as compared with the open sea are due to the more frequent mixing.

4. Confirmation of the fact that diatom increases begin at the surface and gradually spread into deeper water has been obtained.

5. The occurrence of Peridinians is apparently related to high temperature and low salinity.

6. The amount of sunshine in the early part of the year does not exert any apparent influence on the date of the spring diatom increase in the Clyde Sea Area.

7. The regeneration of phosphate in the deep water of Loch Strivan has been described.

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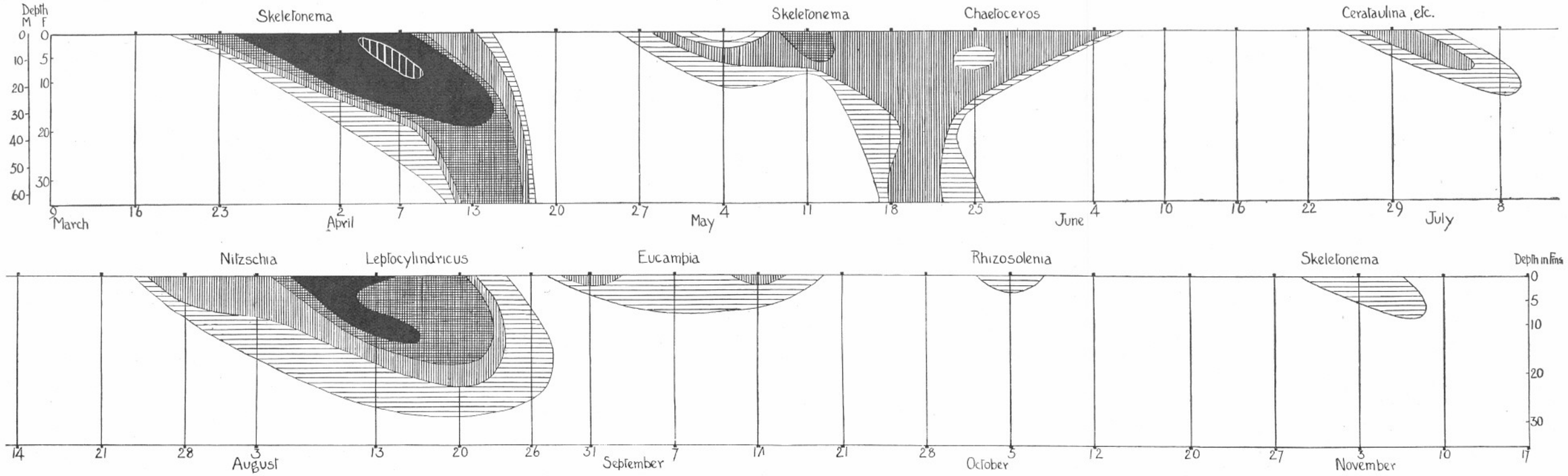

FIG. 1. Diagram of the diatoms at Clapochlar in 1926.

□ under 500, ▤ 500 to 2,000, ▥ 2,000 to 5,000, ▩ 5,000 to 10,000, ■ 10,000 to 25,000, ▮ over 25,000, diatom chains in 20 c.c.

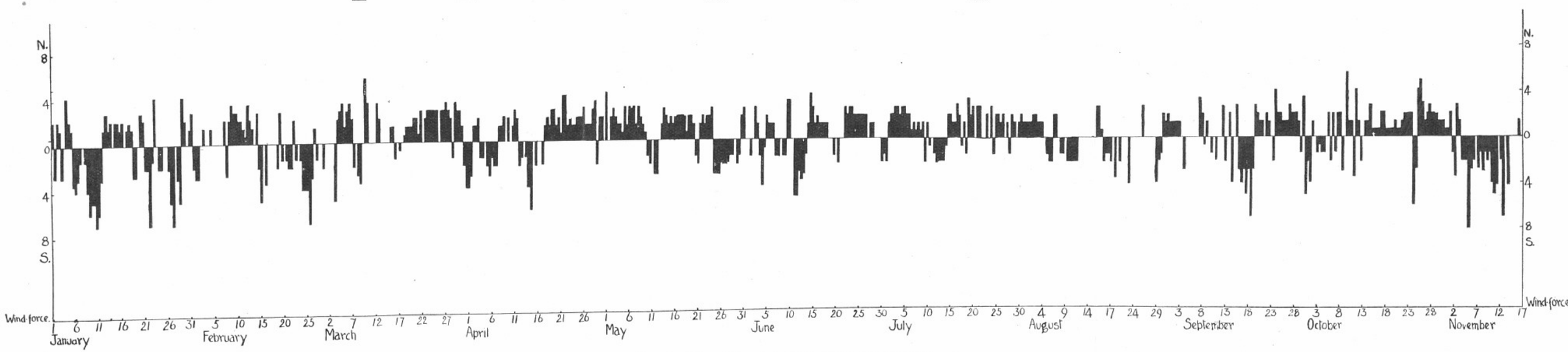

FIG. 2. N. and S. components of the wind in 1926.

To face p. 868.

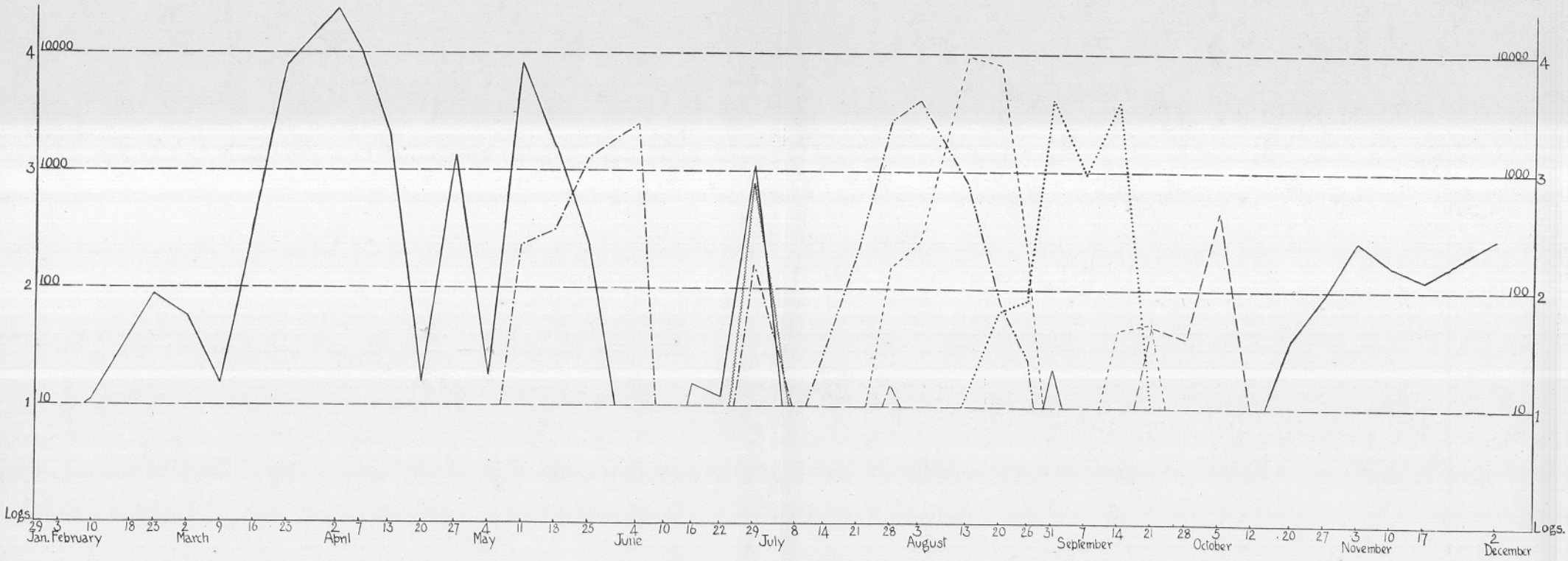

FIG. 3. Loch Strivan, 1926. Clapochlar. Number of diatom chains in 20 c.c. at the surface. —— *Skeletonema costatum*, —.—. *Chaetoceros cinctum*, ~~~~ *Cerataulina bergoni*, —.—.—. *Nitzschia seriata*, - - - - - *Leptocylindricus danicus*, ... *Eucampia zoodiacus*, —— —— *Rhizosolenia setigera*. Numbers below 10 omitted for the sake of clearness.

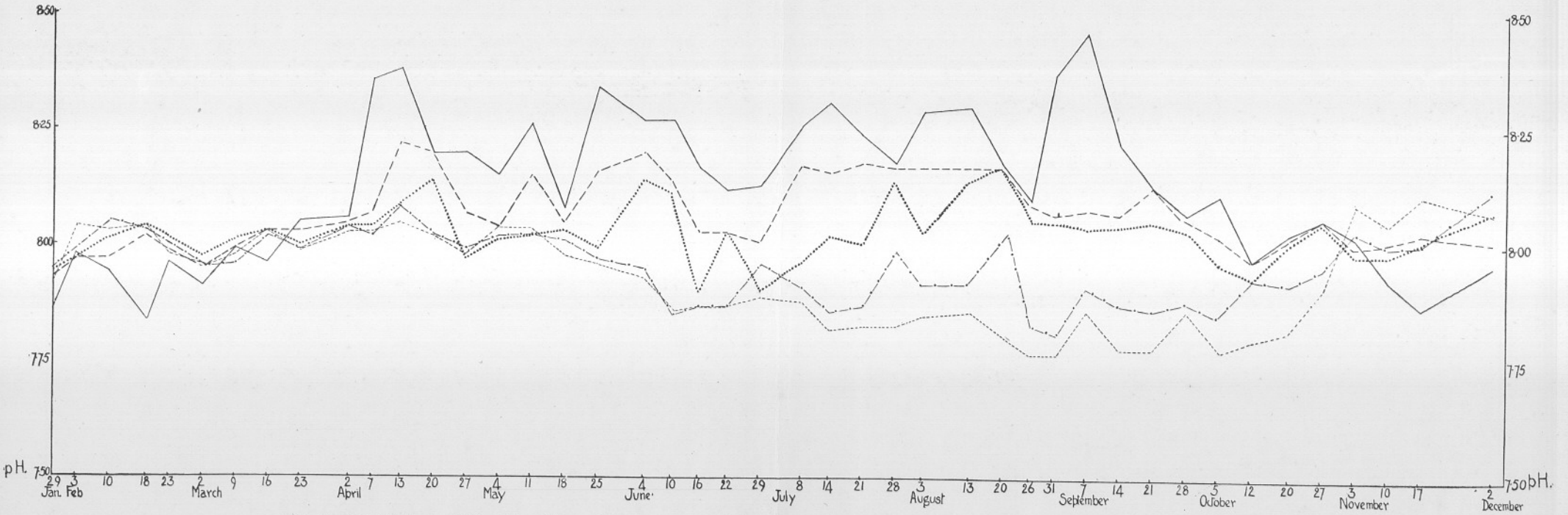

FIG. 4. Loch Strivan, 1926. Clapochlar. pH value. ——— 0 fm., — — — — 5 fm., ... 10 fm., —.—.—. 20 fm., - - - - - - bottom.

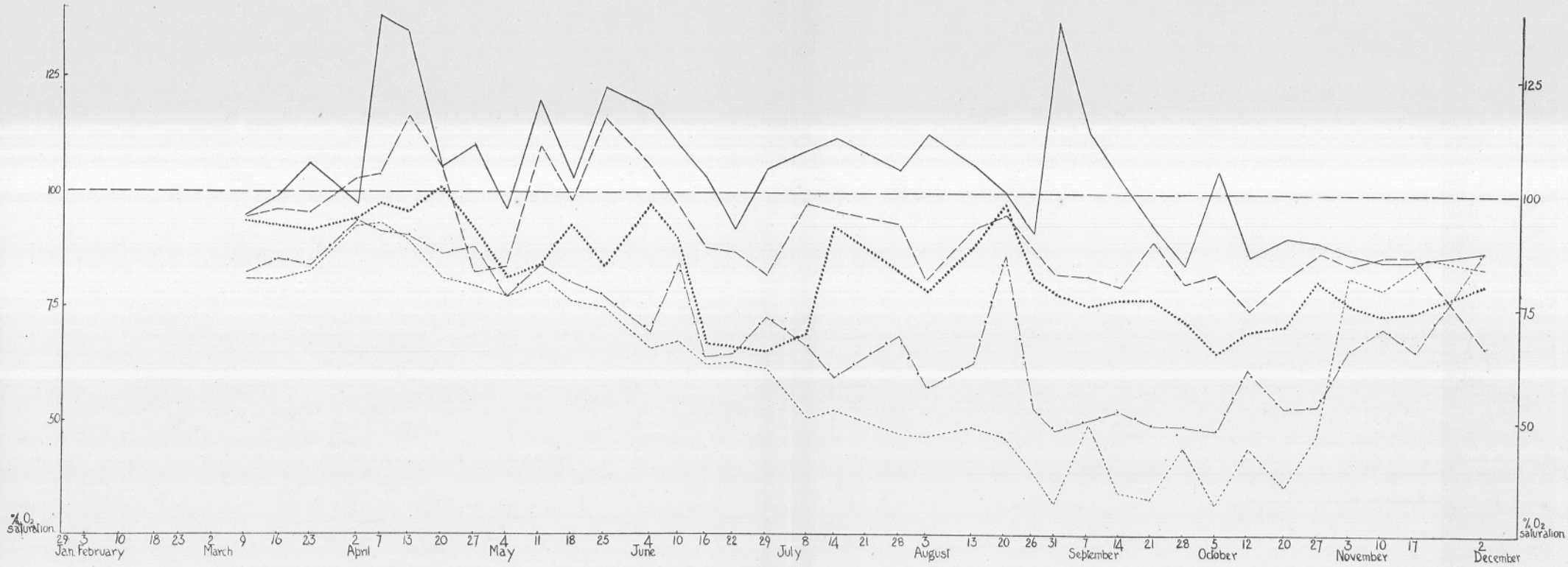

FIG. 5. Loch Strivan, 1926. Clapochlar. Percentage saturation of oxygen. —— 0 fm., — — — 5 fm., ... 10 fm., —.—.—. 20 fm., - - - - - bottom.

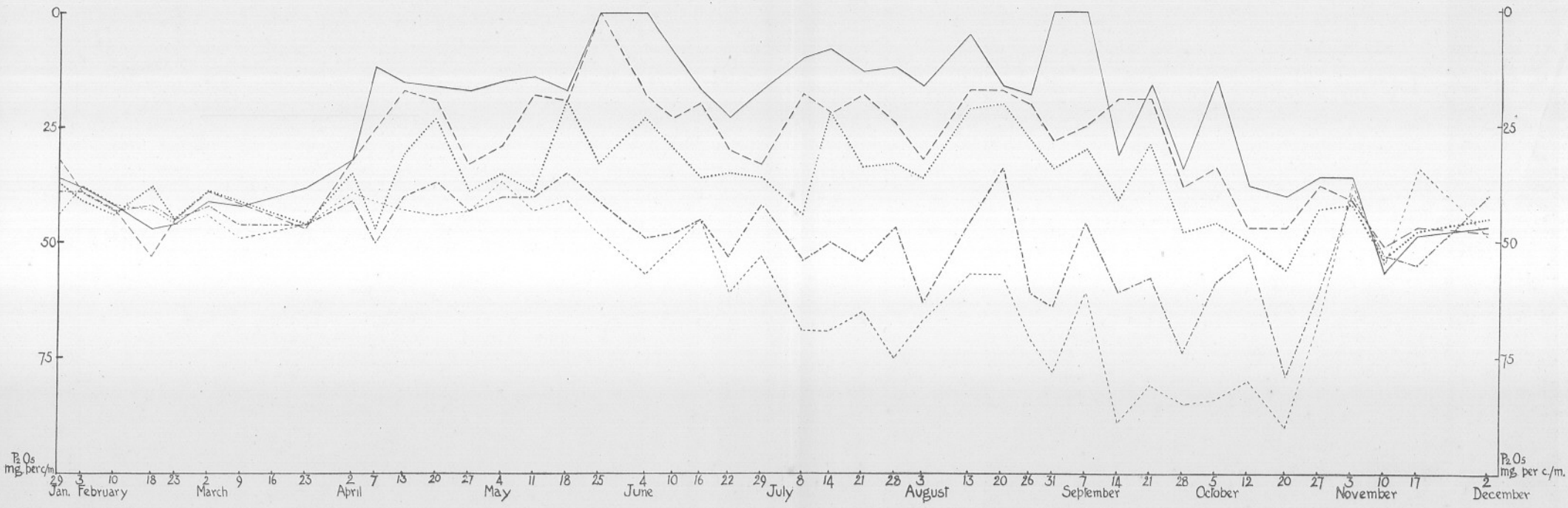

FIG. 6. Loch Strivan, 1926. Clapochlar. Phosphate. —— 0 fm., — — — — 5 fm., ... 10 fm., —.—.—. 20 fm., - - - - - bottom.

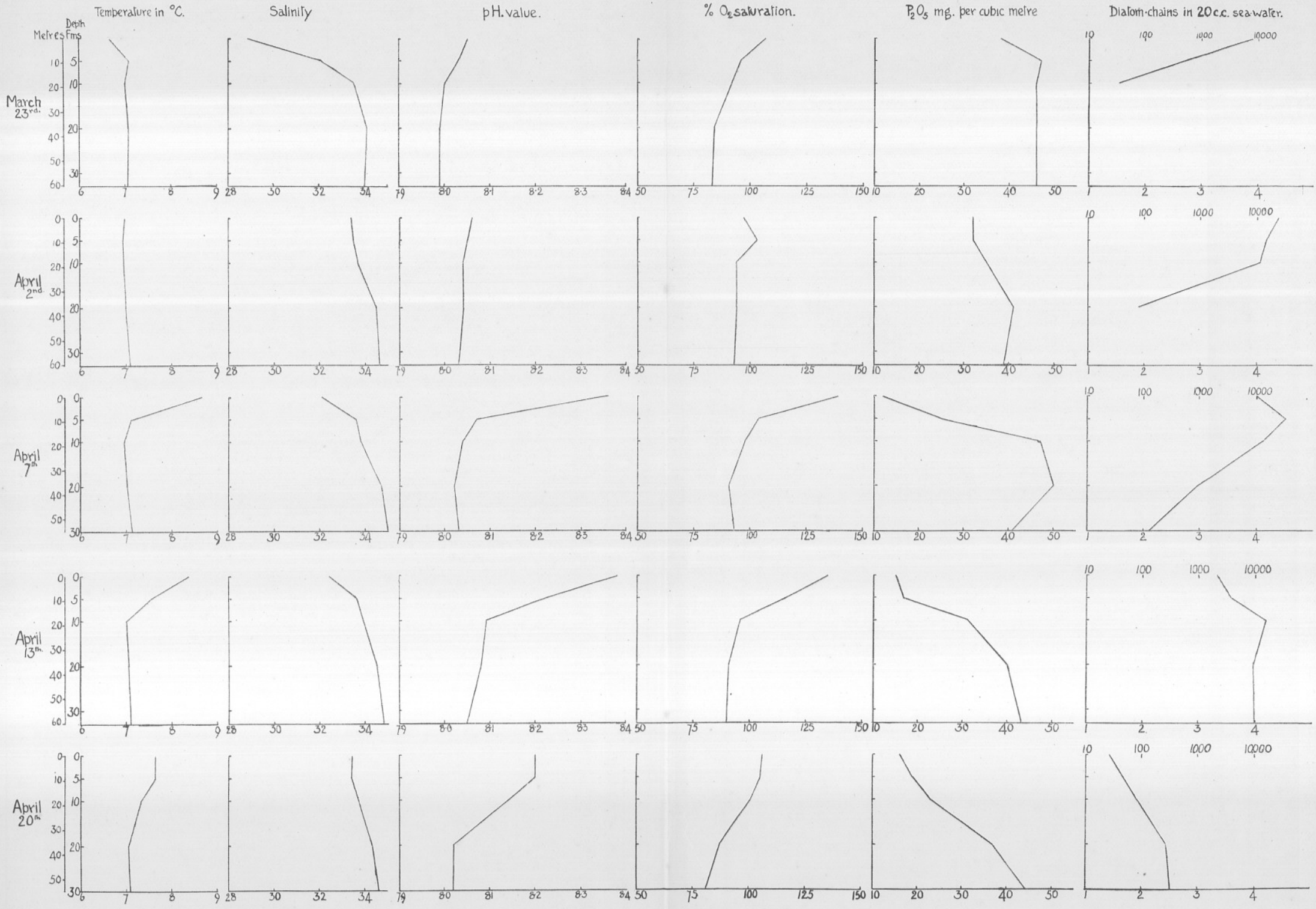

FIG. 7. Loch Strivan, 1926. The changes during the spring diatom maximum.

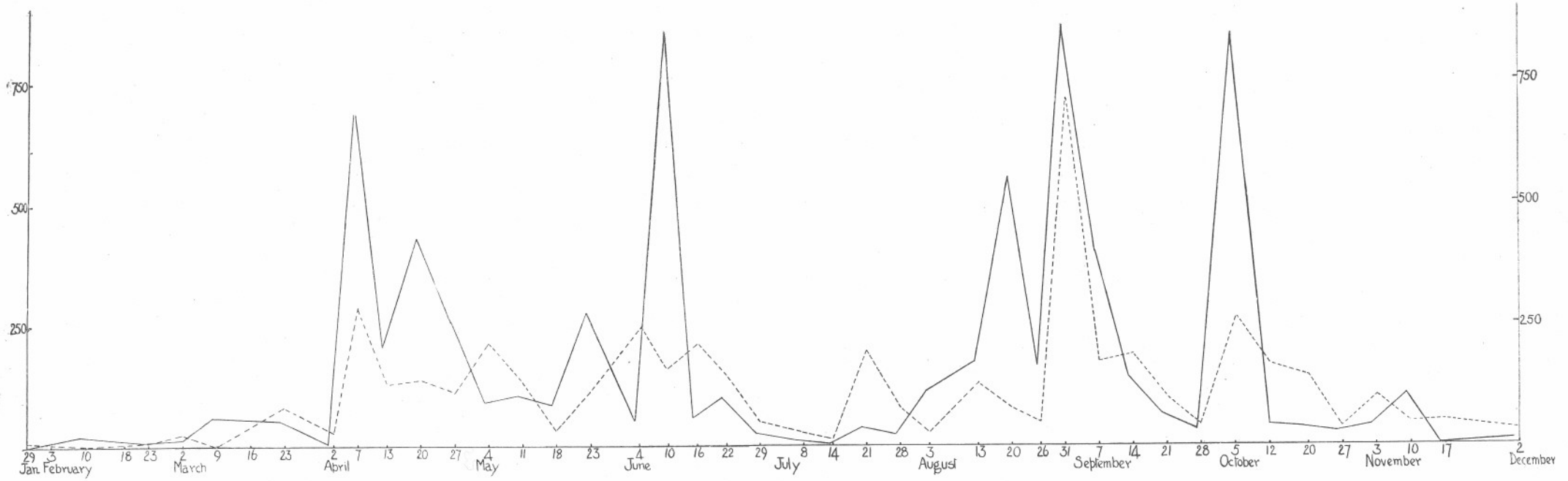

FIG. 8. Loch Strivan, 1926. Dinoflagellates in 20 c.c. at the surface. —— Loch Strivan head, - - - - Clapochlar.

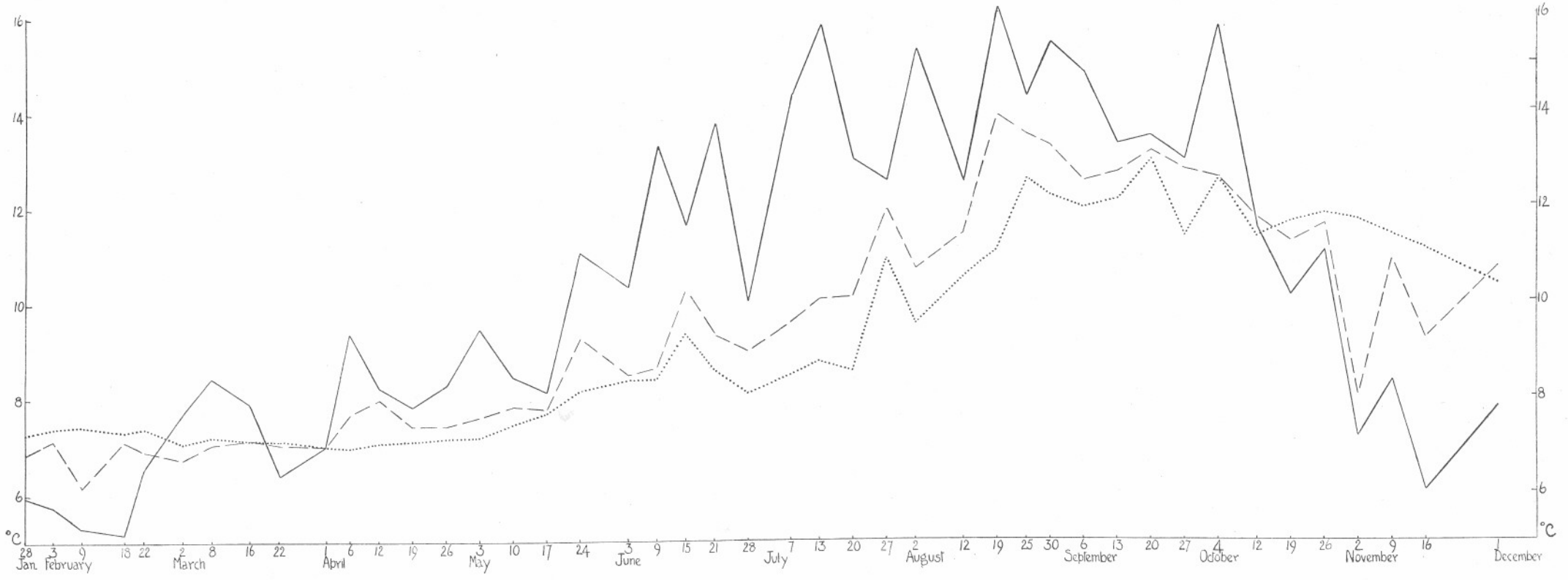

FIG. 9. Temperature at Loch Strivan head, 1926. —— 0 fm., - - - - - 5 fm., ... bottom.

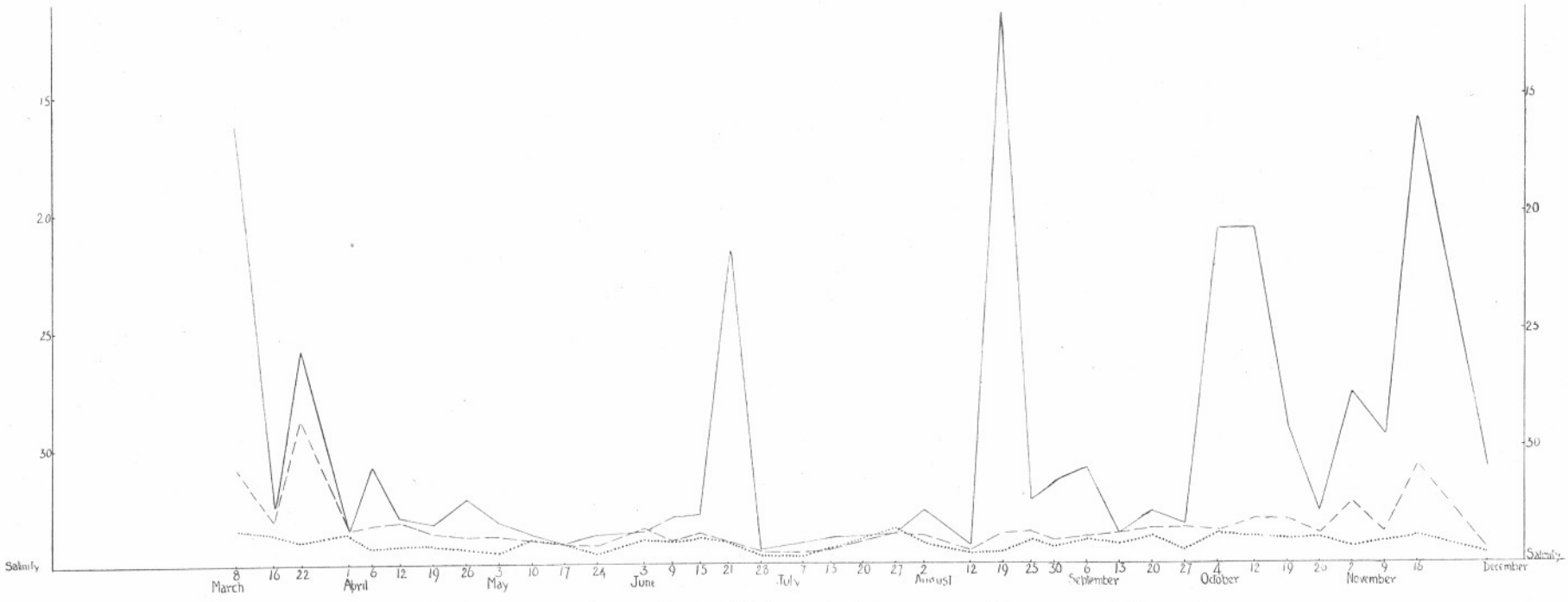

FIG. 10. Loch Strivan, 1926. Head. Salinity. —— 0 fm., — — — 5 fm., - - - - - - bottom.

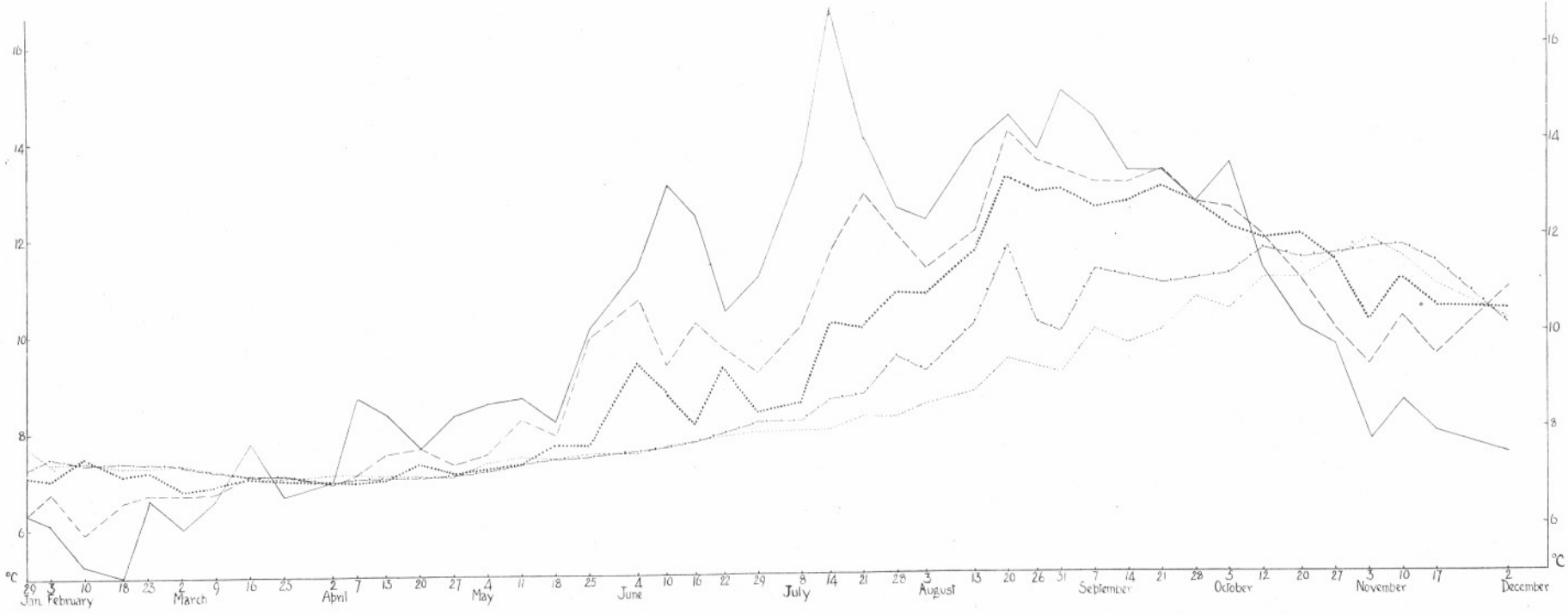

FIG. 11. Loch Strivan, 1926. Clapochlar. Temperature. —— 0 fm., — — — — 5 fm., ... 10 fm., —.—.—. 20 fm., - - - - - - bottom.

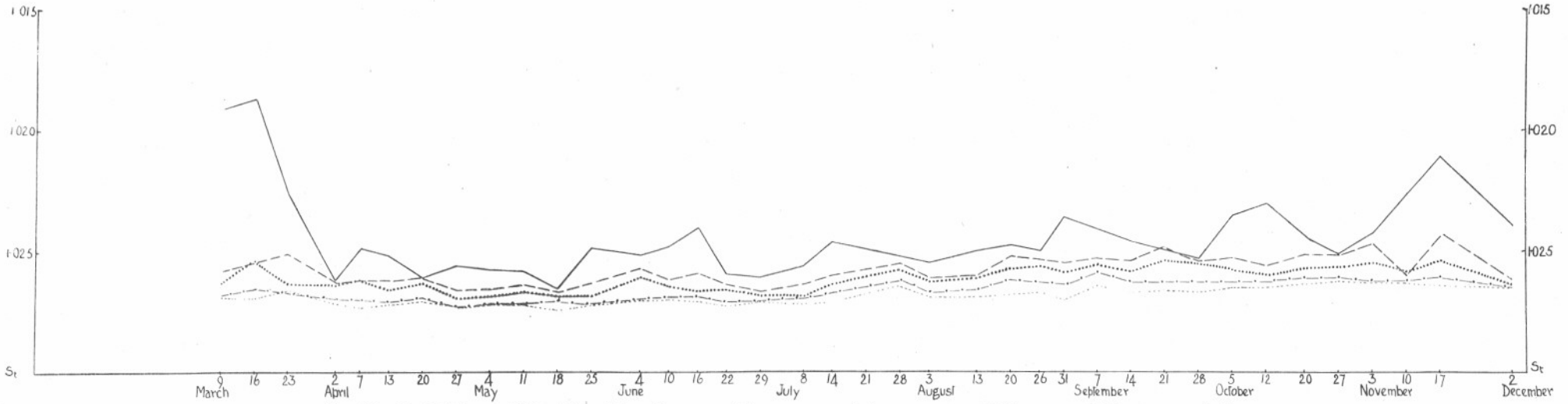

FIG. 12. Loch Strivan, 1926. Clapochlar. St. —— 0 fm., — — — 5 fm., ... 10 fm., —.—. 20 fm., - - - - bottom.

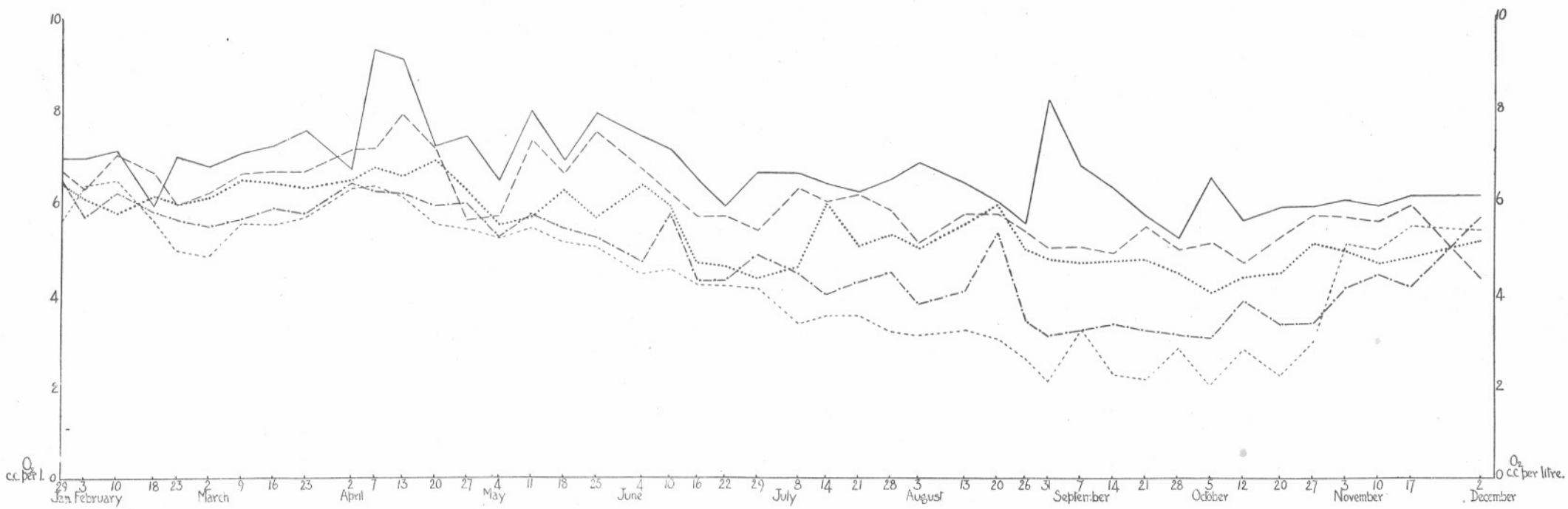

FIG. 13. Loch Strivan, 1926. Clapochlar. Dissolved oxygen. —— 0 fm., — — — 5 fm., ... 10 fm., —·— 20 fm., - - - - bottom.

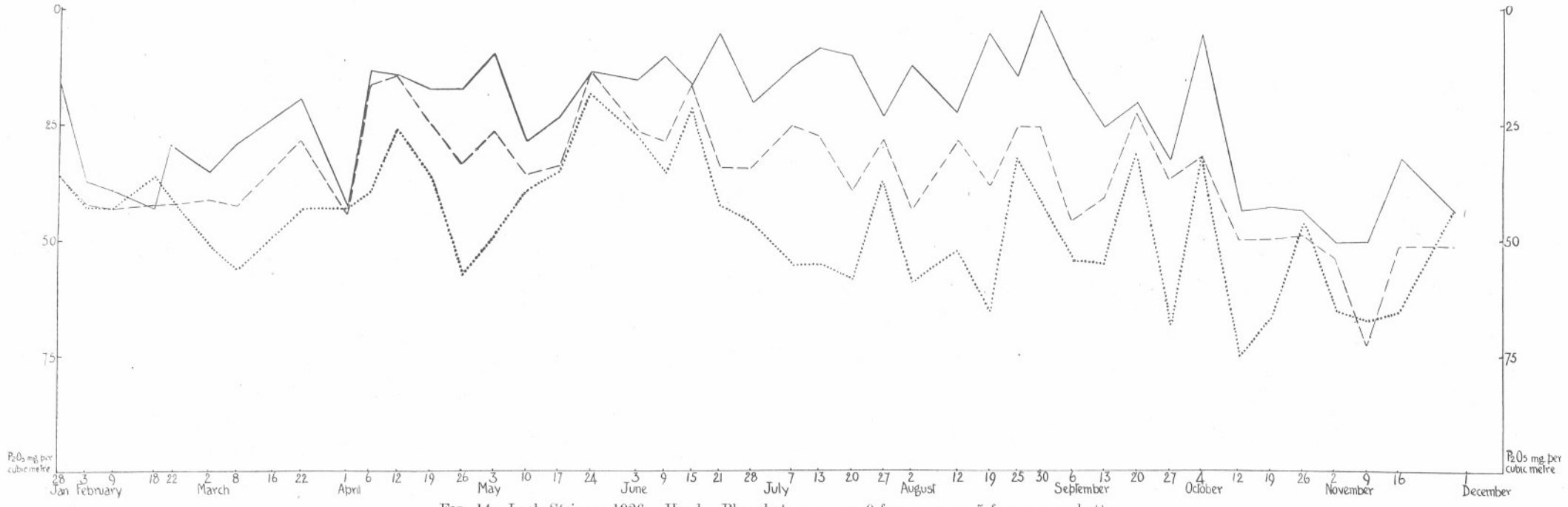

FIG. 14. Loch Strivan, 1926. Head. Phosphate. ——— 0 fm., — — — 5 fm., ... bottom.

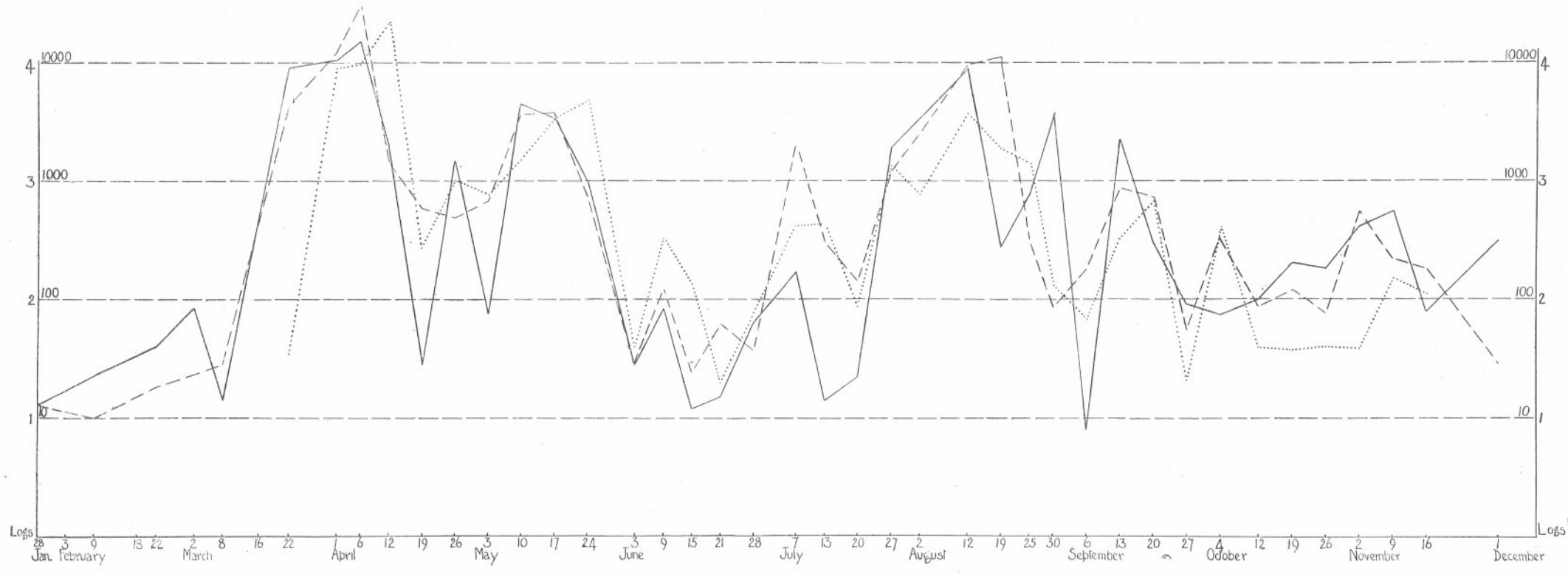

FIG. 15. Total diatoms in 20 c.c. at Loch Strivan head, 1926. ——— 0 fm., — — — 5 fm., ... bottom.

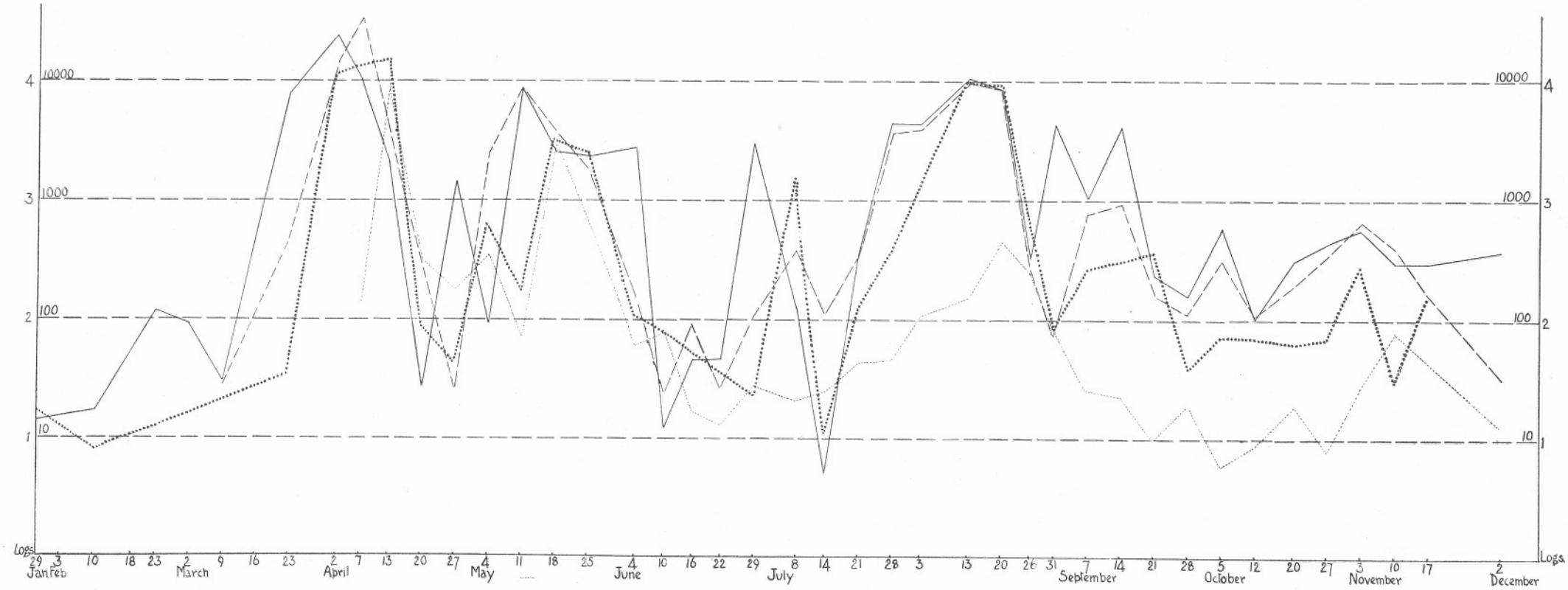

FIG. 16. Total diatom chains in 20 c.c. at Clapochlar, 1926. —— 0 fm., — — — 5 fm., ... 10 fm., - - - - - bottom.

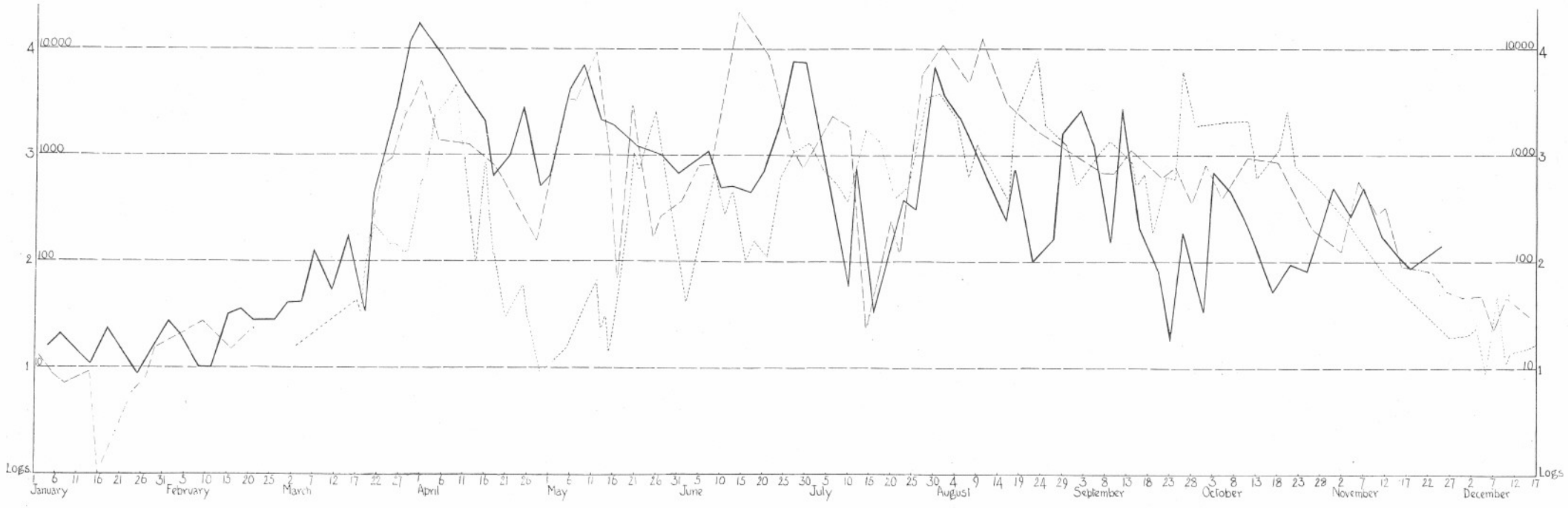

FIG. 17. Total number of diatom chains in 20 c.c. at Keppel in - - - - - 1924, — — — 1925, —— 1926.

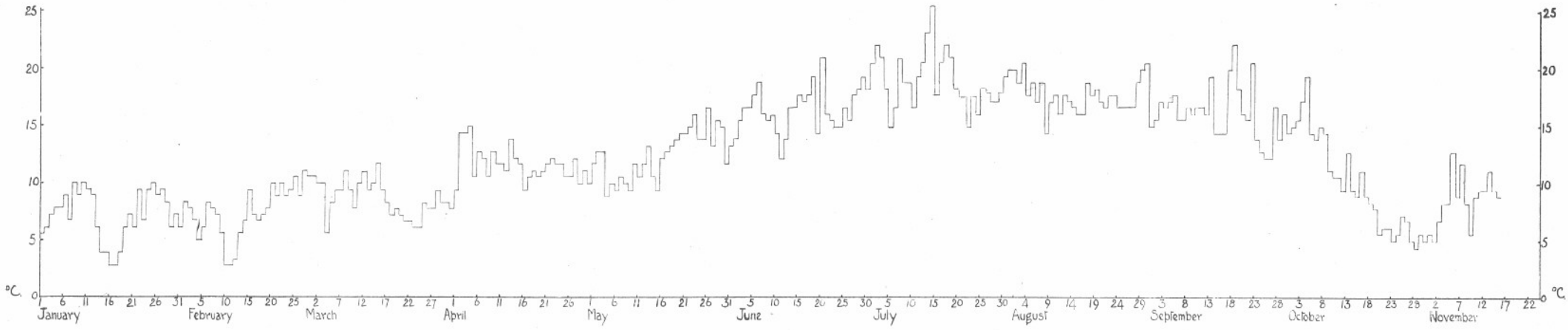

FIG. 18. Air temperature. (Shade maximum.) 1926.

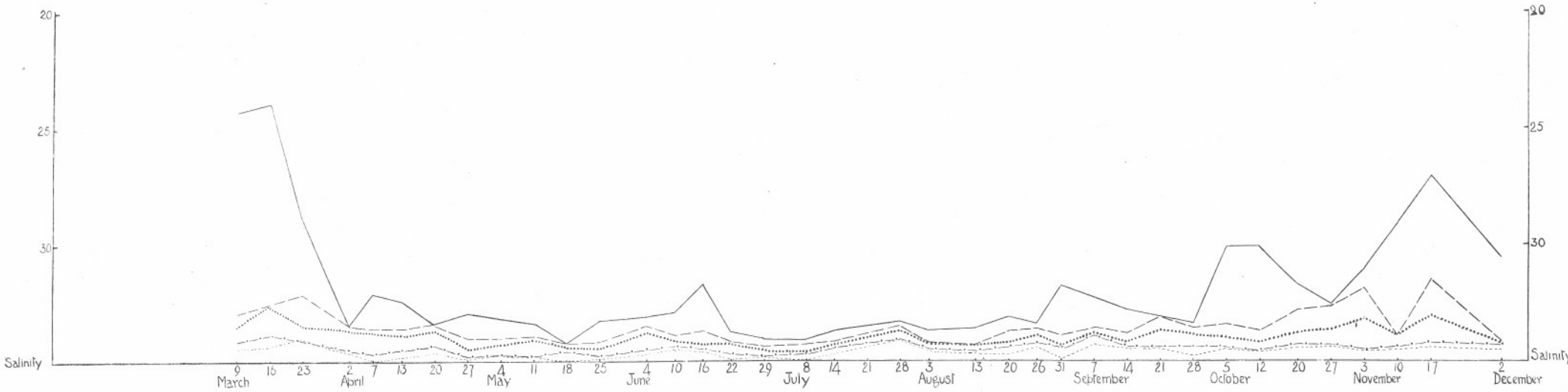

FIG. 19. Loch Strivan, 1926. Clapochlar. Salinity. —— 0 fm., — — — 5 fm., ... 10 fm., —.—.—. 20 fm., – – – – bottom.

Fragmentation in the Genus *Autolytus* and in other Syllids.

By

E. J. Allen, D.Sc., F.R.S.,

Director of the Plymouth Laboratory.

With 1 Figure in the Text.

In a former paper (Allen, Phil. Trans. Roy. Soc. B., Vol. 211, p. 131, 1921) it was shown that the Syllid *Procerastea Halleziana* Malaquin, in addition to the ordinary mode of sexual reproduction which occurs in this group, reproduced asexually by a process of fragmentation, followed by the regeneration by each fragment of a new head and series of anterior segments and of a new pygidium and posterior segments. The fragments usually consisted of sections of two, three, or four segments each, in the region of the body behind the seventh setigerous segment. It was further shown that this breaking up of Procerastea, which could be produced artificially at any time by treating the worms with sea-water of low salinity, made by adding distilled water to natural sea-water, took place according to a definite law. The first section consisted normally of the head and setigerous segments 1 to 7, then followed three sections of two segments each (Segments 8 and 9 ; 10 and 11 ; 12 and 13), then three sections of three segments (14–16 ; 17–19 ; 20–22), followed by four or five sections of four segments each, and then a number of sections of three segments. This was expressed as a formula thus :—

H7+2+2+2+3+3+3+4+4+4+4(+4)+3+3+3+3+ . . . P

where H represents the head, P the pygidium or tail, and the plus sign the position at which a break occurs. A considerable number of segments at the posterior end do not break up readily and often not at all, these being young segments recently developed.*

* Previous to the publication of my paper on Procerastea, Mesnil and Caullery, in a paper entitled "Sur un processus normal de fragmentation, suivie de régénération, chez une Annélide Polychète, *Syllis gracilis* Gr." (Comptes rendus, t. 169, 1919, p. 926), which I had unfortunately overlooked, had described fragmentation followed by regeneration in *Syllis gracilis*. This case is described further in Mesnil, "Titres et travaux scientifiques (1893–1920)," Laval, Barnéoud, p. 37, and Mesnil et Caullery, "Sur la complexité du cycle évolutif des Annélides polychètes" (Comptes rendus, t. 178, 1924, p. 168). They did not, however, determine in *Syllis gracilis* the serial order of fragmentation,

In *Procerastea Halleziana*, the bud head of the single "stolon," which is formed prior to the sexual reproduction of the species, is always found on Segment 14, the first segment of the first section of three segments.

Similar fragmentation has since been studied in other Syllids, especially in the genus Autolytus, which is closely allied to Procerastea, and an account of this work is given in the present paper.

Autolytus macrophthalma (Marenzeller).

Fragmentation according to a definite law is shown with special clearness in this species, and has been produced in a large number of specimens by treating them with distilled water on a glass slide in the way described for Procerastea. The breaking-points are quite clear long before an actual rupture takes place.

The two following examples observed on February 19th and 20th, 1923, respectively, are typical of many others :—

Feb. 19. H7+2+2+2+3+3+3+4+4+4+4+4+3+3+4+4+4 +4+4+4+4+4+4+11P.

Feb. 20. H7+2+2+2+3+3+3+4+4+4+4+4+3+3+4+4+4 +4+4+4+4+4+4+6P.

The bud head in all cases forms on Segment 14.

Autolytus macrophthalma is a much longer species than *Procerastea Halleziana*, and contains many more segments. A large specimen of *A. macrophthalma* may have from 90 to 100 segments, whereas a large Procerastea seldom has more than 50 to 60.

It will be seen that for the first portion of the body the sequence of breaking-points is the same in the two worms, viz. the head and seven segments, three sections of two segments, three sections of three segments, five sections of four segments. Procerastea then continues with sections of three segments, which persist until the undividing segments in front of the tail are reached. *Autolytus macrophthalma*, on the other hand, has only two sections of three in this position, and then continues with sections of four. These two sections of three, interpolated in the midst of the sections of four, are remarkably constant in this species, and are invariably in the same position, that is, they are segments 43 to 48.

It is interesting that in *A. macrophthalma* the positions at which the breaks occur are in many specimens clearly visible as thin, transverse, transparent lines in the living animal, before it has been treated with

so that we do not know whether it resembles that found in Procerastea and in other Syllids to be described in the present paper. Since the publication of my Procerastea paper Dehorne (Comptes rendus, t. 178, 1924, p. 143) has described asexual reproduction in *Dodecaceria*.

distilled water at all. The worm is of a light yellow colour, except for the rose-coloured proventriculus, but the amount of yellow pigment is very slight. Nevertheless its absence along the lines where the fragmentation occurs gives rise to the distinct transparent lines by which the body is crossed.

Interesting variations in the breaking up of *A. macrophthalma* are seen in a specimen treated with distilled water on February 19, 1923, which gave the following formula :—

H7+2+1+2+2+2+3+3+3+4+4+4+4+4+3+3+4+4+4+4+4
+4+4+4+8P,

and one on March 6, 1923, which gave :—

H7+2+2+1+2+3+3+3+3+4+4+4+4+4+3+3+4+4+4+4+4
+10P.

In both cases it looks as if extra segments had been interpolated in the anterior region of the body (the part usually occupied by segments 1 to 13). The phenomenon is probably due to some irregular regeneration after injury.

Experiments on regeneration were not very successful in this species, though not many were tried. The difficulty was due to the fact that the sections did not live well after they had been separated. The only successful pieces were (1) Head and segments 1 to 13 gave in six weeks a posterior regeneration of ten setigerous segments and two well-developed anal cirri ; (2) Segments 20, 21, and 22 (the last section of the first group of threes) gave in six weeks a posterior regeneration with five well-developed and one rudimentary setigerous segments, and well-developed anal cirri, but with no anterior regeneration ; (3) Segments 23 to 26 (the first section of four) gave in six weeks a posterior regeneration with three setigerous segments and well-developed anal cirri, but again with no anterior regeneration.

Autolytus pictus (Ehlers).

This species breaks under the action of distilled water in exactly the same way as *A. macrophthalma*, excepting that the first break occurs behind Segment 9, that is to say, the first section of 2 is not detached. The following is a typical formula :—

Dec. 18, 1922. H9+2+2+3+3+3+4+4+4+4+4+3+3+4+4
+4+4+4+4+1+3+5P.

As in Procerastea the stolon head always occurs on Segment 14. This species is exceptional amongst British species of Autolytus, on account of its deep pigmentation and definite colour pattern (Fig. 1). The dorsal

surface is covered with a deep deposit of black or dark brown pigment, with the exception of a mid-dorsal longitudinal line (immediately over the intestine), which is free of pigment and hence appears white, and a series of transverse bands free of pigment and hence also appearing white (Fig. 1). We find here in a much more marked and striking form the phenomenon which we have already described in *A. macrophthalma*, namely, that it is precisely along these pigment free white bands that the breaking-points occur when the worm is treated with distilled water.

The following formula shows the positions of the white bands on a specimen of *Autolytus pictus*, the + sign showing the position of a band before the worm was broken up :—

H7+2+2+2+3+3+3+4+4+4+4+3+1+3+3+4+4+. . . .

When this worm broke up on the addition of distilled water it gave the following, the + sign now indicating the places where the breaks occurred :—

H9+2+2+3+3+3+4+4+4+4+3+1+3+3+4+4+4+3+3+3 +3+4P.

This case was specially interesting because the exceptional splitting up of the last (fifth) four of the first group of fours into 3+1 was shown equally clearly by the white bands and by the actual breaks.

The series of facts just described suggests that tissue at the breaking places possesses some definite difference in its chemical properties, which prevents the dark pigment deposited on the rest of the back from being laid down.

It may be mentioned that the pigment is a highly resistant substance, being insoluble in water, in alcohol, in ether following treatment with absolute alcohol, and in strong hydrochloric acid.

It was noted that in specimens in which the sexual products were ripening the dark pigment became lighter, somewhat greenish and more diffuse, the white longitudinal band and the white transverse bands becoming much less conspicuous behind Segment 14, the segment upon which the stolon head is budded.

Regeneration in this species takes place much more slowly than in Procerastea, but heads and anterior regeneration have been obtained as well as regeneration of posterior segments. A description of these results is reserved until further experiments have been made.

LEGEND TO FIG. 1.

FIG. 1.—*Autolytus pictus* (Ehlers). ×8¼. The parapodia and setae of the first setigerous segment do not appear in the drawing, as they cannot be seen in a dorsal view of the worm. They lie immediately below the very long dorsal cirri. (From a drawing by Mrs. E. W. Sexton.)

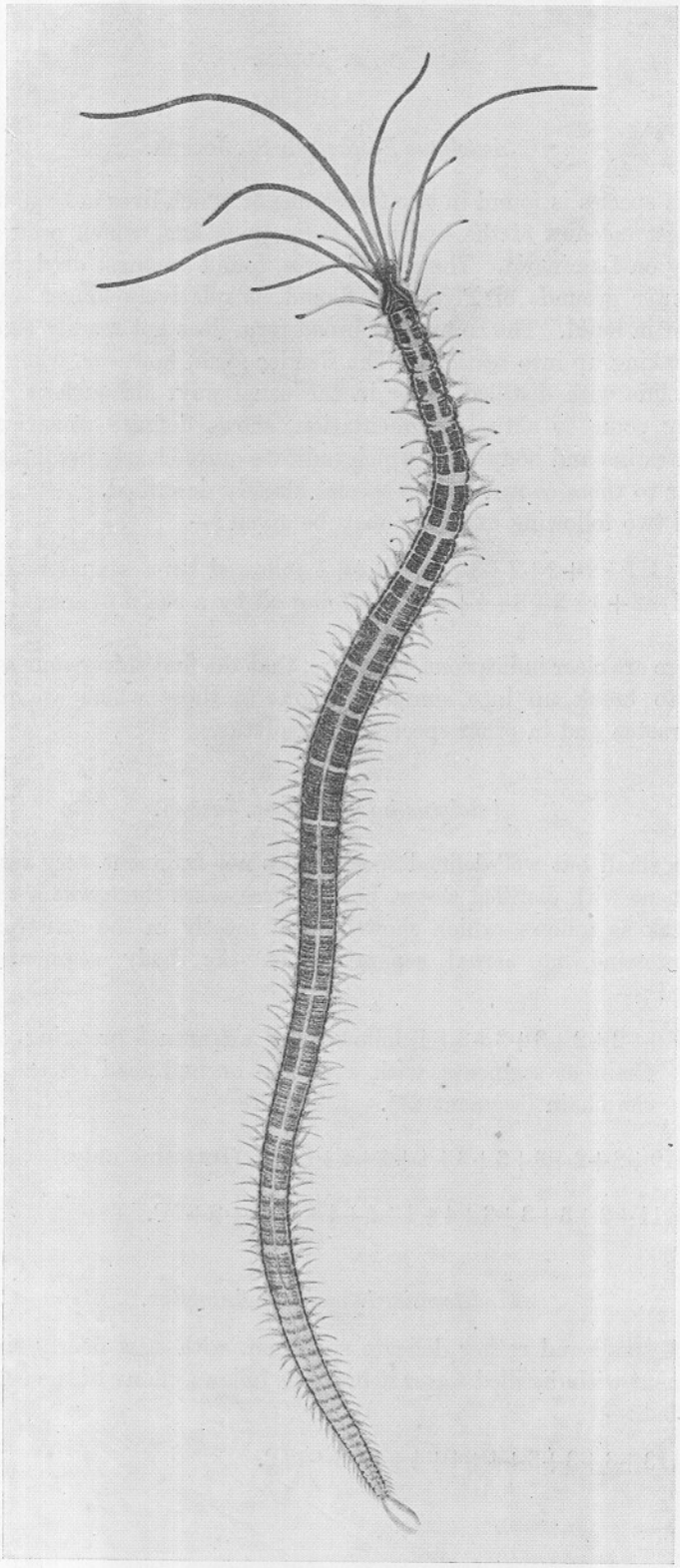

FIG. 1.

Autolytus Edwarsi de St. Joseph.

This species is found in two forms, one of which lives in large numbers amongst colonies of the hydroid *Obelia geniculata*, which occurs abundantly on Laminaria. The second form, found amongst dredgings from the outer grounds of Plymouth Sound, is relatively longer and more slender in build. The commoner broad form does not readily show signs of breaking up into sections. The slender form, however, when treated on a slide with distilled water in the usual way, although it does not usually come to actual fragmentation, shows definite constrictions of the intestine and body wall, which indicate quite clearly breaking-points similar to those shown by the species already described.

The two following examples may be given :—

H7+2+2+2+3+3+3+4+4 followed by a sexual bud.
H11+2+3+3+3+4+4+4+3 followed by a chain of sexual buds.

There are clear indications, therefore, that the first thirty-four segments tend to break up into similar sections to those which are found in Procerastea and in other species of Autolytus.

Autolytus inermis de St. Joseph.

This small but well-defined species does not fragment very readily on treatment with distilled water, but in three cases there was a tendency to break as follows, which showed itself mostly in the constriction of the intestine, no actual separation of the body segments being reached :—

1. H9+2+2+3+3+3+4 followed by an actual breaking off of a chain of segments, with a stolon- or bud-head on the first of the chain (segment 27).

2. H9+2+2+3+3+3+4+4+4+14P. (Intestine only.)

3. H11+2+3+3+3+4+4+4+4+4+3+3+7P.

Undetermined species of Autolytus.

1. A small and rather delicate specimen, with eggs nearly ripe. On treatment with distilled water it broke as follows, many of the eggs being extruded :—

H13+3+3+3+4+4+4+4+3+12P.

2. A specimen resembling *A. Ehbiensis* de St. Joseph, but with no definite teeth on the proboscis gave :—

H13+3+3+3+4+4+ca. 12P.

3. A specimen resembling the last, but with about twenty-five equal teeth on the proboscis, gave with the intestine, but with no break or great constriction of the body :—

H9+2+2+3+3+3+4+4+a bud head and ca. 15P.

4. A specimen which was probably *Autolytus prolifer*, but the teeth on the proboscis could not be seen clearly enough to be sure that the number was 10, gave on treatment with distilled water :—

H7+2+2+2+3+3+3+4+4+4+4+4+4+3+3+4+4+4+25P.

This is similar to what occurred in *A. macrophthalma* and *A. pictus*.

From the observations recorded above it is clear that the tendency to fragment according to a definite scheme is widespread in the genus Autolytus, and that the scheme for the first forty or fifty setigerous segments is the same as that previously described for Procerastea. In the case of the longer members of the genus possessing considerably more than fifty segments a new regularity of fragmentation is continued in the posterior segments, of which the arrangement found in *Autolytus macrophthalma* is typical.

There is one species of the genus, however, *Autolytus rubropunctatus*, which, in spite of many attempts, has shown little or no tendency to fragment. The tissue of this worm seems to be tougher and more compact than that of allied species of about the same size.

In the genus Autolytus I have met with no evidence that fragmentation followed by regeneration is a normal process of asexual reproduction occurring in nature, as it certainly is in the genus Procerastea. In no instance have I found worms which appeared to have originated from segments of the body, which were regenerating new anterior and posterior ends. The only cases of obvious regeneration which were seen, and these were not infrequent in *Autolytus pictus*, were posterior regenerations from old heads and anterior segments, arising generally from the thirteenth setigerous segment, and thus replacing that part of the body which had broken away as the ripe stolon, or free-swimming bud.

Attempts have been made to cause other Syllids to fragment by the addition of distilled water. Positive results were obtained for the two following species :—

Syllis (*Pionosyllis*) *lamelligera* de St. Joseph.

This gave quite distinctly :—

H9+2+2+3+3+3+4+3+4+2+2+6P.

Syllis (*Pionosyllis*) *divaricata* Keferstein.

H9+4+3+3+3+4+5+3+4+4+4+5P.

There were signs that regeneration had occurred after the section of 5 (i.e. after the thirty-first setigerous segment).

No sign of fragmentation on addition of distilled water was found in the following Syllids : *Odontosyllis ctenostoma* Claparède, *Syllis* (*Typosyllis*) *armillaris* (Müller), *Trypanosyllis zebra* (Grube), *Syllides longocirrata* Oersted, *Myrianida pinnigera* (Montagu).

My best thanks are due to Mrs. E. W. Sexton for the figure of *Autolytus pictus*.

A Revision of the Genus *"Portunus"* (A. Milne-Edwards, Bell, etc.).

By

Richard Palmer, B.Sc.(Lond.).

Student Probationer at the Plymouth Laboratory

With 9 Figures in the Text.

I. Introduction.

It is to-day realised very generally that such superficial characters as colouration and ornament, though in many cases of value for approximate identification, may frequently be mere effects of environment, not attributable to actual genetic differences at all. The characters of the adult animal are seen to be a complex resultant of both genetic and environmental factors, and taxonomy, if it is to have a firm genetic basis, must take both of these influences into account. These considerations point to the need for a critical re-examination of many of the doubtful species and varieties with which zoology abounds, with the object of determining whether their distinguishing characters are sufficiently definite and numerous to admit of their being regarded as genetically distinct types.

The swimming crabs, "*Portunus*" *holsatus* and "*Portunus*" *marmoreus*, are cases in point. Typical specimens are readily distinguishable by their colouring, but on the basis of the descriptions so far published it is understandable that considerable doubt has existed as to their complete distinctness. The majority of authors have considered them as very closely allied, and several, notably Stimpson (1869), A. Milne-Edwards and Bouvier (1899), and Bouvier (1922), have regarded them as identical. With the object of deciding the question finally, the present author therefore examined in detail large numbers of both fresh and preserved specimens of both species, and found as a result a number of definitely diagnostic characters clearly separating the two forms. These characters and others were found to be of value in considering the relationships of all the species of the genus, and to justify a short paper on the subject, especially as no detailed revision of the genus had appeared since A. Milne-Edwards' monograph on the Portunidæ (1861, a).

In considering the relationships of the species the probable degree of genetic complexity of a character has been borne in mind in estimating its morphological value. Much more genetic work in all groups requires, of course, to be done, before this criterion can be used in any exact sense, but it was felt that some such conception will ultimately be of importance in taxonomic work, and that even to-day it is not without value as a guiding principle. Further examples of its application in other groups could be given were space available.

It was found that the species arrange themselves fairly naturally in the phylogenetic scheme shown in Fig. 1. In view of the paucity of the

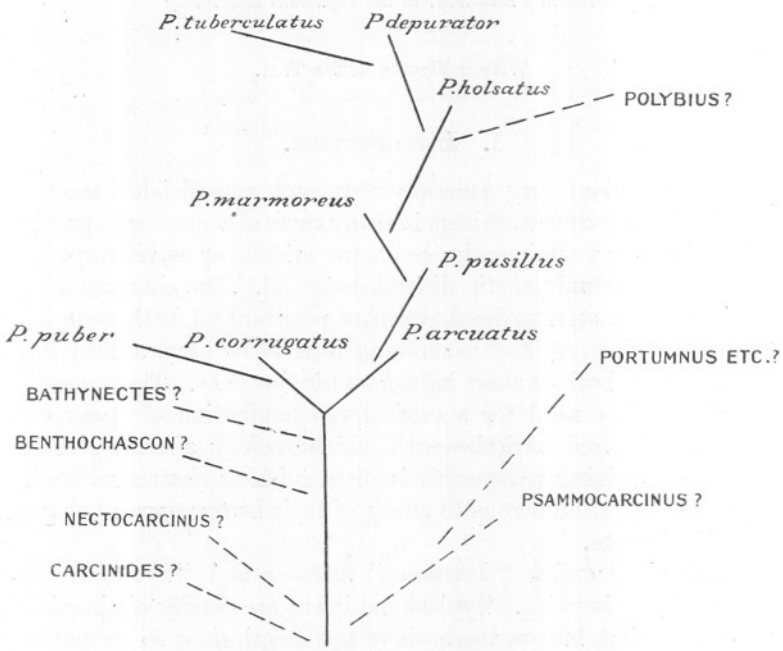

FIG. 1.—Tentative scheme of relationships of "Portunus" and its allies.

fossil evidence, this scheme is very tentative; but it was thought to be useful as a working hypothesis, and it is implicitly referred to in the discussions of specific characters. No attempt has been made to describe exhaustively those specific characters which have already received adequate attention in previous accounts, and the descriptive portion is to be regarded as, in the main, merely a guide to the figures. The latter have, with the exception of those of *P. tuberculatus*, been drawn from the mean of a large number of specimens, all of which approached the maximum size found in the species. The same precaution of using only full-sized individuals was employed in arriving at the statistical

data, so that errors arising from the heterogonic growth that Huxley (1927) has shown to exist in certain characters of various Brachyura might be avoided. The figures of the carapace are only outlines and follow at the postero-lateral corners the raised rim that is in most cases continuous round the carapace, rather than the less definite margin.

I wish to express my thanks to Dr. W. T. Calman for his kindness in permitting me to examine and revise the collection in the British Museum; to Dr. Mary Rathbun of the U.S. National Museum, for information on a number of points; and to Dr. Marie Lebour, for the the use of unpublished data on the developmental forms.

II. The Synonymy of the Generic Name.

The generic name of the species included under the genus "*Portunus*" in the sense of Milne-Edwards and the vast majority of authors, presents a very tangled problem in nomenclature. The name *Portunus*, as originally published by Weber (1795) and used by Fabricius (1798), included practically all the members of the Portunidæ then known. In 1810 the genus was restricted by Latreille to those species which were later placed by Leach in his genera of *Portunus* and *Lupa*. Subsequent authors until 1897 have consistently followed Leach in considering the name *Portunus* to be applicable (with various further restrictions of minor importance) to the familiar forms with five teeth on each side, that are dealt with in this paper. Rathbun (1897) pointed out, however, that this usage was an infringement of the rule of specification of type. Latreille (1810) had mentioned a number of species as types of their respective genera, and had given *P. pelagicus* (L.) as that of *Portunus*. Subsequent restrictions have made this form, first *Lupa pelagica* of Leach, and, secondly, *Neptunus pelagicus* of de Haan. Provided, then, that Latreille intended by "type," "*the type* of the genus" rather than merely "*an example* of the genus," *Neptunus pelagicus* of de Haan, being synonymous with *Portunus pelagicus* of Latreille, becomes the type of *Portunus*. *Neptunus* de Haan therefore becomes *Portunus* Weber and Fabr., and the species included by the majority of authors under *Portunus* Weber and Fabr., are left without a generic name. Dr. Rathbun has since pointed out to me that actually Latreille appears to have designated the type of *Portunus* at a much earlier date. In "Additions" to Vol. 6, Hist. Nat. Crust. et Insectes, an. XI (1802–1803), p. 336, he says: "Portune réticulé; *portunus reticulatus*. Herbst a donné la figure de cette espèce, Pl. L; et nous l'avons fait copier, comme type du genre, Pl. XLIII, fig. 3, tome V. Nous l'avions oubliée en mentionnant les espèces:" etc. Herbst's *P. reticulatus* is a synonym of *Neptunus pelagicus* (L.). If these two cases are to be taken as constituting a specification of type, and if, in that

case, the rule is to be strictly enforced, a new name is required for the species of " *Portunus* " in the more usual sense. Rathbun has suggested *Liocarcinus* Stimps., 1869 (see below, Section XIV), as an available name.

Such is the history of the name *Portunus*. While it has to be admitted that Dr. Rathbun has made a strong case for her use of the name, there are certain considerations which have to be taken into account. In the first place it is still open to question whether Latreille used the word " type " in the modern sense, or whether he merely meant " example." So far as his 1810 list is concerned this seems very debatable, especially as in certain genera (e.g. *Maia*) he has there " specified " more than one type species. The same doubt applies to the earlier " specification." If Latreille had forgotten *P. reticulatus* in mentioning the other species in the main part of his work, it seems hardly likely that he would proceed to make it the type species in the modern sense. Two citations from a later work by Latreille give further support to this view. In " Cour d'entomologie " Ire ann. 1831, p. 349, he says : " Ce genre est celui de portune ou d'étrille (*portunus*), de Fabricius, mais qu'on a maintenant réduit. Nos côtes offrent communément : 1. Le P. étrille (*puber*, Fab.) . . . 2. Le P. ridé (*corrugatus* Leach) . . . P. de Rondelet de M. Risso . . . Le P. de tranquebar (*tranquebaricus*) a neuf dents à chaque bord latéral." It is obvious from this that Latreille regards *P. puber* as the typical species of the genus since he uses the same common name for both. Furthermore, on p. 350 he mentions *Lupa pelagica*, accepting without any comment Leach's alteration of the generic name of what Dr. Rathbun regards as his type species.

There are other more practical objections to the proposed alteration of the general usage in this case. Firstly, while *Liocarcinus* is a valid name under the Code, there are logical objections to its use since it was originally used for two species of the genus as opposed to the rest. Secondly, the genera " *Neptunus* " and " *Portunus* " are large ones, and the confusion resulting from the change is consequently considerable. Thirdly, " *Neptunus* " contains a species, *N. tuberculatus* Stimps., which if spoken of as *Portunus tuberculatus* is liable to be confused with the totally different species, *P. tuberculatus* Roux. Finally, it may be urged that in the whole of the existing literature with the exception of Dr. Rathbun's papers and to my knowledge, three others, the names *Portunus* and *Neptunus* are used in A. Milne-Edwards' sense, although thirty years have elapsed since Dr. Rathbun published her amendment.

In spite of all this, however, it must be admitted that Dr. Rathbun is legally right under the Code, since in 1910 the International Commission, rightly or wrongly, gave an Opinion validating Latreille's 1810 types. This being the case, I cannot agree with those eminent carcinologists who have, in opposition to the Rules, continued to use the name *Portunus*

without qualification, for the species discussed in this paper. Such individual action is likely to make confusion worse confounded. I consider on the contrary that this is an instance in which an Opinion by the Commission suspending the Rule of specification of type in this case, and legalizing the almost universal usage of the names, is the only practical and permanent way out of the difficulty. A case is being placed before the Commission to this end, and in the meantime the name "*Portunus*" will be used in inverted commas in this paper.

III. P. CORRUGATUS (Penn.).

Cancer corrugatus. Pennant, 1777; Herbst, 1783.
Portunus corrugatus. Leach, 1814, 1816; H. Milne-Edwards, 1834; Bell, 1853; A. Milne-Edwards, 1861, etc.
Portunus puber. Blainville.
Portunus strigilis. Stimpson, 1858.
Liocarcinus strigilis. Rathbun, 1902.
Portunus subcorrugatus. A. Milne-Edwards, 1861.
Portunus carcinoides. Kinahan, 1857.
Liocarcinus corrugatus. Rathbun, 1902.
Portunus Leachii. ? Risso, 1826.

The *carapace* (B. Fig. 2) is slightly convex and rather contracted posteriorly. Nineteen males had a mean value for $\frac{\text{breadth}}{\text{length}}$ of 1·29, and thirteen females a mean value of 1·27. (In this and subsequent statements as to the proportions of the carapace, by "breadth" is meant the distance between the tips of the posterior antero-lateral teeth, and by "length" the distance between the anterior side of the posterior rim of the carapace and the tip of the median frontal tooth or lobe. In *P. puber*, where there is no median tooth, the tips of the two inner frontal teeth formed the anterior limit.) The species varies within wide limits in regard to this character, all variations from females with value 1·24 to a male with the value 1·35 having been found. The *front* is divided into three crenulated lobes, and is moderately advanced. The *antero-lateral teeth* are strong, pointed, and sub-equal. The first two teeth show slight traces of the grouping seen in *P. arcuatus*. The *orbits* have a somewhat sinuate ventral margin (G), this term being understood to include in this and subsequent descriptions the whole ventral side of the orbits shown in the figures. The *epistome* (D) is considerably extended laterally in the majority of specimens, but is a rather variable character in this species. The *merus of the third maxillipeds* (F) is rather short, with its inner margin obliquely truncate. The slight notch seen in ventral view at the antero-lateral corner is due to an in-turning of the edge at this point to

meet the edge of the opposite face over the next joint, whose base is thus enclosed between the two faces of the merus. The *carpus of the chelipeds* (H) is somewhat rectangular, and in common with most of the surfaces of this form is considerably crenulated. A group of tubercles on the outer margin below the equally tuberculate antero-external corner form together a sort of blunt tooth. The chelæ are bluntly carinate, and are slightly unequal, the right being usually the larger. In the *last pair of thoracic limbs* (A) the dactylus is lanceolate, with a mean value for $\frac{\text{length}}{\text{breadth}}$ of about 2·35. The propodus is short and rounded. Both joints have a well-marked ribbing. The *abdomen of the male* (C) shows a very abrupt narrowing at the penultimate joint, and its proximal joints are very broad. The sutures between the 3rd, 4th, and 5th joints, are obscure. The tip of the 1*st abdominal appendage* in the male (E) is bent almost at right angles. The *colour* is usually a uniform light red-brown, sometimes rather darker. The *surface* of the carapace is covered with transverse rows of crenulations, each row being set with a fringe of hairs. The regions are rather indistinct.

P. corrugatus is moderately common on shelly gravel at Plymouth.

IV. P. PUBER (Linn.).

Cancer puber. Linnæus, 1758.
Portunus puber. Fabricius, 1798; Leach, 1816; H. Milne-Edwards, 1834; Bell, 1853, etc.
Cancer velutinus. Pennant, 1777.

The *carapace* is broad and flattened, and very little contracted posteriorly. The mean value for $\frac{\text{breadth}}{\text{length}}$ in sixteen individuals measured was 1·36. There was no significant difference in this character between the males and the females measured. The *frontal teeth* are usually from eight to ten in number, and are frequently asymmetrical as in the figure. On each side of the middle line is a large tooth, which in some specimens appears to be made up of a number of crenulations. Occasionally these two inner teeth are fused. Beyond this tooth on each side are two or three small spike-like teeth. External to these is a large crenulated tooth whose outer edge slopes down towards the orbit. In the 5th and subsequent juvenile stages the two inner teeth are represented by crenulated lobes with only a slight depression between them (Fig. 3, juv.), and in

FIG. 2.—*Portunus corrugatus.*—A, left propodus and dactylus of last pair of thoracic limbs. B, outline of carapace. C, male abdomen. D, epistome. E, tip of left first abdominal appendage of male. F, ventral view of merus of right third maxilliped. G, ventral view of sub-orbital margin. H, carpus of right cheliped.

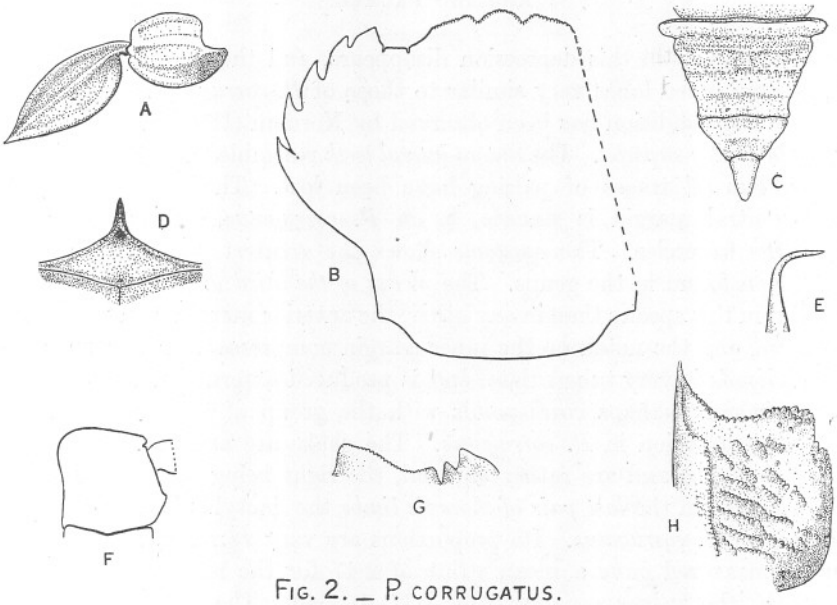

FIG. 2. — P. CORRUGATUS.

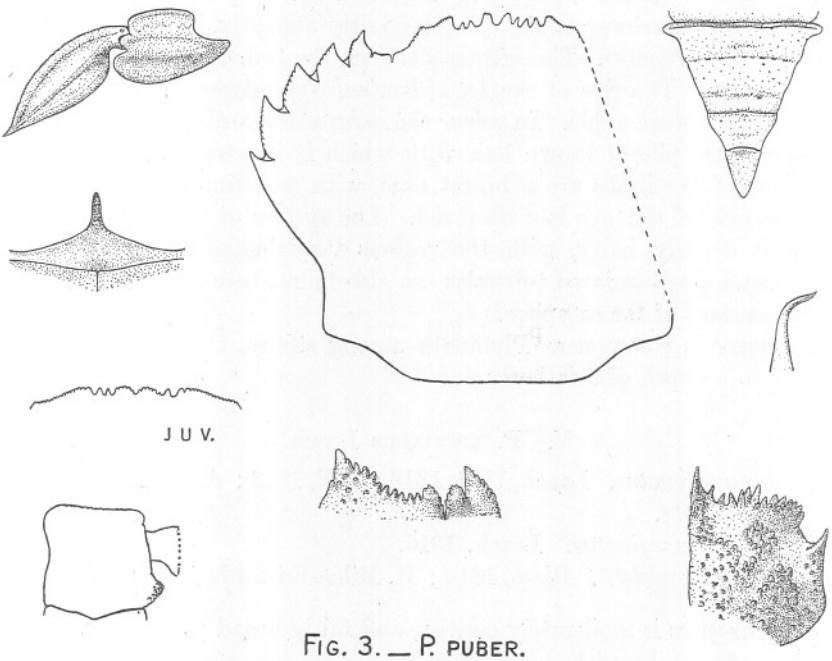

FIG. 3. — P. PUBER.

JUV., front of juvenile.

earlier stages still this depression disappears, and the front consists of three crenulated lobes very similar to those of *P. corrugatus*. A similar three-lobed condition has been observed by Norman (1891) in the young of *Bathynectes superba*. The *antero-lateral teeth* resemble those of *P. corrugatus*, but all traces of pairing have been lost. The *orbits* are large. The ventral margin is sinuate, as in *P. corrugatus*, but is bordered by large tubercles. The *epistome* shows the greatest degree of lateral extension found in the genus. The *merus of the third maxillipeds* is also shorter in this species than in any other, the anterior margin being slightly concave, and the notch on the inner margin compressed. The *carpus of the chelipeds* is very tuberculate, and is produced externally into a sharp tooth, which perhaps corresponds with the group of tubercles seen in the same position in *P. corrugatus*. The chelæ are armed with tuberculated carinæ and are rather unequal, the right being more frequently the larger. In the *last pair of thoracic limbs* the dactylus is very similar to that of *P. corrugatus*. Its proportions are very variable, but sixteen males measured gave a mean value of 2·47 for the ratio of length to breadth, the values ranging from 2·37 to 2·60. The propodus has a prominent distally-projecting lobe on its posterior side, rather resembling that of *P. holsatus*. Both joints are even more strongly ribbed than in *P. corrugatus*. The *abdomen of the male* is moderately broad proximally, and becomes narrower at the 6th joint fairly abruptly, but much less so than in *P. corrugatus*. The sutures between the 3rd, 4th, and 5th joints, are obscure. The tips of the 1*st abdominal appendages* of the male are bent at an obtuse angle. In *colour* the carapace is a dirty brown, owing to the dense pile of brown hair with which it is covered. The naked portions of the limbs are a bright blue, with sometimes specks of red. The cornea of the eye is a deep red. The *surface* of almost the whole body is densely hairy, with the regions very indistinct. Crenulated ridges and small isolated tubercles are also found here and there on the dorsal surface of the carapace.

P. puber is common at Plymouth among stones, from between tide marks to a depth of 5 fathoms.

V. P. ARCUATUS Leach.

Portunus arcuatus. Leach, 1814, 1816 ; Bell, 1853 ; A. Milne-Edwards, 1861, etc.

Portunus emarginatus. Leach, 1816.

Portunus Rondeletii. Risso, 1816 ; H. Milne-Edwards, 1834 ; A. Costa.

The *carapace* is moderately convex, and fairly broad posteriorly. The mean value for $\frac{\text{breadth}}{\text{length}}$ of thirty-two specimens of both sexes was 1·27.

In the specimens measured there was no significant difference between the sexes in this respect. The *front* is entire, though there are three faint undulations on its edge reminiscent of *P. corrugatus*, and these undulations are more marked in juveniles. It is fringed with a sparse row of hairs. The *antero-lateral teeth* show a marked grouping into pairs, the 1st and 2nd and the 3rd and 4th being associated. The 2nd and the 4th are considerably reduced, the 4th sometimes almost obsolete. The 5th is very strongly developed, suggesting comparison with *Bathynectes longipes*. The *orbits* are in dorsal view very like those of *P. corrugatus*. The ventral margin is, however, more rounded and concave. The *epistome* is intermediate in lateral extension between that of *P. corrugatus* and that of *P. puber*. The *merus of the third maxillipeds* is rather more obliquely truncated than in *P. corrugatus* and the region in front of the notch on the inner edge is more extended. The *carpus of the chelipeds* is longer, smoother, and more rectangular than in *P. corrugatus*, and is without the cluster of tubercles seen on the outer margin in that species. The chelæ are nearly smooth, somewhat stout and rather unequal, the right being usually the larger. In the *last thoracic limbs* the dactylus is very slender, the mean proportion of length to breadth being about 3·1. The propodus is longer than in *P. corrugatus*, and in general rather nearer to the probable primitive type. The ribbing of both joints is less distinct than in *P. corrugatus*. The *abdomen of the male* differs strikingly from that of *P. corrugatus*, having its sides almost straight. The sutures between the 3rd, 4th, and 5th joints, are obscure. The tips of the 1*st abdominal appendages* of the male are bent at an obtuse angle. The *colour* is dark brown, the limbs being generally rather lighter than the carapace. The *surface* of the carapace is covered with minute transverse rows of crenulations, resembling on a smaller scale those of *P. corrugatus*, but less continuous and without hairs. The regions are rather indistinct.

I have not taken Leach's "*P. emarginatus*." This form differs from *P. arcuatus* only in the concave character of the front, and is certainly no more than a variety of that species, though a remarkable one. It appears to be extremely rare since Leach only saw one specimen—that in the British Museum—and Bell found none among some hundreds of *P. arcuatus* examined.

P. arcuatus is moderately common at Plymouth on coarse shelly gravel.

VI. P. PUSILLUS Leach.

Portunus pusillus. Leach, 1814, 1816 ; Bell, 1853 ; A. Milne-Edwards, 1861, etc.

Portunus pusilus. H. Milne-Edwards, 1834 ; Lucas, 1840.

Portunus maculatus. Risso, 1826 ; Roux, 1828.

Liocarcinus pusillus. Rathbun, 1900.

The *carapace* is fairly convex, and is not greatly narrowed posteriorly. Its proportions vary enormously. Of twenty-six female specimens measured the mean value for $\frac{\text{breadth}}{\text{length}}$ was 1·20, the limiting values being 1·17 and 1·24. Thirteen males had a mean value of 1·215. This number included one exceptional specimen with the very low value of 1·06. Several such abnormally long specimens are in the British Museum collection, one of them actually being longer than broad. $\left(\frac{\text{Breadth}}{\text{Length}} = \cdot 95\right)$ In other characters such specimens appear to be quite normal. The *front* is greatly advanced as a broad shelf between the orbits, and is divided into three lobes, of which the median is the more advanced. The greatly produced front is by far the most striking character of the species. The *antero-lateral teeth* show the same kind of paired arrangement as was seen in *P. arcuatus*, but the size differences are less marked. The first four teeth are rather blunt, and the fifth spiniform and curved somewhat upwards. The *orbits* are modified dorsally by the forward extension of the front. The ventral margin is very similar to that of *P. arcuatus*, but, taken as a whole, rather shallower. The *epistome* is less extended laterally than in *P. arcuatus*. The *merus of the third maxillipeds* shows a further increase in the size of the anterior extension, and is still more oblique than in the last species. The *carpus of the chelipeds* is very similar in general shape to that of *P. corrugatus*, but agrees with that of *P. arcuatus* in being without a tooth of any sort on its external margin. The chelæ are in most specimens practically smooth, but slight carinæ may occasionally be present. The right is more usually slightly the larger. In the *last thoracic limbs* the dactylus is broader than in *P. arcuatus*, and less acutely lanceolate, the mean proportion of length to breadth being about 2·4. The median rib is almost obsolete, but traces of it are visible if the joint is held up to the light. The propodus resembles that of *P. arcuatus* in general form, but the ribbing is much less distinct than in that species. The *abdomen of the male* differs little from that of *P. arcuatus* in shape, but is rather narrower proximally, and the sutures between the 3rd, 4th, and 5th joints, are even more obscure. The tips of the *1st abdominal appendages* of the male are similar to those of *P. arcuatus*. The *colour* varies enormously, from a yellow variegated with red-brown, both on the carapace and the limbs, to a uniform dark brown on the carapace, with the limbs variegated in shades of lighter brown. The *surface* of the carapace is also variable, being sometimes quite smooth, and in other specimens coarsely and irregularly granulated. The regions vary greatly in degree of distinctness.

P. pusillus is fairly common at Plymouth on shelly gravel.

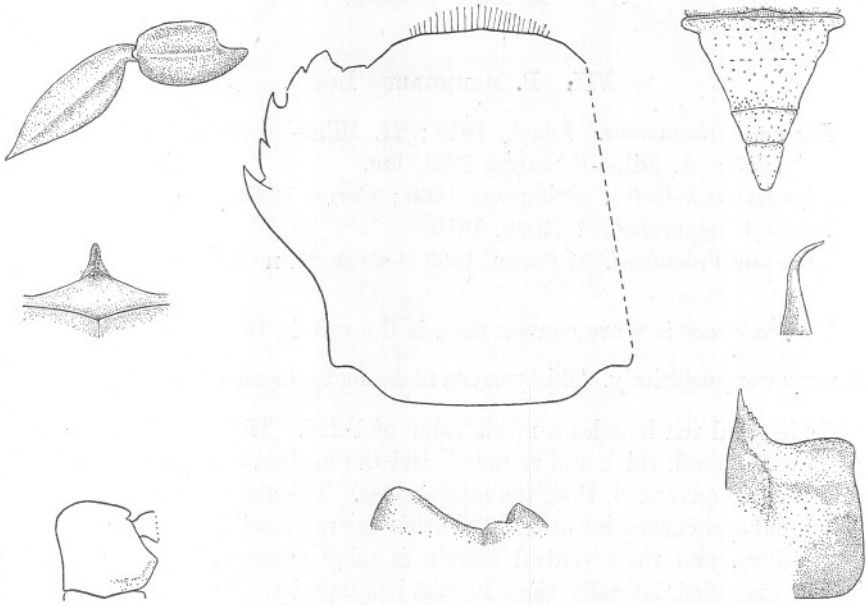

FIG. 4 _ P. ARCUATUS.

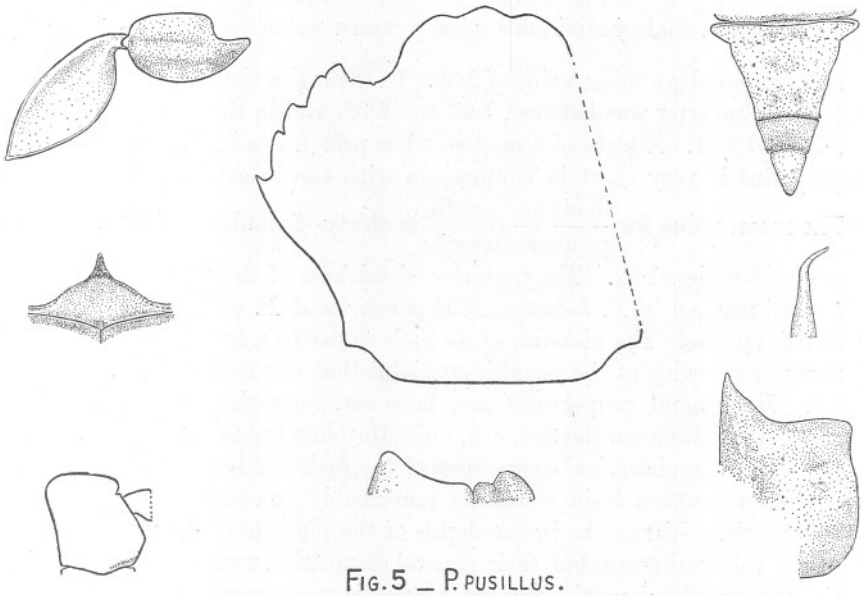

FIG. 5 _ P. PUSILLUS.

For description see Fig. 2.

VII. P. MARMOREUS Leach.

Portunus marmoreus. Leach, 1815; H. Milne-Edwards, 1834; Bell, 1853; A. Milne-Edwards, 1861, etc.
Liocarcinus holsatus. Stimpson, 1869; Carus, 1885.
Portunus depurator. ? Risso, 1816.
Portunus Valentieni. ? Cocco, 1833 (*teste* A. Milne-Edwards).

The *carapace* is more convex than is the rule in the last species, and is narrower posteriorly. Thirty-seven males had a mean value for $\frac{\text{breadth}}{\text{length}}$ of 1·254, and ten females a mean value of 1·224. The *front* is not projecting, the teeth thick and rounded, and the median one less advanced, or not more advanced, than the lateral ones. The *antero-lateral teeth* are sub-equal and curved inwards. The *orbits* are not modified dorsally as in *P. pusillus*, and their ventral margin is more concave. The *epistome* is less extended laterally than in the last species. The *merus of the third maxillipeds* is considerably longer, particularly in its anterior extension. The carpus of the chelipeds is more rounded, and the large tooth at the internal angle more produced than in *P. pusillus*. The carinæ of the chelæ are indistinct. The right chela is usually slightly the larger. In the *last thoracic limbs* the dactylus is rather broader than in *P. pusillus*. Thirty-seven male individuals gave a mean value for $\frac{\text{length}}{\text{breadth}}$ of 2·12, and ten females a mean value of 2·36. In the males the range of variation in this character was between 1·95 and 2·32, and in the females between 2·27 and 2·51. A trace of a median rib is present, as in *P. pusillus*. The propodus is very short in comparison with the length of the dactylus. The mean value for $\frac{\text{dactylus length}}{\text{propodus length}}$ in thirty-six males was 1·47, and in twelve females, 1·52. The posterior distal lobe of the propodus, that is so well marked in *P. holsatus*, *P. depurator* and *P. puber*, is very slight in this species. The *abdomen of the male* shows to a less extent the same abrupt narrowing at the penultimate joint that was noticed in *P. corrugatus*. Its general proportions are, however, near those of *P. pusillus*. The sutures between the 3rd, 4th, and 5th joints are fairly distinct. The tips of the 1*st abdominal appendages* of the male are bent at right angles. The *colour-pattern* is in essentials remarkably constant and regular in this species. Variations in the depth of the pigmentation affect the size of the coloured areas, but their general disposition varies very little. In the matter of colour the present species is more nearly approached by *P. depurator* than by *P. holsatus*. In the former species all variations

exist from the typical whole-coloured forms to specimens which exhibit a colour-pattern closely resembling in a simplified form that of *P. marmoreus*. The *surface* of the carapace is very smooth, and the regions indistinct.

I have taken three abnormal examples of this species. One of these, a male, differs from the typical form only in that it is completely whole-coloured, like *P. holsatus*. Another, a female, approaches *P. holsatus* to some extent in the ventral margins of the orbits, in the frontal teeth, and in the possession of two small teeth on the outer margin of the carpus of the chelipeds. In other respects it is normal. The third differs from the type only in being whole-coloured over most of the carapace, but marbled quite typically on the antero-lateral teeth and legs.

P. marmoreus is moderately common on fine sand at Plymouth, and is found with *P. holsatus*, sometimes in the same haul. Its distribution in Great Britain appears, however, to be more local and southerly than that of *P. holsatus*, although it has been recorded by T. Scott (1888) as occurring occasionally as far north as the Firth of Forth.

VIII. P. HOLSATUS Fabr.

Portunus holsatus. Fabricius, 1798; H. Milne-Edwards, 1834; Bell, 1853; A. Milne-Edwards, 1861, etc.
Cancer depurator. Pennant, 1777.
Portunus lividus. Leach, 1814, 1816; Thompson, 1843.
Liocarcinus holsatus. Stimpson, 1869.
Portunus dubius. Rathke, (*teste* Heller).
Portunus Valentieni. ? Cocco, 1833, (*teste* Carus).

The *carapace* is less convex than in the previous species, and is considerably narrowed posteriorly. Forty-four males gave a mean value for $\frac{\text{breadth}}{\text{length}}$ of 1·30, and twelve females a mean value of 1·28, these differences from *P. marmoreus* being found highly significant by the χ^2 method. The *frontal teeth* are angular, and the median tooth the most advanced. The *antero-lateral teeth* are sinuate or flattened externally, sharply pointed and somewhat thin. The *orbits* are small relative to the breadth of the carapace. In ventral view the sub-orbital margin appears as a symmetrical curve, or even, in some cases, is more concave internally. This point of difference from *P. marmoreus*, though very striking in actual specimens, is difficult to bring out completely in any figure. In comparing the two figures in regard to this character, the ventral fissure should be ignored and the curves treated as if continuous. It is a case in which the presentation of structural details diverts attention from the general form, which is, in this instance, of greater diagnostic value. The *epistome* is almost rhomboidal in shape, showing the least degree of lateral extension to be found

in the genus, though a closely comparable condition is seen in Polybius. The *merus of the third maxillipeds* differs very little from that of the last species, but the anterior margin is usually more flattened. The *carpus of the chelipeds* differs strikingly from that of *P. marmoreus*. It is considerably more rectangular in shape, and possesses on its outer margin two well-marked teeth. Of these, the posterior is acute, and forms the termination of a sharp carina bounding the postero-external margin of the joint. The anterior tooth is more rounded, and in young specimens is sometimes nearly obsolete. The antero-external corner of the joint is more produced than in *P. marmoreus*, and may almost be said to constitute a third rounded tooth. The chelæ are fairly sharply carinated and are slightly unequal, the right being usually the larger. In the *last pair of thoracic limbs* the dactylus is broader than in the last species, but not rounded at the end as has been stated by some authors. Forty-three males gave a mean value for $\frac{\text{length}}{\text{breadth}}$ of 1·95, and twelve females a mean value of 1·99, the differences from *P. marmoreus* being found highly significant when tested by the χ^2 method.

Traces of a median rib are present, as in *P. marmoreus*. The propodus differs noticeably in shape from that of the last species, and is longer in proportion to the dactylus, the mean value for $\frac{\text{dactylus length}}{\text{propodus length}}$ in forty-four males examined being 1·34, and in nine females 1·37, differences from *P. marmoreus* which again were shown to be highly significant by the χ^2 method. The posterior margin of the propodus is extended distally in adult specimens into a rounded lobe, as in *P. puber*.* The *abdomen of the male* agrees with that of *P. marmoreus* in becoming abruptly narrower at the penultimate joint, but is proximally considerably broader in the adult than in that species, and the sutures between the 3rd, 4th, and 5th joints, are more clearly marked. The tips of the *1st abdominal appendages* of the male are bent at a right angle, as in *P. marmoreus*, but the bent portion is rather longer. The *colour* is usually a brownish grey with a tinge of green and with a row of lighter-coloured spots following the cervical groove on each side and curving backwards to the postero-lateral margins. In *P. marmoreus* these spots are present, but are obscured by the rest of the colour-pattern. The *surface* of the carapace is typically almost smooth with the regions indistinct, but specimens are occasionally taken which possess to a greater or less degree the coarse irregular

* Since this was written the merus of this pair of legs has been found to be a further difference between *P. holsatus* and *P. marmoreus*. In *P. holsatus* the mean value in twenty-two male individuals for $\frac{\text{merus length penultimate limbs}}{\text{merus length last limbs}}$ was 1·97, with a range from 1·87 to 2·15. In *P. marmoreus* the value for twenty-two males was 1·52 with a range from 1·45 to 1·60.

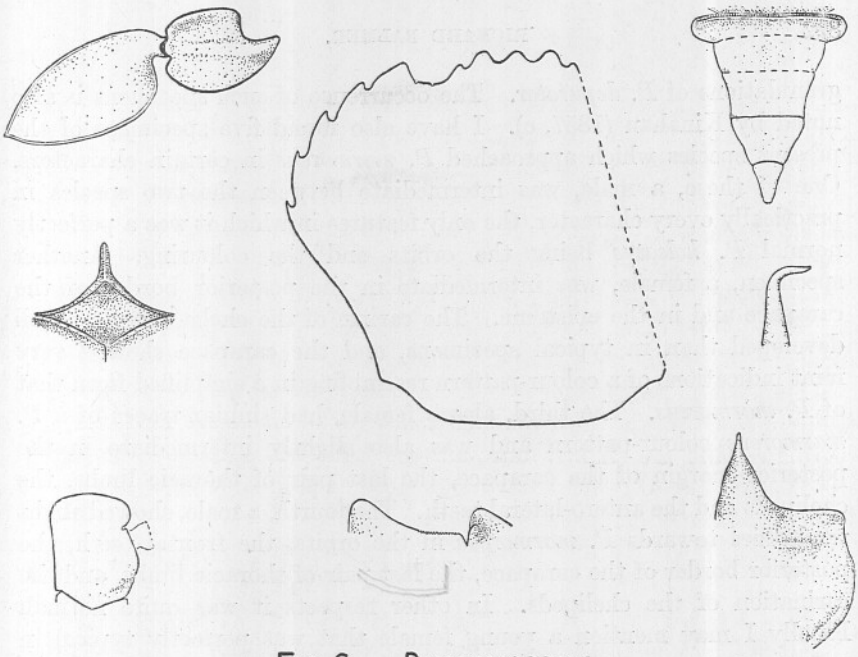

FIG. 6. — P. MARMOREUS.

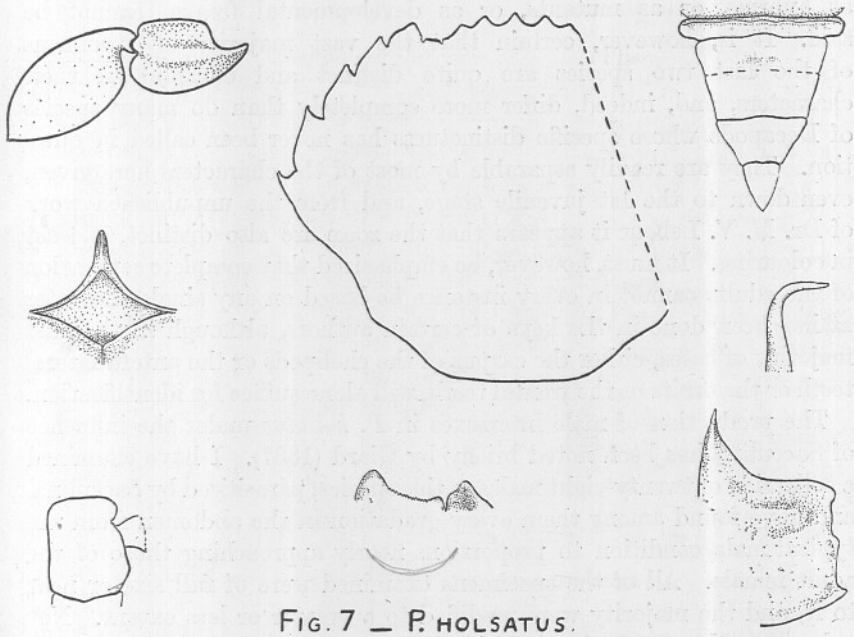

FIG. 7 — P. HOLSATUS.

For description see Fig. 2.

granulations of *P. depurator*. The occurrence of such specimens is also noted by Kinahan (1857, c). I have also found five specimens of the present species which approached *P. marmoreus* in certain characters. One of these, a male, was intermediate between the two species in practically every character, the only features in which it was a perfectly normal *P. holsatus* being the orbits and the colouring. Another specimen, a female, was intermediate in the posterior border of the carapace and in the epistome. The carinæ of the chelæ were less well developed than in typical specimens, and the carapace showed very faint indications of a colour-pattern resembling in a simplified form that of *P. marmoreus*. The third, also a female, had similar traces of a *P. marmoreus* colour-pattern and was also slightly intermediate in the posterior margin of the carapace, the last pair of thoracic limbs, the chelipeds and the antero-lateral teeth. The fourth, a male, showed slight tendencies towards *P. marmoreus* in the orbits, the frontal teeth, the posterior border of the carapace, the last pair of thoracic limbs, and the carination of the chelipeds. In other respects it was quite normal. Finally I may mention a young female that was perfectly typical in every respect except that it had a fairly well-developed colour-pattern of the *P. marmoreus* type.

Whether such atypical specimens as the above are to be considered as hybrids, or as mutants, or as developmental freaks, cannot be said. It is, however, certain that the vast majority of specimens of the last two species are quite distinct and constant in their characters, and, indeed, differ more completely than do many species of Decapods whose specific distinctness has never been called in question. They are readily separable by most of the characters here given, even down to the 1st juvenile stage, and from the unpublished work of Dr. M. V. Lebour it appears that the zoeæ are also distinct, at least in colouring. It must, however, be emphasized that complete separation of the adults cannot in every instance be based on any single character as has been done in the keys of certain authors, although in the vast majority of cases, either the carpus of the chelipeds or the antero-lateral teeth or the orbits or the frontal teeth, will alone suffice for identification.

The production of male intersexes in *P. holsatus* under the influence of Sacculina has been noted briefly by Giard (1887). I have examined a collection of twenty-eight males of this species, parasitised by Sacculina, and have found among them every gradation in the abdomen from the typical male condition to proportions nearly approaching those of the adult female. All of the specimens examined were of full size or near to it, and the majority were modified to a greater or less extent. Not only were the proportions of the abdomen affected, but the sutures between the 3rd, 4th, and 5th segments were distinct as in female

specimens. The abdominal appendages appeared to be normal. Thirteen parasitised females showed no signs of sexual abnormality. Six parasitised males of *P. marmoreus* were examined, but appeared to be unmodified. It might not be out of place to suggest in this connection that new light might be thrown on the physiology of the production of such intersexes in Brachyura, if the abnormal condition of the abdomen were treated as a problem in heterogonic growth.

P. holsatus is moderately common in small numbers at Plymouth, being occasionally taken on fine sand with *P. marmoreus*.

IX. P. DEPURATOR (Linn.).

Cancer depurator. Linnæus, 1758.
Cancer depurator (var.). Pennant, 1777.
Portunus depurator. Fabricius, 1798 ; Leach, 1814, 1816 ; Bell, 1853 ; A. Milne-Edwards, 1861, etc.
Portunus plicatus. Risso, 1816 ; Roux, 1828 ; H. Milne-Edwards, 1834 ; Lucas, 1849.
Portunus vernalis. ? Risso, (*teste* Carus).

The *carapace* is broad and flattened and little contracted posteriorly. The mean value for $\frac{\text{breadth}}{\text{length}}$ in one hundred individuals (fifty males and fifty females) was 1·33,* with a standard error of ·0023. There is no significant difference between the males and females in this character. The *frontal teeth* are sharp, the median one being the narrowest and most advanced. The outer teeth differ from those of *P. holsatus* in having their external edge convex. The *antero-lateral teeth* are sharp, somewhat flattened externally, and in general rather intermediate in form between those of *P. holsatus* and *P. marmoreus*. The *orbits* are large and shallow. In ventral view the sub-orbital margin is sinuate and advanced, almost completely covering the eyes when the latter are retracted. The *epistome* is rather broader in proportion than that of *P. holsatus*. The *merus of the third maxillipeds* is rather longer than in *P. holsatus*, and is somewhat oblique. The *carpus of the chelipeds* closely resembles that of *P. holsatus*. In this case, however, the anterior of the two teeth of the outer margin is the more pronounced. The chelæ are more sharply carinated than in *P. holsatus*, and are rather unequal, the right being usually the larger. In the *last pair of thoracic limbs* the dactylus is somewhat more rectangular

* Warren (1896) obtained a rather lower figure, through using slightly different criteria of "length." He found no significant change in this value with absolute size. From other carapace measurements he reached the interesting conclusion that the correlation between the two sides of the body is greater in *P. depurator* than in *Carcinides mœnas*, and that this greater symmetry is probably connected with the swimming habit of the former.

than in the last species. The mean value for $\frac{\text{length}}{\text{breadth}}$ of the dactylus in fifty males was 1·8682 with a probable error of ·01063, and in fifty females 1·9348 with a probable error of ·01225. Using the χ^2 method, it was shown that the difference obtained between the male and female frequency curves for this character was a significant one, the male dactylus being on the average rather broader than the female dactylus. There are indications that this is so in other species of "Portunus," but sufficient data have not been obtained to decide the matter finally. In all cases the figures of this and other characters have been drawn from male specimens. The posterior lobe of the propodus is greatly produced distally as a rectangular expansion. The median rib of the dactylus is faintly suggested in *P. holsatus*. The *abdomen of the male* differs sharply from that of *P. holsatus* and *P. corrugatus*, and to a lesser extent from the other species discussed above, in that its shape is regularly triangular without any abrupt narrowing at the 6th joint. The sutures between the 3rd, 4th, and 5th joints, are rather obscure. The *1st abdominal appendages* of the male are bent nearly at right-angles. The *colour* is usually a uniform red-brown, or occasionally dark brown, especially in juveniles. In some cases, however, the frontal region is sharply marked off in a lighter colour, and all stages exist from this condition to a pattern closely resembling in a less complex form that of *P. marmoreus*. A very constant character is the violet coloration of the tips of the swimming dactylus. The surface of the carapace is irregularly covered with coarse rows of crenulations, and is moderately hairy. The regions are rather indistinct.

P. depurator is abundant, and generally distributed at Plymouth at a depth of 3–30 fathoms.

X. P. TUBERCULATUS Roux.

Portunus tuberculatus. Roux, 1828; A. Milne-Edwards, 1861, etc.
Portunus macropipus. Prestandrea, 1833.
Portunus pustulatus. Norman, 1861.
Ellipticodactylus rugosus. Doflein, 1904.

The *carapace* is flattened and very broad, its breadth being, however, accentuated by the length of the last antero-lateral tooth. $\frac{\text{Breadth}}{\text{Length}}$ is normally about 1·6, but some specimens in the British Museum are considerably less broad. The carapace is fairly broad posteriorly. The *frontal teeth* differ hardly at all from those of *P. depurator*. The *antero-lateral teeth* are sharp and pronounced, the last one in particular being

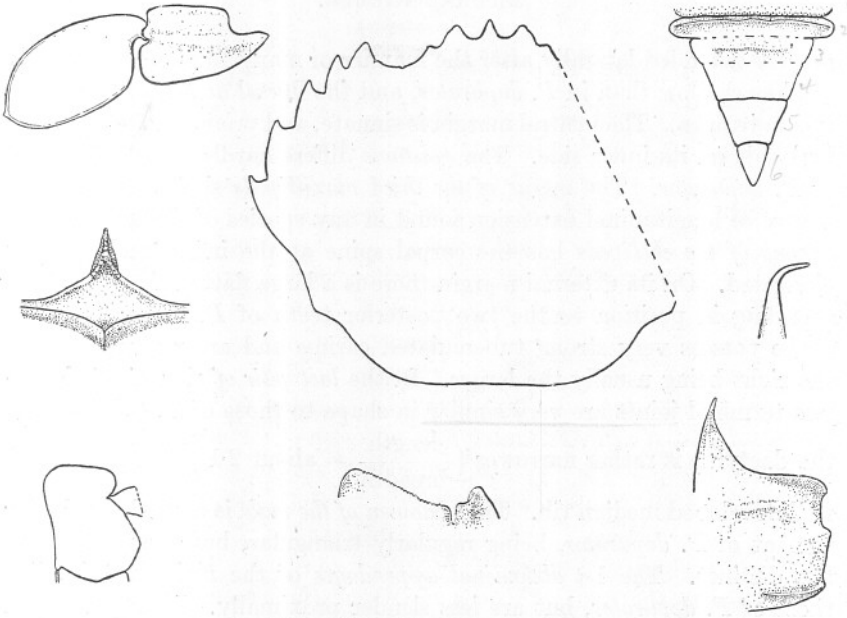

FIG. 8. — P. DEPURATOR.

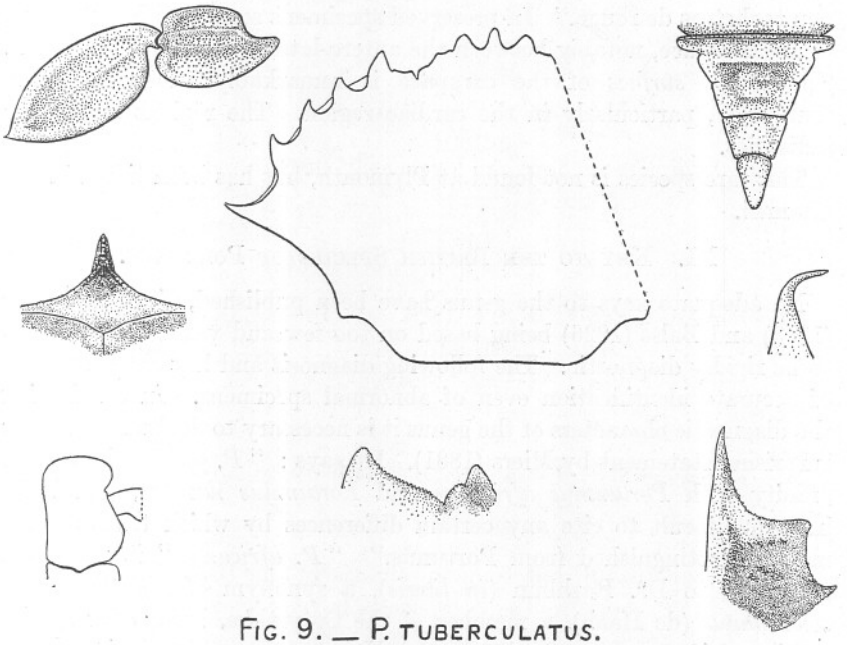

FIG. 9. — P. TUBERCULATUS.

For description see Fig. 2.

greatly extended laterally after the manner of many Lupinæ. The *orbits* are less shallow than in *P. depurator*, and the dorsal and ventral fissures are more open. The ventral margin is sinuate, and produced considerably forwards on its inner side. The *epistome* differs hardly at all from that of *P. depurator*. The *merus of the third maxillipeds* shows the greatest degree of longitudinal extension found in any species of the genus. The *carpus of the chelipeds* has the carpal spine at the inner angle greatly elongated. On its external margin there is a large flattened tooth corresponding in position to the two posterior teeth of *P. depurator*. The chelæ possess very strong tuberculated carinæ and are rather unequal, the right being usually the larger. In the *last pair of thoracic limbs* the two terminal joints are very similar in shape to those of *P. holsatus*, but the dactylus is rather narrower $\left(\frac{\text{length}}{\text{breadth}} = \text{about } 2{\cdot}1\right)$ and possesses a well-developed median rib. The *abdomen of the male* is essentially similar to that of *P. depurator*, being regularly triangular, but the sutures are less distinct. The 1*st abdominal appendages* of the male are also like those of *P. depurator*, but are less slender proximally. I have not seen living specimens, nor ones in which the *colour* has been perfectly retained after death. A. Milne-Edwards (1861a) states, however, that the colour is "d'un roux jaunâtre, avec les pinces un peu plus claires et un peu tachetées de rouge." In preserved specimens some polished portions of the carapace, notably between the antero-lateral teeth, are iridescent. The whole *surface* of the carapace is remarkably tuberculate and sculptured, particularly in the cardiac region. The regions are rather indistinct.

This rare species is not found at Plymouth, but has been taken in the Channel.

XI. Key to the British Species of Portunus.

No adequate keys to the genus have been published, those of Heller (1863) and Balss (1926) being based on too few and variable characters to be rigidly diagnostic. The following diagnosis and key should permit of accurate identification even of abnormal specimens. In considering the diagnostic characters of the genus it is necessary to deal with a rather surprising statement by Miers (1881). He says: "*P. pusillus* has much affinity with *Portumnus africanus* and *Portumnus nasutus*, and it is, indeed, difficult to cite any certain differences by which these species may be distinguished from Portunus." "*P. africanus*" is probably, according to Dr. Rathbun (*in literis*), a synonym of *Nautilocorystes octodentatus* (de Haan), a member of the Corystidæ, but so far as the species of Portumnus, Ovalipes, and Xaiva are concerned, I consider they are very sharply distinct from "Portunus." The orbits, the eyes,

the male abdomen, and the merus of the third maxillipeds may be mentioned as specially important characters in this connection. There is, in fact, such a degree of fundamental agreement in these characters in the three genera mentioned, as distinct from Portunus and its allies, that I cannot agree with the separation of Ovalipes (type *O. ocellatus* (Herbst)) and Portumnus in different sub-families in Alcock's classification (1899b). I agree also with Balss (1921) and others in considering the characters separating Portumnus and Xaiva to be too small to admit of a generic separation. It will be noticed that Bathynectes has only been separated from Portunus in the following diagnosis by the character of the front. It is, indeed, difficult to find any character of importance in which this genus can be said to be sharply distinct from Portunus and the wisdom of placing it in a separate genus seems, therefore, very questionable.

DEFINITION OF PORTUNUS.

Portunidæ in which : (1) The carapace is typically of moderate breadth with five antero-lateral teeth on each side. (2) The front is typically with three teeth or lobes or with eight to ten teeth, or entire ; never with four lobes. (3) The median suture of the sternum occupies only the last two thoracic segments. (4) The palatal crests are present and well defined. (5) The inner infra-orbital angle is never fused with the inner supra-orbital angle. (6) The eye-stalks are short and narrower than the eyes. (7) The basal joint of the external antenna is usually narrow and fused to the front. (8) The last pair of thoracic limbs are modified for swimming ; other pairs normal.

KEY TO THE SPECIES.

1. Front with 8–10 teeth ; (carapace broad and densely hairy) — *P. puber.*
   Front with 3 teeth or lobes, or entire 2
2. Front entire, ciliated ; (swimming dactylus very narrow with distinct median rib, antero-lateral teeth very unequal) . . . . — *P. arcuatus.*
   Front with 3 teeth or lobes 3
3. Front with 3 lobes, the median being the most advanced ; (swimming dactylus acutely lanceolate) 4
   Front with 3 teeth 5
4. Front much advanced ; swimming dactylus without distinct median rib ; male abdomen not abruptly narrowed at the 6th joint ; carapace almost hairless and usually smooth . . . . . — *P. pusillus.*
   Front not much advanced, crenulated, swimming dactylus with strong median rib ; male abdomen very abruptly narrowed at the 6th joint, carapace hairy and transversely crenulated . . . — *P. corrugatus.*
5. Posterior antero-lateral tooth greatly extended laterally ; (carapace flattened, at least half as broad again as long, and very coarsely tuberculate ; carpus of chelipeds with one large tooth on the postero-external margin) . . . . . — *P. tuberculatus.*
   Posterior antero-lateral tooth not greatly extended 6

6. Carapace broad, flattened, and coarsely tuberculate; swimming propodus with large rectangular, distally-projecting lobe; male abdomen regularly triangular; (carpus of chelipeds with 2 teeth on the postero-external margin; frontal teeth acute) . . . *P. depurator.*
These characters not combined 7

7. Frontal teeth acute, the median the most advanced; antero-lateral teeth externally sinuate or flattened; carpus of the chelipeds with 2 teeth on the postero-external margin; orbits small and with their ventral margin forming a symmetrical curve; chelæ sharply carinate; merus of penultimate pair of thoracic limbs twice as long as that of the last pair; colour brownish grey with a tinge of green . . . . . *P. holsatus.*
Frontal teeth rounded, the median typically the least advanced; antero-lateral teeth externally convex; carpus of chelipeds untoothed on its postero-external margin; orbits large, with their ventral margin most concave externally; carinæ of chelæ obsolete; merus of penultimate pair of thoracic limbs only half as long again as that of the last pair; colour marbled in various shades of brown . . . . . *P. marmoreus.*

XII. Doubtful, Non-British and Fossil Species of *Portunus*.

P. parvulus Parisi.

This species has been described by Parisi (1915) from the Bay of Naples, but has not been figured. His description is as follows (translation) :—

" This species has close affinities with *P. pusillus* Leach, from which it is distinguished by the following characters : (1) The carapace is proportionately broader and the regions more distinct. (2) Of the five teeth of the antero-lateral margin, the 1st or extra-orbital is not lobiform, but triangular and similar to the rest ; the 2nd and 4th teeth are small and the 5th spiniform ; (in some examples the 3rd tooth has the point acute as in the 5th). (3) The chelipeds have the carpus rugose and are furnished at the antero-internal angle with a robust acuminated spine, and at the antero-external angle with a small spiniform tubercle. The propodus has two carinæ on its superior margin, and another one, less marked, on its external face. (4) The first three walking-legs increase gradually in length from the 1st to the 3rd. (5) Between the basal joint of the external antenna and the sub-orbital margin there is a well-marked hiatus, represented in *P. pusillus* only by a simple fissure. The colour is very varied : generally greenish brown and reddish brown predominate, with lighter spots and bands."

Dr. Parisi has very kindly sent me two specimens of this form for examination. After careful comparison of these specimens with a long series of *P. pusillus*, I am somewhat doubtful as to the specific distinctness of the two forms. The great degree of variation in the proportions of the carapace of *P. pusillus*, which I have mentioned above, makes this

character of doubtful value for the separation of *P. parvulus*. The degree of distinctness of the regions of the carapace is also a variable character, though I have seen no specimens of *P. pusillus* from Plymouth that approach the condition seen in Parisi's form. I have specimens of *P. pusillus* which approach *P. parvulus* very closely in the antero-lateral teeth and this character is also, therefore, of doubtful value. One specimen of *P. pusillus* that I have taken agrees with *P. parvulus* in the carpus of the chelipeds, and to a less extent in all the other characters that he mentions. Dr. Parisi considers it, however, to be nearer to *P. pusillus*. Most of the Plymouth specimens of *P. pusillus* that I have examined hardly differ from *P. parvulus* in the walking-legs. Finally, while in most examples of *P. pusillus* the fissure between the sub-orbital margin and the base of the external antennæ is narrow, I have met with a number of specimens showing the well-marked hiatus found in *P. parvulus*. Since Dr. Parisi has no doubt based his species on a large number of living specimens, I hesitate to question its distinctness. It seems to me, however, from the two specimens I have seen, that the characters in which it differs from *P. pusillus* are of varietal rather than specific value, and that a fuller redescription of the form is required.*

P. subcorrugatus A. M-E. and *P. strigilis* Stimps.

P. subcorrugatus is described by A. Milne-Edwards (1861, a) from the Red Sea, and is, according to him, probably conspecific with de Haan's *P. corrugatus* from Japan and Savigny's "*P. Rondeletii*" from Egypt. The specimen from Naples in the British Museum agrees with Milne-Edwards' figure in that the front is only faintly trilobed, though in the text Milne-Edwards contradicts himself on this point. The carapace is also less strongly corrugated than in *P. corrugatus*. *P. strigilis* was described by Stimpson (1858) from a single specimen ·28″ long taken off the south of Japan. In his description it differs from *P. corrugatus* only in that the front is "indistincte trilobata," and in that it possesses a small spine on the propodus of the chelipeds above the base of the dactylus, whereas in *P. corrugatus* the spine is long and placed rather further back. As, however, he does not mention *P. corrugatus* in his description, it is possible that this last character is not intended to be distinctive. Rathbun (1902) has since described under the name of *Liocarcinus strigilis* (Stimps.) a form from Japan. She states, however, that in contradistinction to *P. corrugatus*, *L. strigilis* has "the median tooth of the front more triangular, its sides at right-angles to each other,

* Since this was written I have received a letter from Dr. Parisi, in which he says: "I find that your observations are very accurate, and it is possible that my species is only a 'variety' or 'form' of *P. pusillus*."

tip acute." This account of the front differs, therefore, inexplicably from Stimpson's original description. She also states that *L. strigilis* is longer and narrower than *P. corrugatus*, the value for $\frac{\text{length}}{\text{breadth}}$ of the carapace in the former species being ·85–·87. In view of the contradiction that exists between the two accounts of this species it is impossible to say anything definite as to its validity. It is, however, of interest to note that Rathbun gives *P. corrugatus* of de Haan as a synonym of *L. strigilis*. And since Milne-Edwards regarded *P. corrugatus* of de Haan as synonymous with his *P. subcorrugatus*, it seems probable, as Miers considers (1879), that *P. subcorrugatus* and *L. strigilis* are identical. Whether, further, they are only to be regarded as local varieties of *P. corrugatus* can only be decided by future investigations.*

P. barbarus Lucas.

This name was applied by Lucas (1849) to a form which he says is widely distributed and very abundant on the coasts of Oran and Algeria. It is described as being intermediate between *P. marmoreus* and *P. depurator*, differing from the former " par la carapace qui est plus bombée, dont la partie postérieure est moins rétrécie, et surtout par la granulation assez forte dont elle est entièrement parsemée, ainsi que par les poils courts et peu serrés que l'on aperçoit parmi cette granulation," and from the latter " par le front, qui n'est pas relevé, et par la carapace qui n'est pas ridée." The colour is said to be bottle green. The figure given, though very beautiful, is admittedly inaccurate in showing four frontal teeth instead of three, a fact which leads one to doubt its reliability in other respects. A. Milne-Edwards regards this as a variety of *P. marmoreus*. It has not been since described.

Ellipticodactylus rugosus Doflein.

This form was described by Doflein (1904) on the basis of two specimens from the Congo region. Doflein suggests affinities with *Lupocyclus* and *Ovalipes*, and does not mention *P. tuberculatus*, with which, however, his species is undoubtedly conspecific, as Balss (1921) has pointed out. Going by Doflein's figures his specimens were rather less broad, and with the last antero-lateral tooth less produced than in typical specimens of *P. tuberculatus ;* but all gradations exist in this character in the examples

* Dr. Rathbun has since written me: "I have re-examined the *strigilis* and *corrugatus* specimens together with more recent accessions and think you are right to combine the species and also *subcorrugatus*, on account of variation. There is, however, something odd about the Japanese specimens—more elongate and more deeply areolate."

of that species at the British Museum, and it is therefore doubtful whether Doflein's specimens are even varietally distinct.

P. carcinoides Kinahan.

Kinahan (1857, b) describes this species as follows : " Carapace smooth, without raised ridges, regions marked out by rounded prominences only, sparsely hirsute. Front *three-lobed*, middle lobe largest, *edges of lobes entire*. Antero-lateral margin of carapace five-toothed. First pair of legs equal, surface nearly smooth, hirsute ; two flattened triangular teeth at anterior superior angles of wrist ; hand with two well-marked carinæ on the upper sides, *the inner terminating in a very minute, obtuse tubercle*. Upper edges of second, third, and fourth pair of legs very sparsely hirsute ; fourth joint broadly keeled above ; fifth and sixth acutely keeled ; sixth joint slender, styliform ; terminal joint of posterior pair of legs narrowly lanceolate, with a raised central line, hairy on the edges." The species is based on three young specimens. Kinahan states that it is " easily mistaken for young of *Carcinus mœnas*," and A. Milne-Edwards (who seems, however, only to have seen the figure (1857, a) and not the description) considered it to be this species. From Kinahan's figure it appears more probable, however, that it is the young of *P. corrugatus*, and this apparently was the view taken by Miers (1886) since he cites *P. carcinoides* as a synonym of *P. corrugatus*. It has not been recorded since as a distinct species.

P. guadulpensis H. de Sauss.

This species, described by de Saussure (1858) from Guadeloupe, is defined by A. Milne-Edwards as follows : " Carapace bombée et longue, régions à peine indiquées. Bords latéro-antérieurs découpés chacun en cinq épines aiguës. Front à cinq dents, dont les deux externes rudimentaires, les trois autres également avancées, la mediane aiguë, les mitoyennes plus arrondies. Bras court et lisse. Avant bras armé d'une seule épine à son angle antéro-interne. Mains fortement carénées portant une petite épine au-dessus de la base du pouce. Pattes suivantes grêles." Milne-Edwards includes the internal angles of the orbits among the frontal teeth, so that this species is not to be taken to differ from most members of the genus in this respect. From the above description it does not appear to approach closely any known member of the genus, and may be a distinct species. It has not, to my knowledge, been since recorded.

P. Brouweri Van Straelen.

This name has been given by Van Straelen (1924) to a fossil impression of the carapace of a crab found in the Lower Miocene of Celebes. The

carapace is half as broad again as long and somewhat hexagonal, with six antero-lateral teeth, including the extra-orbital, on each side, and four acute frontal teeth. From the figure given, this crab is, in the present author's opinion, much more closely allied to Charybdis de Haan (=Goniosoma A.M.-E.) than to "Portunus."

XIII. Distribution.

No attempt will be made in this section to include every locality from which the species have been recorded, but merely to indicate the present state of knowledge regarding their general distribution. In certain cases (e.g. Heller) the authority given is not the original recorder of the species at the locality, but a later compiler of a list of localities such as this.

P. corrugatus.—British Isles, France, Belgium, Mediterranean, Adriatic, Canary Is. (Heller, 1863); Scotland to Cape Verde, Azores, and Canaries (Bouvier, 1922); Oran (Lucas, 1849); Red Sea (A. Milne-Edwards, 1861); Senegambia (Miers, 1881); Senegambia to Sierra Leone (Balss, 1922); Japan (Miers, 1879); Victoria, Australia (Miers, 1886); New Zealand (Borradaile, 1916).

P. puber.—British Isles, N. France, Belgium, Mediterranean (Heller, 1863); Holland (Balss, 1926); North Sea and Mediterranean (Bouvier, 1922); Adriatic (Parisi, 1915).

P. arcuatus.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Adriatic (Heller, 1863); Holland (Balss, 1926); West Indies (Neumann, 1878) (?); Black Sea (Blohm, 1915); Algeria, Oran (Lucas, 1849).

P. pusillus.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Adriatic (Heller, 1863); Senegambia (Miers, 1881); Senegambia to Sierra Leone (Balss, 1922).

P. marmoreus.—British Isles, France, Belgium, Mediterranean (Heller, 1863); Portugal (Blohm, 1915); Azores (A. Milne-Edwards and Bouvier, 1899).

P. holsatus.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Canary Is., Black Sea (Heller, 1863); Portugal (Blohm, 1915); Holland, Denmark (Balss, 1926); Iceland, Faröes (Hansen, 1908).

P. depurator.—British Isles, France, Belgium, Scandinavia, Spain, Mediterranean, Adriatic (Heller, 1863); Scandinavia to Mediterranean (Bouvier, 1922); Algeria, Oran (Lucas, 1849).

P. tuberculatus.—Mediterranean (Heller, 1863); rare from Shetlands to Azores and Mediterranean (Bouvier, 1922); Adriatic (Parisi, 1915); mouth of Congo (Doflein, 1904).

XIV. Relationships.

Apart from the somewhat crude and inaccurate divisions of Leach, the only attempt at a sub-generic classification of "Portunus" is due to Stimpson (1869). This author went, indeed, beyond a mere sub-generic division. He proposed to divide the genus generically into *Portunus*, including "*P. puber*, *corrugatus* etc.", and *Liocarcinus* "for *P. holsatus* and its allies." Except for the fact that he regards *P. marmoreus* as identical with *P. holsatus*, he gives no indication regarding which genus the other species belong to. In addition to this, the characters upon which he bases his generic division are all of them ones which vary either within the species or continuously throughout the genus. For instance, he states that the basal joint of the second antenna is slightly movable in *P. holsatus*. The examination of living specimens (which were not available to Stimpson) shows that this character varies within the species, probably in relation to the length of time since the last moult. It is in any case a negligible character, easily affected by developmental conditions. He also mentions the median rib of the swimming dactylus in *P. puber* and *P. corrugatus* as a generic character. It has been shown above that this character varies continuously throughout the genus, and the same is true of the other characters that he cites. Some species, such as *P. depurator* and *P. tuberculatus*, could not be placed in either of his genera since they exhibit characters of both.

In discarding Stimpson's genera, it may be said further, that until new evidence is available there appears to be no justification for a generic or sub-generic division of any kind. The most widely different species are linked together by intermediate forms, a fact which has been sufficiently brought out in the description of the species. The *order* of relationship suggested in Fig. 1 (p. 878) is fairly strongly supported by the characters discussed. More room for debate exists regarding the precise *direction* in which the series is to be read, and there is little indication within the genus upon this point. A consideration of allied genera suggests, however, the use of the scheme shown in Fig. 1 as a working hypothesis. The adaptation to a swimming habit which exists in the majority of the Portunidæ is undoubtedly a secondary one, and in the absence of contrary evidence those forms have to be regarded as the most primitive which approach most nearly the non-pelagic Cancroid type. We have, therefore, to seek links between the more typical Portunidæ and the other Cancroid families. One such link is provided by Carcinides Rathb. (Carcinus of Leach, of which the common shore-crab, *C. mœnas*, is the only living representative), or its ancestors. This form is spoken of by Alcock (1899, b) as linking the Portunidæ with the Cancridæ, and it is actually included by Ortmann (1899) in the latter group. Its

almost world-wide distribution lends further colour to the view that it is to be considered as a primitive form. Among the species of "Portunus," *P. corrugatus* and *P. arcuatus* approach more nearly to this primitive form than do any other members of the genus. Another stage in the progress towards a pelagic habit is, perhaps, represented by Nectocarcinus. This form, though specialised in many respects, is nevertheless intermediate in a number of features, between Carcinides and "Portunus." In certain characters, particularly in the species *N. integrifrons*, it has distinct affinities with *P. corrugatus* and *P. arcuatus*, and the fact that it has only four antero-lateral teeth is, no doubt, secondary since the large flat first tooth probably corresponds to the first two teeth of other forms, and since a tendency towards the suppression of the second tooth has already been noted in *P. arcuatus*. (Alcock (1899, b) considers Nectocarcinus to form a link with the Xanthidæ. In this case the Portunidæ are diphyletic, and should be split up.) The fossil, Portunites (A. Milne-Edwards, 1861, b), found in the London clay, so far as it is known, appears to be intermediate in some respects between Carcinides and *P. arcuatus*, and certainly has much less affinity with forms at the other end of the series. The genus Banthochascon may, perhaps, represent another link in the chain. While its nearest affinities are probably with Bathynectes, as Alcock (1899, a) has suggested, it is reminiscent in some features, of Nectocarcinus and Carcinides. Finally, Bathynectes may be mentioned as a form which, though considerably specialised in certain characters, notably in the lateral extension of the carapace and legs and in the four frontal teeth of the adult, is in other characters closely similar, in some features to *P. corrugatus*, and in others to *P. arcuatus*. It will be seen, therefore, that it is possible tentatively to trace a progression of forms from Carcinides to "Portunus," and that this chain links up most closely with the species, *P. arcuatus* and *P. corrugatus*. The most significant feature of this evolutionary sequence is the gradual increase in the degree of adaption for swimming, found in the last pair of thoracic limbs. The modification of this pair of appendages is not confined to the last two joints, but affects the proximal joints also, notably the merus. In the Cancridæ and Xanthidæ this joint hardly differs from that of the penultimate pair of thoracic limbs. In Carcinus it is somewhat specialized, and this process can be traced through the series mentioned above, to "Portunus." In this genus the species *P. arcuatus* and *P. corrugatus* show the least degree of modification of the merus, while the greatest specialization is seen in *P. holsatus* and *P. depurator*, both strong swimmers. Polybius has carried the process even further than in these two species, the merus being practically as broad as it is long. I have no suggestions to make as to the origin of the other sub-families of the Portunidæ, except to point out that the fossil

Psammocarcinus (Miocene), forms a possible link between Carcinides on the one hand and Portumnus and its allies on the other.

It will be seen, therefore, from the above discussion of allied genera, that the evidence points, on the whole, to *P. corrugatus* and *P. arcuatus* as being the nearest species to the primitive ancestor of the genus. This view is also supported to some extent by the early juvenile stages, most of which have been investigated by Dr. M. V. Lebour. All of the forms studied, including even *P. depurator* and *P. holsatus*, show to a greater or less degree the partial suppression of the second and fourth antero-lateral teeth which has been noted in the adult of *P. arcuatus*. The same fact has been observed by Milne-Edwards and Bouvier (1899) in the young of Bathynectes. The swimming dactylus in the young stages of all species is of the narrowly lanceolate, acutely pointed type. Again, *P. corrugatus* has a world-wide distribution, and *P. arcuatus* is said by Neumann to have been found in the West Indies, whereas the other species with the exception of *P. pusillus* and *P. tuberculatus*, described from Senegambia and the Congo region respectively, are confined to Europe, or the Mediterranean coast of Africa.

Assuming that the ancestral "Portunus" lay somewhere between *P. corrugatus* and *P. arcuatus* in its characters, no further comment need be made on the evolutionary tendencies within this genus, which have been sufficiently brought out in the descriptive text. Some consideration must, however, be given to the position of *Polybius henslowi*. This form has been widely separated from "Portunus" by some authors following H. Milne-Edwards (1834), and considered to be nearer to Portumnus, and its allies, Ovalipes Rathb. and Xaiva MacLeay. This grouping appears to be based almost exclusively on a supposed similarity in the external antennæ. The literature on this point is confused and contradictory, and no attempt will be made to follow its intricacies. It may, however, be mentioned that H. and A. Milne-Edwards regard the basal joint in Polybius as slender and movable, and that Ortmann (1899) mentions the second joint as being cylindrical—in both cases in contradistinction to "Portunus." After examining in detail a large number of specimens I can find no basis for a division on this character. The basal joint in Polybius is almost indistinguishable from that of *P. holsatus*, and is slightly movable or completely fused, in different specimens, as in that species. The second joint does not differ from that of "Portunus." Borradaile (1900) groups Polybius and Carcinides in the same sub-family entirely on the grounds that the basal joint of the external antenna is slender as opposed to that of "Portunus" and its allies, whereas actually in Carcinides the basal joint is broader than in any species of "Portunus" except *P. puber*. There appears to be no reason, therefore, for grouping Polybius with Portumnus and its allies

on these grounds, and, in fact, the genera differ most markedly, notably in the eyes, the orbits, the male abdomen, and the merus of the third maxillipeds. On the other hand, Polybius shows very close affinities with *P. holsatus* in a number of characters, particularly in the ventral margin of the orbits, the epistome, the carpus of the chelipeds, the antero-lateral teeth, and the last pair of thoracic limbs. The merus of the third maxillipeds is also of the elongated type, and the first abdominal appendages of the male and the male abdomen are almost identical with those of *P. holsatus*. For these reasons Polybius is regarded provisionally, in Fig. 1, as fairly closely allied to *P. holsatus*, but as very greatly specialised in adaptation to a semi-pelagic existence.

XV. SUMMARY.

1. The characters of the species of "*Portunus*" are redescribed in detail and comparatively.

2. On the basis of the characters studied an attempt is made to determine the relationships of the constituent species, both within the genus and with allied genera, *P. corrugatus* and *P. arcuatus*, being regarded as the more primitive forms.

3. *P. marmoreus* and *P. holsatus* are separated by a large number of characters.

4. The status of various foreign, fossil and doubtful species is discussed.

5. An account is given of the present state of knowledge regarding the distribution of the species.

6. The synonymy of the generic name is considered at length.

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On the Mode of Feeding of the Hermit-crab, *Eupagurus Bernhardus*, and some other Decapoda.

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CONTENTS.

INTRODUCTION.

Whilst working on the oyster beds in the Fal Estuary, hermit-crabs, *Eupagurus Bernhardus*, were being frequently taken in the dredge-hauls and systematically killed, and the question was raised whether this hermit-crab might be in any way responsible for the shortage of oysters. I replied that I did not know, and that it seemed unlikely that the hermit-crab would be a serious enemy of the oyster; but as these crabs are numerous on the beds the matter might be important, and it would probably not be difficult to obtain definite data on the subject. The following observations were made in attempts to obtain the required information.

Experiments with the Hermit-crab (*E. Bernhardus*) and Oysters (*O. edulis*).

On December 21st, 1926, a sample of hermit-crabs was forwarded from the oyster beds, and of the twenty sent eleven recovered after arrival on December 23rd. It was considered advisable to examine individuals from the beds where oysters occur, since *E. Bernhardus* exists in numbers off Plymouth (Allen, 1899), and in other situations remote from oyster beds, where hermit-crabs might not have the same habits, particularly

with regard to bivalves and oysters. The hermit-crabs were placed in well-aerated water and allowed several days to recover from the effects of the journey before a number of young oysters, $1\frac{1}{2}$ to 2 inches long, were added to the dish in which the hermit-crabs were placed. Later fresh batches of hermit-crabs and some smaller oysters, with thin shells only about 1 inch to $1\frac{1}{4}$ inches long, were obtained. At no time have the hermit-crabs been found to show any inimical interest in the oysters with which they were kept, and in view of what has been observed of their mode of feeding, it is highly probable that hermit-crabs are in no sense harmful to healthy oysters, which have attained a size of about 1 inch or more, although like most crabs they would, no doubt, attack weak or dying oysters. This hermit-crab is, however, so clumsy, owing to the impediment of the shell, which it carries, that it would probably be beaten by other crabs, especially *Carcinus mœnas*, which is common on certain parts of the Fal Estuary beds, in a hunt for a weakly oyster.

E. Bernhardus attempts to break barnacles and tubicolous worms (e.g. Pomatoceros) from stones and shells, and in this way will no doubt kill inadvertently a small proportion of very young oysters.

It is possible that *E. Bernhardus* may also obtain oyster larvæ, at the time these settle, by scraping objects with its third maxillipedes; but various Amphipods, worms, and other animals are probably greater enemies of the oyster at this stage of existence than is the hermit-crab.

Observations and Experiments on the Mode of Feeding of *E. Bernhardus*.

Whilst observing the hermit-crabs, it was noticed that individuals scraped various objects in the dish with their third maxillipedes, and as *Porcellana longicornis* is known to use the similar appendages for catching food-particles (Gosse, see Potts, 1916), it was suspected that the hermit-crab obtained food in a similar way. To test this suspicion bunches of *Ascidiella aspersa*, which had accumulated much sediment and extraneous growth, were added to the dish, and the scraping operation was found to be repeated. On confirmation of this fact it was decided to add sediment to the dish to make it resemble the bottom on the oyster bed, which is mainly muddy or muddy gravel. A sediment usually rich in micro-organisms was obtained from walings exposed at low water at the Great Western Docks and made to form a layer on the bottom of the dish.

As a result of this arrangement, an additional act of feeding could be seen. The hermit-crabs now scraped the bottom of the dish—with its covering of sediment—with its smaller claw, and passed on the products of the scraping to the third maxillipedes, whose hairs were used like a brush

to transfer the collected particles towards the mouth. This movement is carried out automatically for long periods, and if arrested can be started by adding fresh material or the juices of fresh Pecten meat to the water. When the captured particles reach the smaller mouth parts they are sifted in some way, since a cloud of rejected material is borne forwards and upwards in the stream of water emerging from the gill-chamber. From these actions it seemed clear that the hermit-crab was feeding on material obtained by sifting and selecting from sedimentary deposits. In order to obtain more definite information a hermit-crab was isolated for a period without food in a clean bottle with circulating water, and to this water was added, after the period of isolation, brushings of the brown incrustations found on stones and other objects on the foreshore. This brown material consists of a feltwork of small filamentous algæ and chain and free diatoms, with Vorticellids, Acineterians, and other micro-organisms. After leaving the hermit-crab in the bottle with this material overnight, the animal was anæsthetised and the contents of the gut examined. The stomach and first part of the intestine were found to contain quantities of the diatoms and algal threads and other material similar in mass to that added to the bottle, but already in a partly digested state.

To test whether the feeding action observed in the Laboratory occurred on the oyster beds, the stomachs and intestines of fourteen individuals, sent to the Laboratory in February, were examined.

In the gut of these hermit-crabs was found a collection of detritic and food material similar to that which may be found in the oyster or Crepidulæ (Orton, 1912) with, in addition, microscopic bits of brown and green algæ, in one case also algal ova, fragments of microscopic shells, crustaceans, and polychætes. The material in the gut which resembles that found in oysters and Crepidula consists of microscopic sand-grains, sponge spicules, diatoms, foraminifera, algal threads, and polychæte and crustacean bristles, but the two latter kinds of material may have been derived in the case of the hermit-crab from captured organisms.

The food found in the stomachs and intestines of hermit-crabs during the winter months is probably small in amount in comparison with what may be taken during the spring and summer, and observations will need to be continued throughout the year to obtain adequate information.

It is clear, however, that the hermit-crab obtains its food *largely* by scooping up loose detritic material from the sea-bottom and objects on the sea-bottom, and selecting therefrom the organic constituents. In this way are obtained small polychætes, small crustaceans, small algæ, foraminifera, diatoms, and other micro-organisms. The relative importance of this kind of food-material in comparison with that derived from larger food-organisms cannot be estimated without seasonal examination

of gut contents of a considerable number of individuals, a research which might not even, on completion, give the desired information (see the work on the food of the American lobster (Herrick, 1911). The writer, however, holds the view that when all the information relating to feeding in the hermit-crab is considered, there remains little doubt that the food obtained by the small pincer and third maxillipede constitutes the main diet. As the hermit-crab can obtain food without its large claws, it is interesting to note that the loss of the latter is not so serious a matter as it would be if the claws were essential for feeding.

Hunt (1925) examined stomachs of *E. Bernhardus* and *E. Prideauxii* from the Plymouth trawling grounds, and remarks that they "feed on small lamellibranchs (Venus, Cultellus, etc.), echinoderms (Echinocyamus, small Echinocardium, ophiuroids), crustaceans (amphipods, crangonids, smaller pagurids), and polychætes (Polynoidæ, Nephthys, Goniada, Terebellidæ, Pectinaria). Detritus and sand are found in their stomachs, but only in quantity that might have been swallowed along with their prey." From this description it would appear that *E. Prideauxii* feeds in the same way as *E. Bernhardus*, but that the size of the food-organisms at the time Hunt examined the stomachs was rather larger than microfauna, and indicates the probability, as suggested above, of seasonal variations in the kind of food capturable by means of the small chelæ and third maxillipedes.

It is well known that *Eupagurus Bernhardus* will eat fish-meat of any kind, and Jackson (1913), in his valuable memoir on this animal, makes the following remarks under the heading of food: "The hermit-crab (*E. Bernhardus*) is an omnivorous feeder. In its early youth it follows the cannibalistic instincts of other zoeas, but the adult seems to be purely a scavenger. It will accept almost any animal or vegetable food. The left chela (the small one) is almost invariably used for carrying the food to the foot-jaws, and it also aids them in tearing the morsels to suitable shreds. *It may be observed very frequently tossing sand with the same appendage between the mouth parts, and letting the grains drop as it rubs them.** There is no doubt M. T. Thompson is right in thinking that the diatoms and foraminifera which are found in the alimentary canal come from this source." It is clear from Jackson's remarks that he had observed this hermit-crab's habit of passing on sedimentary material to the mouth parts with its smaller (left) chela, but would seem not to have realised the full significance of the act; possibly he observed animals in dishes containing only few sand-grains, and was therefore unable to note how the animal behaved in its natural environment, that is, on a bottom containing a fair to a considerable amount of fine sand, sediment, or mud. As *Eupagurus Bernhardus* belongs to that

* The italics have been inserted by the writer.

section of the bottom fauna known as epifauna, it has unfortunately been generally omitted from quantitative surveys carried out recently by naturalists with the Petersen grab, but Allen (1899) made an estimate of the relative frequency of species on and about the 30-fathom line near Plymouth, and remarks that " this hermit-crab is present on grounds of all kinds, though it is most abundant on the sand and on the gravel and sand grounds where the fauna is generally rich." He records the species as most common on grounds II and III with respectively 95·8 per cent fine sand with 1·9 per cent silt, and 82·7 per cent fine sand with 1·1 per cent silt. On the estuarine grounds in the Fal Estuary the nature of the bottom where this hermit-crab occurs in abundance varies from muddy to a muddy gravel, in which the percentage of silt would everywhere be very much higher than on the grounds off Plymouth. These facts indicate that the microfauna on a fine sandy ground may be, as is indicated by Hunt (1925), as great as on an estuarine muddy ground, but it is not impossible that other food-factors may govern the distribution of the hermit-crab. It may be remarked in passing that as this hermit-crab is an important member of those animals which subsist on food-material derived from the sea-bottom, its omission from bottom-communities affords an example of the artificiality of these so-called communities.

On the Function of the Mouth Parts, and some Unusual Features in the Gut, of *E. Bernhardus*.

When it was found that the stomach and intestines of hermit-crabs taken from the oyster beds contained a large amount of food-material picked up from the sea-bed, the question arose to what extent the mouth parts might be modified for this purpose. Jackson (l.c.) shows the mouth parts to be normal in form, but comparison with the similar appendages in Carcinus or Portunus shows that they are relatively feeble. The mouth parts in a hermit-crab are indeed not adapted in the same way as those of the typical crabs mentioned for cutting up and ingesting such food as fish-meat. In order to obtain some expression of this difference, *E. Bernhardus*, *Carcinus mœnas*, and *Portunus puber* were fed with pieces of squid-meat of approximately the same size. The hermit-crabs could only nibble tiny pieces at a time from their food-masses, while the crabs cut up theirs rapidly. At the end of an hour and a quarter, the hermit-crabs had still one-fourth to one-third of their food left, while both Carcinus and Portunus had eaten and swallowed theirs in four to eleven minutes. Similar time-relations were found with regard to softer food, such as the gills of Pecten or the visceral mass of Tapes. There can be no doubt that these observations show that although *E. Bernhardus*

can eat portions of fish-meat, its mouth parts are not adapted to a regular diet on this kind of food. It is further significant that all hermit-crabs (Anomura) differ from all crabs (Brachyura) in not having the third maxillipedes broadened out to form an operculum over the inner mouth parts (Calman, 1909), and an important function of the opercular maxillipedes in crabs is to retain food-masses under pressure in contact with the cutting inner mouth parts, so that the food can be readily and quickly sub-divided and ingested. It is therefore a reasonable conclusion that the normal food of hermit-crabs and other Anomura is likely to differ from that of the true crabs.

In view of the suggestions made later and the possibility of correlating in detail the structure with the function of the third maxillipede, it is worth while to give here Calman's review of the variations in form of this appendage in Decapoda. He states that " The third maxillipede may, in the Natantia, even exceed in length the next succeeding pair of appendages. The exopodite and basipodite are almost always connected by an immovable articulation. In the Caridea the ischiopodite is quite coalesced with the meropodite, and the dactylopodite is obsolete or coalesced with the preceding segment. A serrate ridge or ' *cresta dentata* ' is commonly present on the third segment, but no endites are developed from the first and second segments. Among the Brachyura the third maxillipedes become greatly modified to form an operculum to the buccal frame and entirely lose their pediform character. The ischiopodite and meropodite become broad plates and the terminal three segments are often hidden behind the meropodite. The peduncle of the exopodite may also be expanded and share in forming the operculum. Its terminal flagellum is either folded out of sight or may be entirely lost. The epipodite forms a long curved blade in most Brachyura."

With regard to the ossicles in the stomach of *E. Bernhardus*, Jackson (l.c.) notes that " The cardiac ossicle is far more slender than is usual, and is bow-shaped ; the pterocardiac ossicles are also slender. . . . The lateral teeth are unusually massive and are prolonged backwards into strongly pectinated ridges. The summit of the cardiopyloric valve also bears a ridge of great blunt setæ like a comb." The slender nature of some of the ossicles gives a hint that the need for these organs for the manipulation of ingested food is not the same in this crustacean as in such a form as Cancer, while the occurrence of pectinate lateral teeth and the development of setæ is in harmony with a mode of feeding on the smaller organisms in sedimentary material. Potts (1916) shows that an extreme reduction of the gastric ossicles occurs in the plankton-feeding crabs, Hapalocarcinus and Cryptochirus.

The form of the gut in *E. Bernhardus* is interesting in that Jackson has found (l.c.) the achitinous—and absorptive—portion of the mid-gut to

be unusually long. This fact would lead one to infer that the food ingested is either of a detritic or vegetable nature in conformity with the general occurrence of a relatively long intestine in animals which feed on the organic contents of detritus or on vegetable matter. But it would appear that this conclusion can hardly be permitted in the present state of our knowledge of the natural food and physiology of digestion in crustaceans. The mid-gut in *E. Bernhardus* gives off long-paired anterior cæca and a long unpaired posterior cæcum. These facts are again suggestive of an effort to increase the absorptive area of the intestine in correlation with the nature of the food, but the interpretation is not at present justifiable from the occurrence as noted by Jackson (l.c.) of a very short achitinous mid-gut in *E. longicarpus*, an American hermit-crab, which M. T. Thompson (1904) found to feed in the same way as *E. Bernhardus*. Moreover, the lobster (Homarus) and the Norway lobster, *Nephrops norvegicus*, both have a long mid-gut, and both these animals are believed to be carnivorous according to Herrick (1911) and Yonge (1923). The natural food of these forms is, however, very difficult to determine, and it will be well worth while to review their feeding habits in the light of the information which is accumulating with regard to the use of the third maxillipedes as a food-collecting organ. Herrick examined stomachs of *H. Americanus* preserved during a period of seven months (December to June), and makes the following remarks: "A considerable number of these stomachs were empty; more than half contained remnants of recently devoured fish, a mass of scales and bones, mixed with fragments of the indigestible parts of other organisms. In many cases it was quite evident that the bait of traps formed the only food found in their stomachs." . . . "The stomachs examined contained remnants of the following organisms placed in the order of their relative abundance: fish (procured independently of the traps); crustacea, embracing chiefly isopods and decapods; mollusca, *consisting largely of small univalves;* algæ; echinoderms and hydroids. . . . In the large lobster found at the Vinal Haven Islands I have seen the muddy bottom scored in all directions—the work of lobsters in their search for clams. . . . As a fisherman remarked, if you put lobsters in a pound and *do not feed them, they will soon turn over the bottom as effectually as it could be done with a plough.*" * From these observations the information regarding the natural food of the American lobster must be regarded as unsatisfactory, and as our information regarding the English lobster (*H. vulgaris*) is similar to that of its American relative, there is reason to believe that a special study of the food and mode of feeding of these and allied forms, especially Palinurus, the crawfish, would be profitable. It would be easy to overlook the possibility of small organisms serving

* The italics have been inserted by the writer.

as food in the case of these large animals. In any event a physiological explanation of the occurrence of a large achitinous mid-gut in some forms and a small one in others is required.

With regard to the histology of the gut and its appendages in *E. Bernhardus*, Jackson (l.c.) notes that "The histology of the digestive gland differs somewhat from that described by Pearson (1908) in Cancer. The so-called 'fat-cells' are never scattered round the lumen, but bulge out (like a typhlosole) from one point only at a time. It seems doubtful whether the division into 'fat' and 'ferment' cells can be justified, and whether the fat-cells are not to be considered only as ferment-cells. The lining of the mid-gut is characteristic. The cells are columnar with large nuclei and considerable contents of fatty matter." From Jackson's observations there is an indication that the physiology of digestion in two such forms as Eupagurus and a truly carnivorous ally, such as Cancer probably is, is different, and in conjunction with that in *Porcellana longicornis* and *Pinnotheres pisum* ♀, would afford an interesting comparative study.

On the Mode of Feeding and Food of some other Decapoda and the Function of the Third Maxillipedes.

Now that it is established that *E. Bernhardus* obtains micro-organisms for food by means mainly of its third maxillipedes, it is worth while reviewing and, indeed, investigating the mode of feeding in all the forms closely allied to Eupagurus. With regard to *E. longicarpus*, the American hermit-crab, M. T. Thompson (1904) remarks: "Like many other Decapods, *Eupagurus longicarpus* is crepuscular, and during the day a majority of individuals remain buried in the sand or congregated in the shade. They are omnivorous and must glean very closely, as they pick up bits of gravel or detritus from the bottom and brush them over between the maxillipedes. They also toss sand—usually with the smaller chelipeds only—to the mouth parts, brush it between them, and let the grains fall again in a continuous stream. Probably it is in this manner that they obtain the diatoms and foraminifera, which are found in the stomach and intestine. But although the food is thus very largely diatomaceous, no sort of vegetable or animal matter is refused." It is seen, therefore, that M. T. Thompson found that *E. longicarpus* feeds in the same way as *E. Bernhardus*. The experiment described on p. 910 with regard to *E. Bernhardus*, if repeated on *E. longicarpus*, would apparently speedily prove that the latter does obtain its micro-organisms by the intermediary of the third maxillipede. It has been noted that other organisms than diatoms are obtained by this mode of feeding, and some of these may have greater total food value than diatoms; for instance, foraminifera and microscopic bivalves, polychætes, and crustacea.

It is thus clear that two hermit-crabs obtain a large portion of their food from micro-organisms and others slightly larger, and there can be no doubt that allied species will be found similar in this respect. It is known that *Porcellana platycheles* also uses its third maxillipede for obtaining food (Borradaile, 1921), and the writer has observed that *Porcellana longicornis* uses the same organs, which when extended are as long or rather longer than the cephalothorax, like whips or lacrosse rackets, throwing out the left and right one alternately, for catching suspended particles, which are removed from the basket-like organs by a scooping action of one of the inner mouth parts; Hunt (1925) has observed that the stomach contents of this crab—and other crustacea, which feed similarly, such as cirripedes and an amphipod—" consist of an assortment of detritus and micro-organisms quite comparable to that found in the ciliary feeding suspension-feeders." Hapalocarcinus, like Porcellana, uses its third maxillipedes for collecting plankton, which provides the sole form of food (Potts, 1916). It is also well known that the females of the pea-crab, *Pinnotheres pisum*—and no doubt other pea-crabs—feed on the food caught in the mucus strings of its hosts, such as Mytilus, Cardium, and others (Orton, 1921); Pinnotheres thus takes the same kind of food second-hand, as *Porcellana longicornis* obtains at first-hand. Hunt's valuable investigations on the food of the bottom fauna (1925) indicate, as might now be anticipated, that many decapoda may be found to obtain their food by using the third maxillipedes either for collecting organisms in suspension, or in the sediments on the sea-bottom. For example, Hunt shows that the burrowing forms, Callianassa and Gebia, had " nothing but a mixture of sand, mud and detritus with the usual associated small organisms " in the stomachs of the specimens examined, and other burrowing forms are probably largely similar in their habits. In the stomach of *Galathea nexa* Hunt found small crustaceans, small polychætes and detritus, with foraminifera, diatoms, copepod eggs, peridinians, a congeries of organisms very similar to that occurring in the gut of hermit-crabs from the oyster beds. This species of Galathea, and no doubt also its related species and genera, probably feeds with its third maxillipedes in the same—or a similar—manner as Porcellana.

In addition to these forms, the sluggish crabs, Hyas, Pisa, Dromia, Inachus, Macropodia, and possibly Maia, may be found to obtain a major portion of their food by means of their third maxillipedes after the manner described above for hermit-crabs and other Anomura. It will be interesting to learn in what way the third maxillipede is modified throughout the Decapoda to subserve different functions, but there can now be no doubt that its form is directly correlated with its function, and that the difference in the form of this organ in crabs and other

Decapoda, especially the old group, Anomura, denotes a fundamental difference in the mode of feeding. The modifications of this appendage in Hapalocarcinus, Macropodia, and Porcellana, figured by Potts (1916, Fig. 6), and the curious anomaly in the structure and disposition of the same organs in Pinnotheres, described by the same writer, support the conclusion that the form of this organ is closely correlated with its function. The degree to which these appendages and the related mouth parts are modifiable in response to change in function, even in a crab, is well brought out by Potts (l.c.), who shows that the mouth parts of Hapalocarcinus and Cryptochirus are modified to such a degree as to resemble those of a Branchiopod.

Some Relationships of the Hermit-crab with its Commensals.

The details of the mode of feeding of the hermit-crab, as described in the preceding pages, enable the relationships of the commensals, Hydractinia, Calliactis (Sagartia), and perhaps *Nereis fucata*, to be better understood.

It has been noted that the hermit-crab is almost continuously, or at least very frequently, scooping up portions of the sediment on the sea-bottom with such an inefficient scooper as the small claw, and sifting the sedimentary material in the outgoing respiratory current. As a result of these actions a small cloud of the bottom sediment containing micro-organisms is frequently produced in the region surrounding the hermit-crab. If the hermit-crab is facing the tidal current, this cloud will be carried around the inhabited shell and the polyps of Hydractinia situated thereon will receive a gratuitous supply of food-material and be thereby enabled to grow and multiply into large colonies on the shell. When the hermit-crab is not facing the tidal current, or in situations where there is no current, the sedimentary material may frequently be carried away from the region of the shell, or a portion only be brought in contact with the hydroids on the shell according to variable complex conditions, but there can be no doubt that Hydractinia obtains a greater supply of food-material as a result of the hermit-crab's habit of sifting bottom deposits than it would if the food of the latter were entirely large organisms. Hydractinia will, however, obtain food also from the sediment which is disturbed and lifted up in the water merely as a result of the hermit-crab dragging its shell over the bottom, and a greater amount of food would be obtained in this way on bottoms where the micro-fauna is easily disturbed, as, for example, on muddy grounds and the softer deposits. It is interesting that Allen (l.c.) found Hydractinia only sparingly associated with *E. Bernhardus* on fine sand, whereas the hydroid

is commonly present on the muddy beds in the Fal Estuary, but other conditions may also govern the distribution of this hydroid.

The frequent scraping of the sea-bottom by the hermit-crab along with the movement of the inhabited shell will certainly disturb organisms such as polychætes, small crabs and similar forms; and as the anemone, *Calliactis* (*Sagartia*) *parasitica*, which is frequently carried on the shell, has the habit of pressing its disc on to the surface of the bottom (Sinel, 1906; and Orton, 1922), the anemone must in this way obtain its main supply of food. The anemone will also obtain additional food from that scattered by the hermit-crab in its inefficient rending apart of large masses of food-material, such as a weak or dying mollusc or small crab. Further, as the hermit-crab can only ingest food of the latter kind slowly, it must frequently happen that when the hermit-crab has accumulated between the maxillipedes all the food it can carry, the remainder will become the share of the anemone or anemones. A hermit-crab with its foot-jaws crammed with food will sometimes drag about the remainder of the unattacked food by means of its big claw. In these circumstances a quick turn by the hermit-crab, such as no doubt frequently occurs owing to other crabs smelling the food, and hunting for it, would often bring the spare food within reach of the anemone, which at once seizes tenaciously morsels of this kind. The possibility that the hermit-crab may definitely and willingly share a portion of its food, when it has gorged its jaws with enough to eat for several hours, may now be considered not unreasonable (Orton, 1922). In this connexion a little further light is perhaps thrown on the observed act of *Nereis fucata*, the worm frequently present in the shell inhabited by the hermit-crab, taking pieces of food out of the foot-jaws of its partner. If the hermit-crab has captured even a moderately large supply of food in mass, it will probably seldom be able to eat it all itself, owing to its slow rate of eating and the probability of other crabs soon finding and capturing the spare food which it cannot adequately defend. The loss of one portion of food, if others are available, would not therefore necessarily be a net loss, and the worm might obtain a portion of food without detriment to the hermit-crab. It is unlikely, however, that the true relations of this worm to the hermit-crab will be properly understood until a close study is made of their mutual behaviour during feeding, and the gut contents of the worm, when freshly caught, have been determined. The only probable advantage to the hermit-crab from its association with the worm is that of having the water in the shell renewed by the rhythmical wave-like motion of the body of the worm, but it is also possible that the worm may assist the hermit-crab by removing from the mouth parts of the latter undesirable food which may inadvertently have been attacked.

SUMMARY.

The hermit-crab, *Eupagurus Bernhardus*, is common in the oyster beds in the upper part of the Fal Estuary, and experiments indicate, while observations and experiments on the mode of feeding virtually prove, that these hermit-crabs do not harm healthy small oysters one inch or more in length, and the larger oysters, but that spat less than one inch may occasionally be damaged or eaten by hermit-crabs picking with their claws indiscriminately at growths on shells and stones.

E. Bernhardus obtains food largely by its small claw and third maxillipedes, and may at certain periods of the year feed mainly on micro-organisms, and at others on macroscopic, but mainly tiny living organisms which have been disturbed and captured in the deposits on the sea-bottom. Food can be obtained by the use of the third maxillipedes alone.

The mouth parts of *E. Bernhardus* are not adapted for rapid ingestion of the meats of animals in bulk, and the gastric mill is less strongly developed than in the carnivorous crabs ; these facts, along with certain features of the gut, indicate morphological and anatomical modification correlated with the food and mode of feeding.

E. longicarpus feeds in the same way as *E. Bernhardus*, and allied species may obtain food similarly.

Some Decapoda are now known to obtain food mainly by use of the third maxillipedes, as Porcellana, Hapalocarcinus, and some subsist entirely on planktonic food-material as *Porcellana longicornis*, *Pinnotheres pisum* ♀, and it is probable that a large number of other Decapoda obtain small or microscopic organisms as food mainly by use of the third maxillipedes. The structure of the third maxillipede in all Decapoda is probably definitely correlated with its function in feeding actions.

Some additional points in the relations of the hermit-crab with its commensals are better understood when the mode of feeding of the former is considered.

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Observations on the Fal Estuary Oyster Beds during 1926, including a study in Over-fishing.

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With 3 Figures in the Text.

CONTENTS.

INTRODUCTION.

During the summer and autumn of 1926 frequent visits were made to the oyster beds in the upper Fal Estuary, and in view of the continued decline in the yield of oysters from these grounds, the opportunity was taken to record any facts which, besides being of value in the study of the bionomics of the oyster, might also be helpful in determining those steps most likely to lead towards an improvement of the general state of the fishery. A special investigation of the spawning in relation to tides and temperature was made, and will be compared in a separate publication with similar work carried out at about the same time on the River Blackwater beds in Essex.

Shell-growth.

A few general observations on shell-growth may be noted. In a sample of oysters dredged from Turnaware Bar and examined the following day, April 22, of 73 individuals with normal shells, 53 had already begun to deposit shell-material and had new shoots of 1 to 9 mm. (measured in the median dorso-ventral line on the left valve). The shells were covered with slight growths of red and brown filamentous algæ. Shell-growth had therefore begun about the middle of April or earlier.

In samples of oysters dredged from Turnaware Bar on May 26, large individuals (over $2\frac{5}{8}$ inches long) with normally-grown shells had thin white new shoots up to 12 mms. and smaller ones had shoots up to 10 mms.; dumpy and slightly dumpy oysters in the same samples showed shoots up to 9 mms., but the proportion of individuals of these kinds with no shoots at all was relatively very high. Similar growth was observed on a sample from the south end of the East Edge on May 21. During June the new growth hardened, that is, thickened, but the shoots did not increase in extent. In the remainder of the summer no special attention was given to observing shell-growth, but it was remarked that no new general outburst of growth occurred until the autumn. On September 21 new small thin shoots of shell appeared on oysters taken on the shore at Turnaware Bar, and a small proportion of shells dredged in the same locality on the 24th showed also slight new growth; but on September 29 oysters dredged from the River, Trelissick Reach, showed new white or yellow shoots from 3 to 14 mms. The River oysters had therefore begun to put on new shoots rather earlier than those in the lower parts of the Estuary.

On October 6 the new shoots in small to medium oysters from Turnaware Bar were mainly about 7 mm., while in a sample of rather larger individuals from the River the new shoots were mainly about 10 mms. During October new shoots up to 10 mms. were found in a high proportion of individuals all over the grounds, but on working out an average shoot, this was found to be generally about 4 to 5 mm. On all the grounds the shoots strengthened towards the end of the month, but there was much soft new shell even in November. On October 28 an important sample from the Falmouth North Bank showed new thin white growths, clearly more recent than that on beds higher in the Estuary and in strong contrast with the hardening shoots on the shells from the Truro beds. New depositions destined to form chambers were also frequently seen in October. On October 28 and 29 samples were examined from the Channel (off the Poles Rocks), Mylor and East Banks, and it was found that whereas new growth had occurred in a high proportion in the shells from the two latter beds, little had occurred in the Channel oysters, in which shoots of only 2 to 3 mm. of indecisive growth were found.

Thus in 1926 shell-growth began in April, or possibly a little earlier, on some parts of the beds and continued generally over the beds in May and June. During the summer this spring growth thickened, but no new *general* growth occurred during the summer. Towards the end of September a new general outburst of shell-growth occurred, beginning in the upper parts of the beds and extending to the lower parts in October. During October and early November this autumn growth was hardening,

and the last new growth was seen on the Falmouth North Bank on October 28, and had probably taken place about the middle of the month.

These observations are of great importance from the point of view of oyster-cultivation. Oysters dredged in October had soft new shoots which were easily broken, and it is well known that oysters with broken shells are unfit to withstand successfully the hardships of transportation for relaying. In addition the oysters were mostly poorly fished, that is, had small reserves of food-material in the early part of October, but many rapidly improved at the end of the month and in November.

Spatfall.

During the examination of different parts of the beds, it was possible to obtain a good general idea of the spatfall in the different parts of the ground. The spatfall in the river, in 1925 and 1926, especially at Trelissick Reach, on the east side, was fairly good, and was apparently equally good in higher parts. On the Edges everywhere spat had settled in fair amounts, and there was also a fair fall on Turnaware Bar. On the Banks the fall was slight, but spat or young brood could generally be seen in a dredge-haul from these beds. The total fall of spat is, however, very small compared with the total amount of oysters taken from the beds. In view of the fact that the summers in 1925 and 1926 were highly favourable for spatfall, in so far as the important factor of weather is concerned, the discrepancy between the input of oysters, as measured by the spatfall, and the outtake, as measured by the dredging-catches, is serious. The outtake of oysters may be measured by the catches of large oysters recorded in Tables I and II (pages 928 and 929), and the input by the catches of brood and spat in the same hauls.

The conclusion to be drawn from the observations on spatfall is that the resources of the authorities should be concentrated on the Banks and Turnaware Bar. These beds would take easily and with profit more than 100 tons of shell-cultch. The cultch on the edges of the Banks, the Channel, and the River is kept sufficiently clean and is present in sufficient amount to give attachment to a relatively great amount of oyster larvæ; these parts of the beds therefore do not need cultivating at present for the capture of spat. As the number of adult spawning oysters on the grounds is decreasing, there is a decrease in the potential number of oyster larvæ, and a corresponding decrease in the expectation of number of spat which will settle on cultch. Therefore, in spite of the promising fall of spat in parts of the River, the spatfall as a whole is inadequate to make up the present loss on the beds.

Spawning.

During May, 1926, and up to June 9, about a thousand oysters were examined mostly from Turnaware Bar and only five oysters found in spawn, of which four were probably forced or premature spawners. From June 15 to June 23 an additional thousand oysters from the same beds yielded only four more spawning oysters, which were also in all probability premature spawners. On the spring tides at about full moon at the end of June, however, regular spawning began and continued throughout the summer until the full moon spring tides about September 23. On Turnaware Bar a high proportion of individuals could be found, in parts of the beds, carrying larvæ after the dredging season opened. For example, on October 4 out of 108 oysters examined 10 were blacksick, and on October 5 in the same place 13 were found blacksick out of 119 examined. This was the end of the spawning in 1926.

The spawning season in 1926 therefore extended from the end of June to the third week in September, but there is evidence that the spawning season varies slightly in extent on different parts of the Fal Estuary beds, beginning and ending early on the upper parts and on the exposed foreshores, as at Turnaware Bar, and beginning and ending rather later in the lower parts of the beds and in the lower parts of the Channel. A full discussion of the information obtained will be given later. The fact that the spawning season in the upper Fal Estuary beds—excluding the higher reaches of the River where no observations could be made—did not begin until the end of June is one of great interest. On the West Mersea oyster beds (Blackwater River, Essex) spawning was well advanced on June 16, as is shown by the fact that a sample of 104 oysters examined on that date contained 7 blacksick and 7 whitesick oysters, while of 1000 examined at the Fal Estuary between June 15 and 23 only 4 were whitesick, which were also in all probability premature spawners. This difference in the time of beginning of a general spawning on the east and west coast beds compared is probably usual, and can be correlated with the different temperature conditions in the two localities. On the east coast beds the temperature of the sea-water rises and falls *rapidly* directly with variations in duration of sunshine and air-temperature, whereas on the west coast beds the change is slower. The slowness of the change on the west coast beds is due to the large body of tidal water flowing into and out of the deep channels in the Fal Estuary beds (10 to 15 fathoms) directly from the English Channel, and this large body of water can only be warmed up slowly. On the east coast beds the shallower water warms up quickly, but in addition the configuration of the north-west portion of the Thames Estuary at the mouth of the River Blackwater is such as to render there even a large body of tidal

water more susceptible to temperature changes in the air than on the Fal Estuary beds. A complete discussion of the matter cannot, however, be given here.

The factor of the time at which regular spawning begins on any oyster bed is an important one in connexion with the size attained by spat in the first year of growth, but an equally important factor also is the extent of the period in which shell-growth occurs on the same beds in the same season. In 1926 spat may have settled on the Fal Estuary beds in fair numbers by the middle of July, and could have continued growth until about the middle of October, a period of about three months, but as the larvæ would continue to settle throughout the summer, *the majority of the spat would have a shorter period of growth than three months.*

The Rate of Dredging in December, 1926.

During the autumn of 1926, visits were paid to the Fal Estuary Oyster Beds for the purpose of obtaining temperature readings at different parts of the beds at different states of the tides. It was hoped to combine this work with observations on the rate of dredging in November to compare with that found in November, 1924, but the weather was so stormy in this month that this work had to be delayed until December; but as relatively little work was done on the beds in November, the results obtained are probably not very different from those which would have accrued if the work could have been carried out as planned.

Dredging was carried out on December 9, 10, 16, and 17, from both rowing and sailing boats, and the whole of the oysters caught recorded and measured as described in the Report on a Survey of the Fal Estuary Oyster Beds, 1926, pp. 9–14. The results obtained during December, 1926, along with those recorded from November, 1924, will form a valuable basis for comparison of the state of the Fal Estuary oyster fisheries in the future.

The details of the dredging from sailing and rowing boats in December, 1926, are given in Tables I and II on pp. 928 and 929 respectively. These tables may be compared with the similar ones given in the report of the work in November, 1924, as follows: Table I herein gives information corresponding to that found in Tables II and III, pp. 29–31, of the November, 1924, survey, and Table II herein corresponds to Table IV, p. 31.

The essential facts obtained from a comparison of the dredging results in 1924 and 1926—shown graphically in Figs. 1 and 2, pp. 930 and 931—are as follows:—

1. That whereas in 1924, 237 dredge-hauls—of average duration of 6·2 minutes—were made from sailing boats, in 1926, 387 similar

TABLE I.

RESULTS OF DREDGING FROM SAILING BOATS ON THE TRURO GROUNDS, UPPER FAL ESTUARY, DECEMBER 9–17, 1926, SHOWING THE AVERAGE CATCH AND TIME OF DREDGE-HAULS AND THE NUMBERS AND PERCENTAGES OF DIFFERENT CATEGORIES OF OYSTERS TAKEN.

Date.	Locality.	No. of dredge-hauls.	Total oysters dredged.			Nos. and percentages of different categories of oysters.				Average No. of oysters per haul.			Working period in mins.	Drifting period in mins.	No. of men dredging.	No. of dredges working.	Aggregate mins. dredges working 15 × 17.	Average mins. per haul 18÷3
			Legal or Large.	Illegal or Small.	Total.	N.*	D.	S-D	Brood and spat.	L.	Sm.	Total.						
1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.	15.	16.	17.	18.	19.
							EAST BANK.											
Dec. 9	North inner	12	22	13	35	(19	9	6	1)	1·8	1·1	2·9	—	15	2	3(4)	45	4·0
			63·0	*37·0*		*54·3*	*25·8*	*17·2*	*2·8*									
Dec. 9	South	58	57	239	296	(99	105	41	51)	1·0	4·1	5·1	125	73	2	3(4)	219	4·0
			19·2	*80·8*		*33·5*	*35·5*	*13·8*	*17·2*									
Dec. 10	N., Middle, and S.	(43)	72	119	191	(68	53	29	41)	1·7	2·8	4·5	318	253	1	2(1)	(506)	11·0
			37·7	*62·3*		*35·6*	*27·8*	*15·2*	*21·5*									
Dec. 16	North outer	52	39	116	155	(52	50	25	28)	0·7	2·2	3·0	78	73	2	4(5)	292	5·5
			25·2	*74·8*		*33·6*	*32·3*	*16·1*	*18·1*									
Dec. 17	Middle and N.	87	133	270	403	(155	109	89	50)	1·5	3·1	4·6	143	(112)	3	7(6)	565	6·5
			32·9	*67·1*		*38·5*	*27·1*	*22·1*	*12·4*									
	Totals, averages and percentages	252	323	757	1080	393	326	190	171	1·3	3·0	4·3	664	501	10	19(20)	1627	6·7†
			30·0	*70·0*		*36·4*	*30·2*	*17·6*	*15·9*									
							MYLOR BANK.											
Dec. 10	Near Edge	(4)	3	11	14	(2	5	2	5)	0·7	2·7	3·5	40	40	1	2(1)	(60)	15·0
Dec. 17	do.	78	103	166	269	(133	70	35	31)	1·3	2·1	3·4	157	96	3	5	480	6·0
			38·3	*61·7*		*49·5*	*26·0*	*13·0*	*11·5*									
Dec. 17	Middle	29	42	50	92	(56	15	6	15)	1·4	1·7	3·1	29	29	3	6	174	6·0
			45·7	*54·4*		*60·9*	*16·3*	*6·5*	*16·3*									
	Totals, averages and percentages	111	148	227	375	(191	90	43	51)	1·3	2·0	3·3	226	165	7	13(14)	714	6·0†
			39·5	*60·5*		*50·8*	*23·9*	*11·5*	*13·6*									
							PARSONS BANK.											
Dec. 17		24	31	95	126	(45	34	16	31)	1·3	4·0	5·3	27	27	3	6(5)	150	6·5
			24·6	*75·4*		*35·7*	*27·1*	*12·7*	*24·6*									
Aggregate totals, averages and percentages		387 (340)	502	1079	1581	(629	450	249	253)	1·3	2·8	4·1	917	693	20	38 (40)	2491 (1969)	5·8†
			31·8	*68·3*		*39·8*	*28·5*	*15·8*	*15·9*									

* N = normal; D = dumpy; S-D = semi-dumpy; L = large; Sm = small.

† In calculating the average time per dredge-haul the work done on December 10th in a very light wind is not included.

During the work on December 17th five long hauls on the middle of the East Bank taken during lunch-time are also excluded from the data for reckoning the time of the average haul. The time of the average haul for all drifts, namely, 5·8 minutes, is the period elapsing between shooting and hauling the dredge; the average time the dredge is working on the bottom is appproximately one minute less.

TABLE II.

RESULTS OF DREDGING FROM ROWING BOATS IN THE UPPER FAL ESTUARY, DECEMBER 9–17, 1926, SHOWING THE AVERAGE TIME AND CATCH OF DREDGE-HAULS AND NUMBERS AND PERCENTAGES OF DIFFERENT CATEGORIES OF OYSTERS TAKEN.

	Rowing Boats.		Total No. and % of Oysters caught.		Nos. and percentages of the different categories of oysters dredged.					Average per haul.			Average minutes per haul (approx.).
	Working period in minutes.	No. of hauls.*	Legal or Large.	Illegal or small.	N.	D.	Sl. D.	Br. and spat.	Total dredged.	Large.	Small.	Total.	
TURNAWARE BAR.													
(1) December 10	360	40	52	646	216	182	116	184	698	1·3	16·1	17·4	9·0
			7·4	*92·6*	*30·9*	*26·1*	*16·6*	*16·4*					
RIVER, EAST TRELISSICK REACH.													
(2) December 10	400	40	61	618	247	82	190	160	679	1·5	15·4	17·0	10·0
			9·0	*91·0*	*36·4*	*12·1*	*27·9*	*23·6*					
MYLOR BANK EDGE.													
(4) December 17	105	16†	33	77	40	21	44	5	110	2·1	4·8	6·9	6·6
			30·0	*70·0*	*36·4*	*19·1*	*40·1*	*4·5*					
EAST BANK, NORTH EDGE.													
(7) December 9	150	18	27	183	78	71	30	31	210	1·5	10·0	11·5	8·3
			12·9	*87·2*	*37·1*	*33·8*	*14·3*	*14·8*					
PARSONS BANK, EDGE AND BANK NEAR PILL CREEK.													
(13) December 10	360	40	75	313	200	80	79	29	388	1·9	7·8	9·7	9·0
			19·3	*80·7*	*51·6*	*20·6*	*20·4*	*7·4*					
Totals, averages and percentages	**1375**	**154**	**248**	**1837**	**781**	**436**	**459**	**409**	**2085**	**1·6**	**11·9**	**13·5**	**8·9**
			12·0	*88·0*	*37·4*	*21·0*	*22·0*	*19·7*					

* The number of rowing-boat hauls given is a close approximation and is not derived from actual records. † Two small dredges used.

dredge-hauls—of average duration of about 6 minutes—were made with the following different results :—

	Average catches of oysters per haul.			Average daily catch per man of large oysters.
	Large.	Small.	Total.	
November, 1924	4·2 ($2\frac{1}{2}$-inch ring)	6·4	10·6	300–325
December, 1926	1·3 ($2\frac{5}{8}$-inch ring)	2·8	4·1	About 100

FIG. 1 (**1926**)

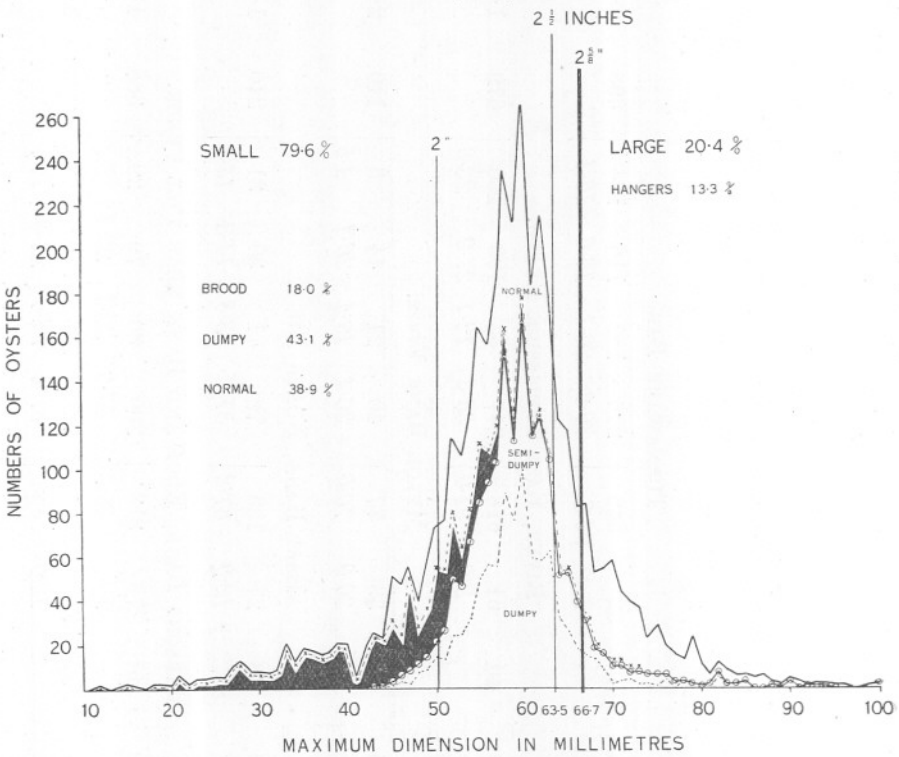

FIG. 1.*—Graph of the maximum shell-dimensions of 3,666 oysters dredged on the Truro beds, Upper Fal Estuary, December 9–17, 1926, in 387 hauls with sailing-boat dredges and about 154 hauls with rowing-boat dredges, showing the size-distribution and the proportions of the different categories of individuals constituting the population at the time.

The graph is built up by plotting successively the dumpy individuals (denoted by the thin broken line with dots), the semi-dumpy individuals (denoted by the thinner continuous line with circles), the brood and spat (denoted by the black area and broken line with crosses), and the normal, which give mostly the main outline of the graph.

The hangers observed constitute 2·7% of the whole catch and 13·3% of the large or legal oysters : it is known that the actual percentage was higher than these figures indicate, but the conditions of working prevented records being made in every case observed.

* I am indebted to Mr. J. H. Bowden for the drawings for this figure and for Fig. 3.

2. That the rowing-boat catches made in 1926, when all the parts of the grounds richest in small oysters were well sampled, and those made in 1924 show the following differences :—

	Average catch of oysters per haul.			Average daily catch per man of large oysters.
	Large.	Small.	Total.	
November, 1924	8·7 ($2\frac{1}{2}$-inch ring)	19·5	28·2	About 325
December, 1926	1·6 ($2\frac{5}{8}$-inch ring)	11·9	13·5	About 50–75 (100)*

3. The oysters on the grounds in 1926, when divided into those (*a*)

FIG. 2 (**1924**)

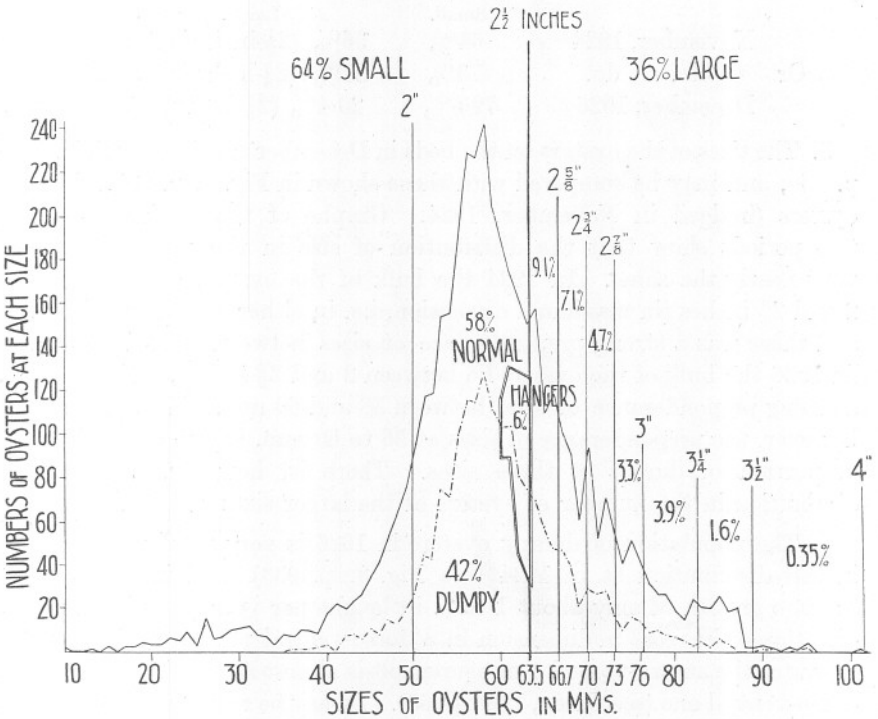

FIG. 2.†—Graph of the maximum shell-dimensions of 4,243 oysters dredged on the Truro beds, Upper Fal Estuary, November, 1924, in 270‡ hauls with sailing-boat dredges and 49 hauls with rowing-boat dredges, showing the composition in size of the stock, and the proportion of dumpy and normal oysters at different sizes.

* When the dredgerman is culling only for large oysters he can work at a quicker rate, but in the rowing-boat catches for December, 1926, one man had to cull both large and small. It is probable that at this time ordinary rowing-boat dredgermen were catching on the average from 75 to about 100 legal oysters per day.

† Reproduced from the Report of the Survey in 1924.

‡ In the Report referred to records are given of 237 dredge-hauls from sailing boats and 49 hauls from rowing boats, from the whole of which 3,897 of the oysters graphed above were obtained. In order to render the graph of these oysters more easily comparable with that of the sample taken in 1926, an additional 33 hauls from sailing-boat dredges (of average catch of 10·6 oysters) have been added to account for the whole total of 4,243.

with normally grown shells, (*b*) with dumpy or semi-dumpy and slow-growing shells, and (*c*) very young oysters, namely, brood and spat of one to three summers' growth, showed the following proportions :—

	Normal.	Dumpy and semi-dumpy.	Brood and spat.
From sailing boats	40%	44%	15·9%
From rowing boats	37·4%	43%	19·7%

In 1924 the proportion of dumpy and semi-dumpy oysters was 42%.

4. The proportions of small and large oysters dredged in the two periods are :—

	Small.	Large.
November, 1924	64%	36% ($2\frac{1}{2}$-inch ring)
Or do. do.	73%	27% ($2\frac{5}{8}$-inch ring)
December, 1926	79·6%	20·4% ($2\frac{5}{8}$-inch ring)

5. The sizes of the oysters on the beds in December are shown in Fig. 1, p. 930, and may be compared with those shown in Fig. 2, p. 931, of the oysters dredged in November, 1924. Graphs of the catches at the two periods show that the distribution of size in the populations is very nearly the same. In 1924 the bulk of the oysters were between 2 and $2\frac{3}{4}$ inches (in maximum dimension, i.e. in either length or height), and there was a strong preponderance of sizes between 56 and 58 mm. In 1926 the bulk of the oysters lie between 2 and $2\frac{5}{8}$ inches, and there is a strong preponderance of sizes between 58 and 60 mm. In both years, however, the preponderance of sizes at 56 to 60 mm. is due to the large proportion of dumps at these sizes. There is, however, a distinct diminution in the number of oysters of the larger sizes in 1926.

6. The population of dumpy oysters in 1926 is very nearly the same in size-distribution as in 1924 (see Fig. 3. p. 933), and indicates an average growth of only about 1 mm. in height per year (that is, in the direction of increase in dimension in a dorso-ventral plane; in this type of oyster the antero-posterior measurement is almost always less than the dorso-ventral one (see Orton, 1926, p. 66). It may be remarked, however, that dumpy oysters increase in dimension on the lateral axis to a much greater degree than normally growing individuals.

7. On the Banks the catches of legal oysters ($2\frac{1}{2}$-inch ring) were in December, 1926, rather less than one-third of similar catches ($2\frac{5}{8}$-inch ring) in November, 1924. On the Edges and in the River the catches of legal oysters in December, 1926, were one-third to one-fifth of similar catches in November, 1924.

8. On the Banks in December, 1926, the average catch of small oysters is less than half of the average caught in November, 1924, while on the Edges and in the River beds the average catch of small oysters in Decem-

ber, 1926, was rather more than half of the average caught per dredge-haul in November, 1924.

9. Thus in comparing catches in 1924 and in 1926, the legal oysters caught are seen to have diminished in the average haul from one-third to one-fifth, while the catches of small oysters have diminished to about a half. There is no doubt that the population of oysters has diminished in about the same ratio.

10. The recent input of oysters on the beds is represented by the brood

FIG. 3.

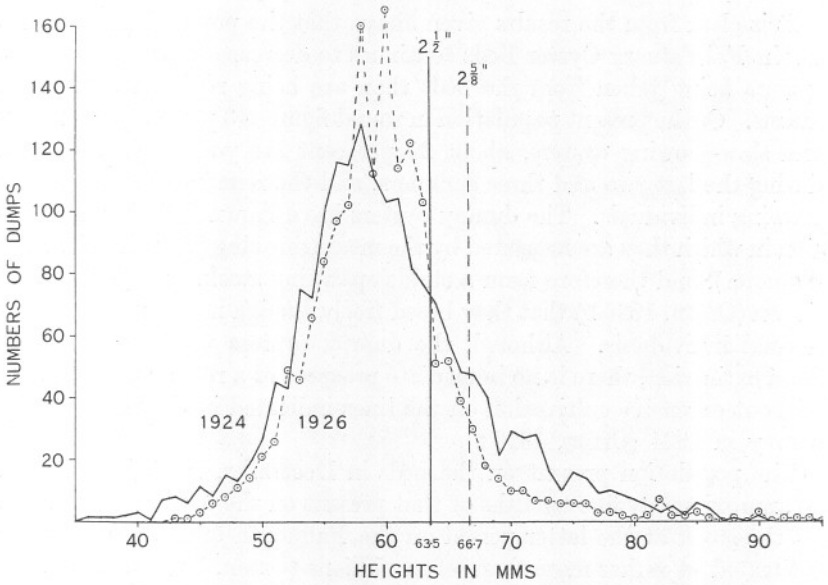

FIG. 3.—Graphs of the height (or depth)* of the shell in samples of dumpy and semi-dumpy oysters taken on the Truro beds, Upper Fal Estuary, respectively, in November, 1924, and December, 1926, indicating the extremely slow rate of increase in height (or depth) of the shell in this kind of oyster.

The graph of oysters taken, in November, 1924, is constructed from 1788 individuals taken from all parts of the beds, and that of the dumps taken in December, 1926, from 1,594 individuals also from all parts of the beds.

and spat, which constituted in December, 1926, about 18 per cent of the population. This recent input of oysters constitutes the addition made to the beds mainly in 1924, 1925, and part of 1926.

11. The outtake of oysters from the beds is represented by the catches of large (legal) individuals, which amounted to 20 per cent of the total catches even in December, 1926. As the number of large oysters dredged

* The height or depth of the shell in this kind of oyster is in 99% of the cases the largest dimension of the shell; occasional shells are, however, longer than deep, and in such cases the longest dimension is included in the graph.

was greater at the beginning of the dredging season in 1926 the outtake of oysters at that time was greater than 20 per cent.

12. The present outtake of oysters from the Truro beds is thus greater than the input during the last few years, since it is shown that the average catch of small oysters (in spite of the addition of brood and spat to the stock) was smaller everywhere in 1926 than in 1924. Therefore the beds are still being over-fished in the sense that a larger quantity of oysters is being taken from them than is being replaced by fresh stock.

CONCLUSIONS.

It is clear from the results given above that the population of oysters on the Fal Estuary Oyster Beds continues to decrease as a result of more oysters being taken from the beds than are being replaced by natural means. Of the present population in round figures 43 per cent are dumpy and slow-growing oysters, about 20 per cent are young oysters added during the last two and three summers, and the remainder are normally growing individuals. The dumpy oysters have grown little in the direction in which they are measured by the measuring ring ($2\frac{5}{8}$ inch in internal diameter), and therefore form a stable spawning stock, since it has been shown (Orton, 1926 b) that they breed freely though not so prolifically as normal individuals. Although the dumpy oysters will save the beds from extinction, there is no immediate prospect of a recovery of the beds without extensive cultivation on the lines indicated in the report of the survey in 1924 (Orton, 1926 a).

The population present on the beds in December, 1926, is estimated at approximately five-twelfths of that present on the beds in April, 1925. As the stock at the latter period on the Falmouth and Truro beds was estimated at rather more than seven millions (Orton, 1926 a, p. 74), the stock in December, 1926, in round figures, is estimated at three millions, since the Falmouth grounds were observed to be even less well stocked in December, 1926, than those under the administration of Truro.

Acknowledgment is gladly tendered to the Oyster Committee of the Truro Corporation for facilities for carrying out these observations.

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ORTON, J. H. 1926 a. Report on a Survey of the Fal Estuary Oyster Beds (November, 1924) with Notes on the Biology of the Oyster. Falmouth, 1926.

ORTON, J. H. 1926 b. On Lunar Periodicity in Spawning of normally grown Falmouth Oysters (*O. edulis*) in 1925, with a Comparison of the Spawning Capacity of normally grown and dumpy Oysters. Journ. Mar. Biol. Assoc., N.S., Vol. XIV, No. 1, 1926.

Notes on Shell-Depositions in Oysters.

By

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With a

Note on the Chemical Composition of "Chalky" Deposits in Shells of *O. edulis.*

By

H. O. Bull,

Student Probationer at the Plymouth Laboratory.

With 3 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE observations recorded in the following pages are regarded as preliminary studies—arising out of work on the bionomics of oysters, especially *O. edulis*—in the physiology of shell-deposition in these bivalves, and, it is hoped, they will be useful in the future in definite investigations designed to elucidate the bio-chemical factors and general conditions controlling shell-deposition.

The Distribution of Chalky Deposits on the Internal Face of the Shell of *O. edulis*.

During the examination of many thousands of shells of *O. edulis* the occurrence of chalk-like areas in a definite region on the internal face of the shell was observed to be almost constant. In these so-called chalky areas the crystalline nacreous layer of shell is replaced by material laid down in an apparently amorphous soft white mass, which is chalky in appearance and consistency. It was noticed that these deposits occurred mainly in the region of the exhalent chamber, but also in a position at the edge of the shell roughly opposite the palps and mouth. In order to obtain a definite expression of the situation of these areas, the internal faces of both valves in samples of shells were divided into arbitrary areas numbered 1 to 14 and lettered A to D, as shown in Fig. 1.

Samples of 100 shells from Thornfleet, West Mersea, and 100 from Brown Rose Bar, Fal Estuary, dredged respectively on October 7 and October 21, 1926, were examined and the distribution of the chalky deposits noted in each of the areas mentioned above, and in each shell.

Any area which contained either a large or a small deposit was recorded as showing a deposit.

The results of this analysis of the shells are given in Table I, p. 938, and are plotted to give the graphs in Fig. 2, p. 939. In Fig. 1, which shows the area-division of the shell, the areas numbered 1 to 9 fall in that part of the shell adjacent to the exhalent chamber, which is divided from the inhalent chamber—in the presumed extended condition of the gills—along a line represented approximately by the thick discontinuous curved line. The area divisions 10 to 16 bound the inhalent chamber; while the part of the shell in contact with the visceral mass of the oyster is divided into areas D, C, B, and in part A; but A is a meeting ground of visceral mass and both chambers, as also to a less extent is B. It was found that the deposits in area 1 to 9 were continuous whatever their extent, but those in 13, 14, and 15 were generally discontinuous and often occurred in small spots.

A glance at the graphs given in Fig. 2 shows that the chalky deposits are distributed in quite definite areas as follows:—

In a high proportion in 2 to 9 in the region of the exhalent chamber (left valve).

In a fair proportion in 7 to 9 in the region of the exhalent chamber (right valve).

In a fair proportion in 13 to 16 in the region of the inhalent chamber (left valve).

In a small proportion in 13, 14, and 16 in the region of the inhalent chamber (right valve).

But very rarely present in 10, 11, 12, and A, B, C, D, in both valves.

In the Mersea sample chalkiness is more general in occurrence but less in extent than in the Fal sample, a fact which is connected with the greater average age of the former sample, and variation due to different local physical conditions.

In both samples, however, the maximal occurrences of deposits fall in area 7 in both valves, and there is no doubt that the deposition of chalky shell-material begins in this locality, namely, about the middle of the exhalent chamber. The deposits in the right valve are less frequent and less extensive than those in the left, as is shown by the blackened areas—indicating deposits—in Fig. 1, below. Areas which had deposits mainly in 50 per cent or more of the shells (including also, however,

FIG. 1.

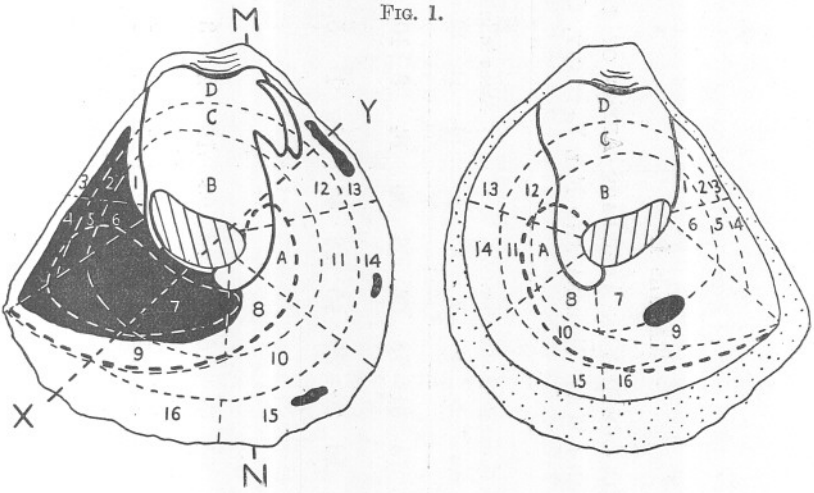

FIG. 1.—Diagrams of the right and left valves of the shell of *O. edulis*, showing

(1) the sub-division of the internal faces of the valves into arbitrary areas (separated by thin broken lines), and

(2) the mean distribution of the chalky shell-deposits on the internal faces of the valves in 100 shells from West Mersea, and 100 shells from the Fal Estuary, October, 1926 (age about 4 to 7 years).

The black regions denote the extent of the chalky deposits in areas affected in about 50 per cent of the shells.

The concentric region denoted by the dotted white line within the large black mass denotes the *extent* of deposits in this locality in about 30 per cent of the shells.

Areas numbered 1 to 9 form mainly the shell-boundary of the exhalent chamber on the sides.

Areas numbered 10 to 16 form mainly the similar boundaries of the inhalent chamber areas. D and C are adjacent to the visceral mass; B and A are mainly adjacent to parts of the visceral mass, but also abut on portions of both mantle chambers. The thick broken curved line marks the approximate dividing-line between the inhalent and exhalent chambers.

The visceral mass is shown in outline by a thick continuous line and the adductor muscle impression by close-set parallel lines.

The dotted region in the right valve shows the extent of the periostracal portion of this valve.

X–Y is the plane of section of the upper section shown in Fig. 3, p. 941.

M–N is the plane of section of the lower section shown in Fig. 3.

TABLE I.

PERCENTAGE FREQUENCIES OF CHALKY SHELL-DEPOSITS IN ARBITRARY AREAS OF THE SHELL OF *O. edulis* IN SAMPLES OF 100 INDIVIDUALS FROM WEST MERSEA AND FAL ESTUARY, OCTOBER, 1926.

	Areas in exhalent chamber.									Areas in inhalent chamber.							Areas adjacent to visceral mass.			
West Mersea—	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	A	B	C	D
Left valve . .	46	53	64	78	81	78	82	66	59	14	8	10	56	58	54	38	5	6	3	5
Right valve . .	12	14	8	16	30	25	45	18	42	6	1	5	27	23	3	20	3	2	1	2
Fal Estuary—																				
Left valve . .	23	34	42	61	75	76	93	68	63	15	2	3	34	39	38	34	8	1	1	1
Right valve . .	9	14	5	8	18	21	56	29	40	1	0	1	12	16	0	8	0	0	0	0

area 1, right valve, and area 7, left valve, in the Mersea sample, and areas 1, 2, 3, 13, 14, and 15, all of left valve, in the Fal sample, all of which areas had rather less than 50 per cent of shells with deposits) are included in the black areas shown in Fig. 1, and the extent of the deposition in 30 per cent of the shells, whose deposit in the exhalent chamber was small, is shown by the concentric white line within the biggest black area.

Deposits of chalky shell-material rarely occur in areas 10, 11, 12, A, B, C, D ; but when such do occur in these regions they form extensions of the main deposits, and occasionally may extend to cover the whole of the shell except the part touching the visceral mass, and in still rarer cases may cover the whole of the shell. This latter condition has been

FIG 2.

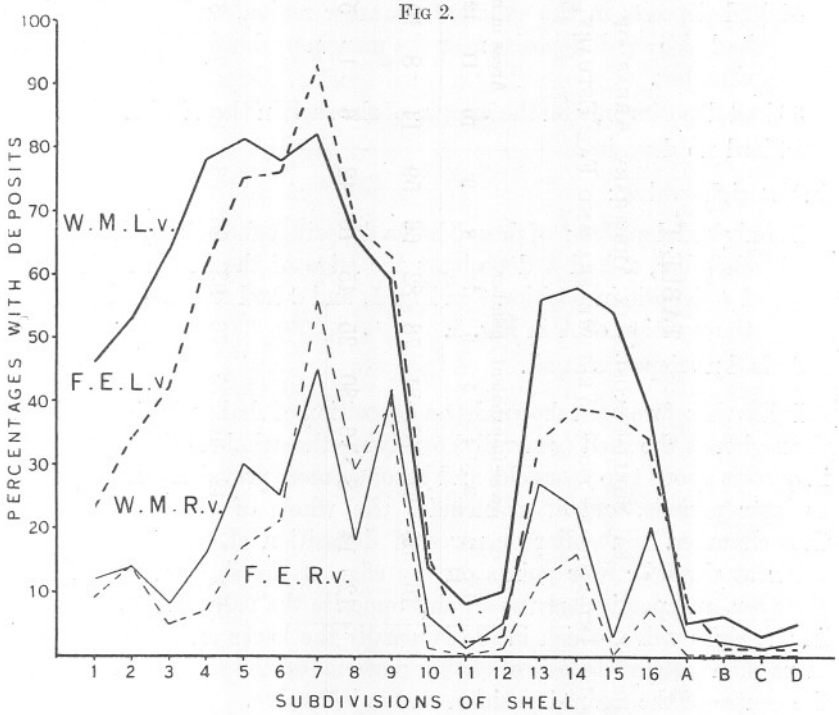

FIG. 2.—Graphs showing the percentage distribution of chalky deposits—of any extent—in arbitrary sub-divisions of the internal faces of the shell-valves in 100 *O. edulis* from West Mersea, and 100 individuals of the same species from the Fal Estuary (October, 1926).

W.M.L.V. The thick continuous-line graph denotes frequencies of chalky deposits in the left valve in the sample from West Mersea.

W.M.R.V. The thin continuous-line graph denotes similar right valve deposits in the West Mersea sample.

F.E.L.V. The thick broken-line graph denotes frequencies of chalky deposits in the left valve in the sample from the Fal Estuary.

F.E.R.V. The thin broken-line graph denotes similar left valve deposits in the sample from the Fal Estuary.

found to be unusually common in oysters dredged from 12 to 15 fathoms in the Parsons–St. Just Channels in the Fal Estuary.

In very young oysters—1 to 2 years old—chalky deposits occur fairly frequently and irregularly, but obviously in places where a thick layer of shell-material is required to fill up a space. In 2 to 3 year-old oysters shells with exposed deposits are rarer than in slightly older oysters from the same bed, and the deposits are less extensive, but the chalky areas are regular and show a concentration around the positions shown in Fig. 1 and especially in area 7.

In a sample of 91 left valves and 90 right valves, from mainly 2-year-old oysters dredged in July, 1925, on the South Shore at West Mersea, in the left valve,

41 had deposits in the exhalent chamber region, and a few of these had also small deposits near the margin of the shell in the inhalent chamber.

38 had deposits only on the margin of the shell in the inhalent chamber.

12 had no deposits.

In the right valve :

10 only had deposits ; of these 5 had a deposit at the edge of the exhalent chamber, 2 had a deposit at the edge of the inhalent chamber, 1 a deposit in position 7 in Fig. 1, and 2 had traces of deposits in the position of A in Fig. 1.

80 had no deposits at all.

It has therefore been shown that a deposition of chalky shell-material on the region of the shell (generally) overlying the exhalent chamber begins in oysters about two years old, and becomes more prevalent and extensive at later periods, and often includes the whole of the shell covering that chamber. Subsidiary centres of deposition of the same material occur at three or four points on the edge of the shell in the inhalent chamber, and particularly at a point opposite the palps in the left valve. In the right valve, which in life is usually the lower one, there is rarely more than a slight deposit of chalky material on the shell about opposite the centre of the main deposition on the left valve.

The chalky areas described above are visible on the internal face of the shell, and are sometimes powdery on the surface and in some cases covered with a nacreous deposit of shell-material. Sections of the shell show that a chalky deposit is not necessarily exposed on the face of the shell throughout life. A section of a shell with a large chalky area—taken in the plane X–Y, shown in Fig. 1—is drawn in Fig. 3, Y–X. In this section it is clear that successive chalky deposits—shown in black—occur alternating with varying thicknesses of nacreous deposits, and

that recent deposits are nearer the edge of the shell than older ones, which, however, would have had a similar relation to the edge of the shell in the younger individual. There may, therefore, during the life of an oyster, be a succession of chalky deposits, which occur in the same relative position on the shell with or without alternating deposits of a crystalline nature. It is hoped later to obtain chemical analyses of the chalky and crystalline material from the same shell, but the analysis of the chalky material as given on p. 953 shows that it has essentially the same composition as the nacreous material.

A Note on the Nature of the Chalky Deposit.

The chalky deposit is composed of very soft material, which easily powders when cut with a knife, and though apparently amorphous to

Fig. 3.

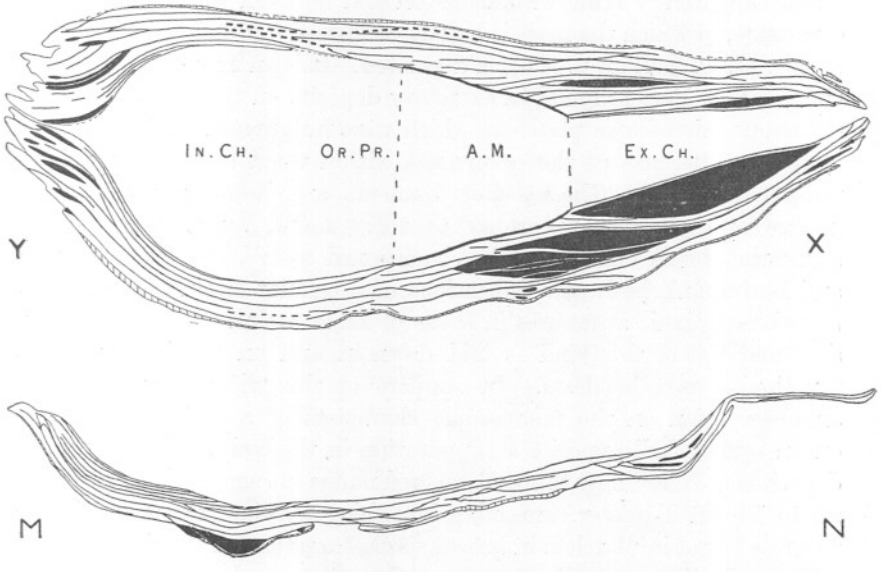

Fig. 3.—Sections of shells of *O. edulis*, with a polished surface, viewed as opaque objects.

Y–X. Sections of both valves of a shell from West Mersea, October, 1926, taken in the direction X–Y shown in Fig. 1. (Age unknown.)

N–M. Section of a left valve of a shell from the Fal Estuary taken in the plane M–N shown in Fig. 1. (Age estimated as certainly not more than five growth-years.)

Chalky deposits are shown in black.

Crystalline layers are shown only by their boundary lines.

Conchyolin deposits are shown as white areas, broken up by short close-set vertical lines, or, in Fig. 3, Y–X, in portions embedded in and overgrown by crystalline shell-material, by a thick black broken line.

In. Ch.=inhalent chamber in section.

Or. Pr.=region of oral process cut by the section.

A.M.=region of adductor muscle.

Ex. Ch.=exhalent chamber in section.

the naked eye, appears to have a microcrystalline structure when examined through a petrological microscope.* Carpenter (1844) noticed these chalky deposits on oyster shells in his work on shell-structure, but he considered that such deposits did not form part of the proper structure of the shell, and states merely that they are composed of particles of carbonate of lime deposited in a chalky or concretionary state.

The crystalline structure of this chalky material is, however, peculiar, and will need to be investigated in a research on its mode of deposition. When microscopic fragments are examined with a high power an apparently organic structure—similar to but finer than that figured by Carpenter (l.c. Figs. 20–21, Plate 9) in shells of *Lima scabra*—can be seen. This structure consists of exceedingly fine branching and anastomosing rod-like bodies—determined by Carpenter in *Lima scabra* as organic tubes—apparently lying in lamellæ on and between which the calcium carbonate, of which the mass is largely composed (see a chemical analysis by Mr. H. O. Bull on p. 954), is deposited. It is an interesting fact that Orton (1923, Part 1) found in excretory deposits on the shells of oysters numerous microscopic platelets, which were interpreted as degenerating leucocytes, because of the occurrence within them of small branching rod-like filaments. These latter filaments are, however, very similar in size and general appearance to those found contributing to the structure of the chalky deposits mentioned above, and as Carpenter and Bowerbank both saw indications of a cellular origin of the similar branching organic structures in shells of *Lima scabra*, it is possible that shell-material of this kind is laid down in and on special leucocytes functioning as calcoblasts. In support of this view may be added an observation on the microscopic characters of a calcareous deposit on an oyster shell opposite a suppuration in the body. The calcareous deposit was exceedingly thin and covered numerous small cells or platelets up to 10μ in diameter containing branching rod-like structures similar to those found in platelets in brown spots (excretion on the shell covered with conchyolin only). At the edge of the calcareous layer was a network formed by chains of living cells (10μ in diameter in the nucleated portion), and in the calcifying portion a reticular organic (conchyolin ?) network which was obviously the basis for the beginning of the process of calcification, as slight calcareous deposits could be seen lining the network on each side. Within the calcified portion of the membrane solid concretions were deposited. Jameson (1912) figures similar concretionary deposits.

Thus there is good reason to infer the existence of a process of formation of shell-material, in which some type of leucocyte is intimately concerned, and the large granular type, which varies in number in different

* We are indebted to Mr. Palmer for assistance in this determination.

oysters, may be especially suspected. The total quantity of leucocytes in oysters is subject to very great variation, as Orton (1923) has previously pointed out, and may be said to be generally small in oysters with well-grown shells, and great in individuals with slow-growing shells (dumpy oysters), and relatively great in individuals which have fairly recently spawned as females.

The Distribution of Chalky Deposits on the Internal Face of the Shell of *O. angulata*.

In the Portuguese oyster, *O. angulata*, deposition of chalky material on the internal face of the shell is much more prevalent and abundant than in *O. edulis*, and is also much more general. An analysis of the position of such deposits in this oyster has not been attempted because of their very general distribution, but it is probable that the region of the shell abutting on the main part of the visceral mass would be found to be less affected by the deposits than any other part. The flat (right) valve in this oyster has chalky deposits much more frequently than that in *O. edulis*. The general characters of these deposits in the Portuguese oyster are very similar to those in the very young *O. edulis*, that is, the deposits have always the appearance of filling up hollows, crevices, and other spaces. Indeed, they frequently seem to have been formed by the pouring out of a liquid matrix into a hollow with subsequent hardening. In the umbo of *O. angulata* there is normally in individuals of medium and advanced ages a deep recess. In a good proportion of cases, however, this recess is filled in with a plug of chalky shell-material which is smoothed off to run into the general contour of the adjacent shell.

Very deep shells of this species frequently have the bottom of the shell-cavity also filled in with a very thick similar deposit. In shells which have been bored—for examination of the internal organs—and have recovered after being put back in the sea, a heavy deposit of chalky material occurred in a few cases around the region of the boring. Such a deposit of chalky material never occurred in bored shells of *O. edulis*, although a much larger number of the latter were experimented upon.

In shells of *O. angulata*, therefore, chalky deposits are much more common and general than in *O. edulis*, and afford one more character of physiological difference between these two species.

On the Function and Causes of the Chalky Deposits.

The cause of the formation of chalky shell-material in the place of the normal crystalline layers has not been demonstrated, but we believe that the explanation now offered will lead to its satisfactory demonstration by experiment in the future.

The formation of soft shell substance, the chalky depositions herein described in the shells of *O. edulis*, is discussed by Southern (1916). After explaining the formation of chambers by the deposition of layers of crystalline shell-material by the epithelium covering the visceral mass of oysters which have recently spawned—a view shared by Orton and Worsnop (1923)—Southern states that: "In order to accommodate the renewed increase in size of the body at the approach of the succeeding spawning* season, the *gonadial cavity* is again enlarged by the rapid deposition of soft shell substance in that part of the shell which *surrounds* the gonadial cavity. The alternation of hard and soft layers of shell substance is clearly shown in sections of the shell. In young oysters and in large (old) oysters without chambers, the shell is relatively thin, with very little soft shell substance."

It may be observed from this quotation that Southern is discussing mainly the function of the soft shell substance, the chalky deposit, in *chambered shells*, while the writers are discussing the function of the same material mainly in normal shells, but it is submitted that the explanation offered of the occurrence of these deposits in normal shells will hold also for abnormal chambered ones. The argument advanced by Southern can best be understood by reference to Fig. 3, Y–X, p. 941. The gonadial cavity referred to is the space occupied by the visceral mass and is well shown in Fig. 1, while the space (Or. Pr.) shown in Fig. 3, Y–X, to the left of the line joining the dorsal margins of the adductor muscle impression constitutes only part of that cavity. If a section similar to this had passed through the hinge, the whole of the space to the left of a similar line would belong to the gonadial cavity. Southern states that the volume of this gonadial cavity (in chambered shells, but normal shells are similar in this respect) "is enlarged by the rapid deposition of soft shell substance in that part of the shell which *surrounds* the gonadial cavity."

This statement is, however, demonstrably inaccurate. Any thickening of the shell outside the gonadial cavity will merely decrease the volume of the mantle cavities, as a glance at the figures will show. In order to increase the volume of the gonadial cavity the valves of the shell must be made to separate more widely (since absorption of shell-material need not be considered) on the dotted line in Fig. 3, Y–X, when the shell is occluded. This divergence of the shells is normally effected by growth of the shell substance at the periphery remote from the hinge. In this regard it has been found that a new rim of shell on the left valve can be formed at a very rapid rate at the beginning of the growing season,

* The word "spawning" has been used to replace "spatting" in Southern's quotation, for the sake of clearness, as spawning, and not spatting, is obviously meant. The italics used in this quotation are the writers'.

which precedes the breeding season. One cannot observe new shell growth on the right valve from external inspection, but it is not unreasonable to suppose that new growth on that valve will occur simultaneously with that on the left. If shell growth occurs in both valves, then—but only then—will the valves diverge and the gonadial space be increased.

A temporary increase in the general shell space could be attained by simple relaxation of the adductor muscle, and a fairly effective closure of the shell could be made even under these conditions, owing to the fact that the edge of the right valve is not calcified (see Fig. 1), but consists of a somewhat extensive and elastic rim of periostracum. In the fully occluded valves the calcareous rim of the right valve fits well inside the rim of the left one, and may leave upwards to $1\frac{1}{2}$ centimetres of the latter covered only by periostracum in a shell 8 centimetres in length.

It is clear, therefore, that an oyster can quickly increase the volume of the occluded shell in the growing season, or at any time temporarily by relaxing the adductor muscle, but in the latter case the shell would not be fully occluded. Although divergence of the valves may be desirable to give the visceral mass room to enlarge as the gonadial products ripen, or fattening or growth occurs, it is also possible for this mass to expand anteriorly and to a less extent posteriorly—or sideways in the view of the shell shown in Fig. 1—without any alteration in the disposition of the valves.

The function of the soft or chalky deposits in the shell of *O. edulis* is therefore not that of increasing the size of the gonadial cavity.

It is submitted that the general character of the depositions in *O. edulis* and *O. angulata* show that the function of these deposits is to fill in rapidly depressions under the mantle, or secreting epithelium, which depressions cannot be maintained in the physiological state of the oyster at that instant, or which can only be maintained with loss of efficiency in functioning.

The general occurrence of amorphous deposits filling in unwanted space, as in the umbo and in deep depressions in the shell in *O. angulata*, in crevices and to bridge over crevices in the very young *O. edulis*, and in deep grooves in all ages of *O edulis*, indicate the function of reducing mantle space at a rapid rate. Nothing is yet known of the rate at which chalky deposits are laid down or when, but the thickness of the deposits in very young oysters—and in old ones—proves that the rate of secretion is rapid in comparison with that of nacreous shell.

Although the function of the deposits noted above seems clear—and the absence of contact of mantle with shell may be regarded as the stimulus which causes such deposits—the occurrence of the large mass of chalky material in the shell over the exhalent chamber in *O. edulis* presented at first a baffling problem, but we now believe that the explanation

of this deposit is the same as for others. The left valve in *O. edulis* is the convex one, and in life usually lies uppermost, and it is in this valve that the large chalky deposits occur ; in the right valve the deposit of the same material is smaller, and occupies a corresponding position, namely, round about the middle of the exhalent chamber. The part of the mantle which covers the chalky deposits consists of a large triangular thin sheet of tissue, which is capable of contraction and extension, and, no doubt, in the exercise of the normal functions of life—particularly in the evacuation of fæces—is constantly extended and contracted. It is suggested that during these movements the central portion of the mantle is restored to its position of close contact with the shell with difficulty, especially in shells in which the contour of the exhalent chamber is markedly concave. If this difficulty is a real one the mantle will tend to sag at a point opposite about the middle of the exhalent chamber, and may form a cavity at this point by a local exudation of liquid under the reduced (suction) pressure. Under these circumstances the conditions will be the same as those observed above, and the stimulus being the same, deposition of chalky shell-material begins and is continued until the contour of the shell is such as to permit the maximum of efficiency in the extension and contraction of the mantle. There are grounds for the view that a contour like that of the right valve, namely, very nearly flat, is the most suitable one, as the effect of the chalky depositions is to flatten out the contour, and some shells moderately flat in the region of the exhalent chamber do not develop chalky deposits at all.

When the chalky deposit has resulted in the attainment of an efficient contour, it ceases, and crystalline deposition should recur. If after nacreous material has been laid down over a chalky deposit there occur a general growth of shell at the periphery, the mantle will extend on to the new growth, and the conditions which stimulate the production of chalky shell-material may recur, moreover, as a shell is usually enlarged in a manner which continues an established mode of growth a recurrence of similar conditions in the spatial contour of the exhalent chamber is possible, and in this way may render necessary a fresh deposition of chalky shell-material.

The similar deposits at the edge of the shell in the left valve (areas 13 to 16 in Fig. 1, p. 937) which occur in hollows and crevices are capable of similar explanation to that given ; but these deposits often form a smooth ridge in this region of the shell, and may then be regarded as having consummated their function of producing a surface over which the mantle can be contracted and extended with a maximum of ease. An additional cause for the formation of these border deposits may also arise from the functions of the ciliated path on the mantle, particularly at the point where this path receives rejected food-masses from the palps.

There is therefore good ground for the view that all chalky deposits of shell-material are due, on the whole, to local unsuitabilities of the contour of the shell to the needs of the oyster, and that the deposits are made to adapt the shape of the shell to the changing needs. In the young oyster shell there frequently occur numbers of grooves and hollows, but these gradually become smoothed out during the course of life in the process of the formation of a shell which has everywhere a smooth and gradual contour.

On reading the preceding discussion on the function of chalky deposits of shell-material, Dr. Allen raised the problem: Why should *O. edulis* form such depositions when *Pecten varians*, which is present on the same beds in great abundance, does not form, or only very rarely shows, similar deposits? The answer to this question brings out a point of essential importance. *Pecten varians* settles in the post-larval stage with a fully formed shell, and merely attaches itself inside or on shells by means of byssus threads, consequently the kind of surface on which the post-larva settles exerts no influence towards modifying the growing Pecten shell, which accordingly develops normally in its specific shape. The corresponding facts with regard to *O. edulis* are quite different: the shelled larva settles on an object to which it cements itself at once by a deposition of shell-material. From this point of development for a considerable time—one to two years—onwards the shape of the object on which a young *O. edulis* has settled bears a very intimate relationship to and largely controls the shape of the young growing shell. Thus the shape of the young shell in *O. edulis* is variable, and is not subject to the same control by the organism as is the case in *P. varians*. Since the shape of the young shell is variable, and if a particular contour of shell in the adult is desirable for a maximum efficiency in functioning, it follows that modification of the contour of the growing shell by internal depositions will often be necessary to attain the desired end. In a similar way variations in shell-shape may be expected to result from moving oysters from one situation to another, for there can be no doubt that there is a general uniformity in shell-shape in a particular habitat, and that a variety of habitats may occur even within the boundaries of one set of beds. Too little is known at present, however, of the relation of shell-shape and other shell characters to the habitat (as Sir Ray Lankester has pointed out in letters) to render further discussion of the problem profitable. It may nevertheless be mentioned that in oysters, especially *O. edulis*, from muddy bottoms in shallow estuarine situations, there is a great tendency to a flat habit of growth with considerable puckering or fluting of the shell in a direction radial from the hinge, while in deeper water and some open water forms, as in Whitstable oysters, this puckering of the shell is greatly diminished. It is not improbable that these shell

formations, which are in turn determined by the shape of the mantle, are controlled largely by the feeding habits imposed by the local conditions, and we know very little about those particular feeding habits of oysters which are concerned in this problem. It is indeed probable that the feeding habits of young oysters are different from those of the adult. All these considerations, however, point to the probability of a changing contour of the shell, with the resultant necessity for the adaptation of the old contour to the needs of the new and changed conditions.

At the beginning of the investigation the chalky deposits in the shell adjacent to the exhalent chamber and those in the region of the palps were thought to be connected with the high degree of acidity of the juices in the alimentary canal of the oyster recently shown by Yonge (1926). It is now, however, regarded as unlikely that the high degree of acidity of the liquid passing through the exhalent chamber can have more than a minor significance, if any, in the process of deposition of chalky shell-material. When the physico-chemical reactions governing the deposition of this kind of material are known, it will be possible to reconsider the effect of the acid medium in the exhalent chamber. The occurrence of a slightly acid medium under the mantle and adjacent to the shell may, however, be an important predisposing factor in the formation of chalky material by attracting leucocytes to the locality.

It is hoped that the preceding discussion on the occurrence and distribution of amorphous deposits will lead to an investigation of the biological and physico-chemical controlling factors.

On the Discontinuity and Frequency of Deposition of the Nacreous Layers of Shell-material in *O. edulis*.

The section of shells of *O. edulis*, shown in Fig. 3, p. 941, are of interest in demonstrating (1) the discontinuity of the nacreous layers of shell-material, which are indicated by the blank spaces and separated and delimited by the sub-parallel lines, and also in showing (2) that more than one such layer may be laid down in one year of growth

The sections shown in Fig. 3 were made for the purpose of obtaining information of the disposition of the amorphous deposits, which are shown in black masses, and the discontinuity found in the nacreous layers has not been fully investigated. The opportunity is taken here, however, to make a few preliminary remarks on the subject. The section in Fig. 3, Y–X, passes through the exhalent chamber region, the adductor muscle impression, a portion of the gonadial cavity containing the oral process, and the inhalent chamber region, in the plane X–Y, shown in Fig. 1, p. 937. The main feature of the section is that there are more numerous layers of nacreous material at the edge of the mantle cavity of the shell

than in other parts, and there is evidence of the deposition of definite layers from the edge of the adductor muscle to the outer edge of the shell.

In a study of shell growth these observations will need to be followed up in order to understand the whole mode of shell formation. The sections in Fig. 3 were prepared by cutting the shell in two and grinding down and polishing the cut faces.

The section M–N is of a thin broody Falmouth shell, about 65 mm. in length and of an age of certainly not more than five summers' growth. The line of section in this case is through the hinge, alongside the anterior edge of the adductor muscle impression, and across the region of the inhalent chamber, that is, almost a median dorso-ventral section. The number of nacreous layers in the hinge region is twice the number of years of the estimated maximum age. There is therefore no doubt that more than one nacreous layer may be laid down in certain parts of an oyster shell in one growing season. It has already been noted (Orton, 1925) that two or more shoots of growth may occur at the edge of the shell in one season, and there is an indication in this section that internal layers of nacreous material are laid down in the hinge part of the shell at the same time as the shoots of shell at the edge.

In the year 1926 samples of Falmouth oysters were examined throughout almost the whole of the year, and distinct periods in spring and autumn were observed when new growth at the edge of the shell was general. New growth of shell occurred during the summer, but not in the same general way as in spring and autumn. It seems highly probable that these rhythmic growth periods are a normal feature in the life-history of the oyster, and are probably intimately related to the general physiological series of seasonal changes in the organism.

The probability that there occurs a minimum temperature below which calcareous material cannot be deposited in *O. edulis* has been previously discussed (l.c. *Nature*, 1925), and in 1926 some definite data on the problem were obtained.

In October, 1926, in the Fal Estuary growth of shell-material at the edge of the left valve occurred extensively on all grounds. On October 7th the general sea-temperature over the beds was 61° F., and fell during the month to a general level of 52° F. on October 28th. During November the temperature varied about 50° to 51° F., when only very occasional individuals were found with thin recent shell-shoots, although the October shoots were then still very obvious and hardening.

A similar general correlation between cessation of autumn shell growth and temperatures between about 60° and about 54° had previously been noticed without, however, definite general observations like those given above being possible. There is therefore in these observations support for the view that when sea-temperature falls to a point not less than

52° F. prismatic—and probably also nacreous—shell-material ceases to be laid down in *O. edulis*, and conversely when the temperature rises above some temperature level between 52° and 60° F., shell-deposition will begin again in the spring. Shell-deposition began in the Fal Estuary in 1926 at some time earlier than April 22nd, when new calcareous growth of shell had attained a median dorso-ventral length of a few to 9 mms. in 53 out of a total of 73 oysters with normal shells examined. Definite temperature observations were not being made in the Fal Estuary at that time, but there can be little doubt that the sea-temperature had risen to a level which would approximate closely to that at which growth ceased in the autumn. It is hoped, however, that it will be possible to follow and correlate the general occurrence of new shell growth and general temperature variations on these beds in the future.

On Deposits of Horny Material on the internal Face of Shells of *O. edulis*.

A very large proportion of the shells of *O. edulis* from the beds in the Fal Estuary have extensive depositions of horny material, which is regarded provisionally as conchyolin, on the internal faces of both valves, but mainly in the areas 6 to 12 (in the region of the inhalent chamber) in Fig. 1, p. 937. In a fair proportion of cases these deposits extend over the remainder of the region of the inhalent chamber and also over the shell in the locality of the exhalent chamber. Nacreous layers of shell-material may be laid down over previous conchyolin deposits (see Fig. 3, Y–X, p. 941), which remain visible for a time through the translucent nacreous layer or layers. It was found, however, that the conchyolin skins peeled off the shells in samples examined in late autumn, but samples examined during the summer months were not noticed to exhibit this peeling phenomenon, and as special attention was not directed at the time to the state of the conchyolin layers, seasonal observations will be required to confirm the observations.

It would seem, however, that the conchyolin deposition occurs mainly in the autumn towards the end of the shell-growing period. As conchyolin is the normal organic basis, and probably forms a matrix, for the deposition of nacreous shell-material, it would seem that at the period when conchyolin is deposited, the physico-chemical—and perhaps in some cases the general physiological—conditions are unsuitable for the completion of a phase in the formation of nacreous shell-material, which had been initiated but could not be completed, and as a result conchyolin alone is deposited. This view is in accordance with the fact that crystalline shell-material ceases to be laid down at the approach of winter—probably at some definite temperature epoch—and with the probability

that a general deposition of conchyolin alone occurs at the approach of winter. Further observations are needed to obtain definite seasonal data, but in the meantime it is clear that conchyolin formation may occur over the whole extent of the mantle and is not necessarily confined to a small layer of cells at the edge of the mantle where the normal external layers of conchyolin are produced to form the periostracum.

Whereas in the Fal Estuary oysters a proportion of over 90 per cent of the shells may have extensive conchyolin deposits on the internal face of the shell, it was found that a sample of shells from West Mersea in October, 1926, had only slight conchyolin deposits in the same situation in about 30 per cent of the shells.

Conchyolin depositions of this kind are certainly more frequent in Fal Estuary oysters than in samples from most of the beds from the Thames Estuary, a fact which appears also to be consistent with the view advanced above on the cause of the deposits, for sea-temperature falls much more rapidly between 60° and 50° F. in the Thames Estuary than in the Fal Estuary, so that a longer time for conchyolin deposition will be available in the latter locality than in the former. The occurrence of small membranes of conchyolin covering excretory deposits on the shell has been dealt with in some detail elsewhere (Orton, 1923); there is no doubt that these latter membranes serve a different function from the extensive conchyolin skins mentioned above, but they also show that conchyolin may be produced by the general outer surface of the mantle.

A Note on Pigmentation in *O. edulis*.

An additional feature of interest in connexion with the shell has been observed in some individuals of *O. edulis* from the Fal Estuary. In a small percentage of thin-shelled individuals—but in no other kind of oyster—it was noticed towards the end of the breeding season in 1925, and again in a few cases at the end of 1926, that black pigment had been laid down on the left side in the epithelium covering the visceral mass. It seems probable that the pigment may have been produced as a reaction to the penetration of the thin shell by certain actinic rays, for black pigment is abundantly produced on the edges of the mantle in oysters which there is every reason to believe have been situated so as to receive light rays.

The pigmentation of the mantle in samples of dredged oysters shows a very wide range of variation, which is probably correlated with the variation in incident light. A similar phenomenon has been noticed in *Cucumaria saxicola* and *C. normani*, whose tentacles become black when exposed to light, and in *C. saxicola* the skin becomes generally dusky black after prolonged exposure to light.

If some form of radiant energy can penetrate thin shells of oysters *in situ* in the water and produce a response in such a remote part of the body as the visceral mass, the phenomenon is probably worth further investigation.

SUMMARY.

The observations recorded form preliminary studies which it is hoped will be useful in special investigations on the physiology of shell-depositions in oysters. The distribution of chalky shell-deposits on the internal faces of the valves in young and old *O. edulis* and *O. angulata* has been studied, and its average distribution determined in shells of *O. edulis* of medium age from West Mersea and the Fal Estuary.

The distribution of this material in the shells of young *O. edulis* and in *O. angulata* is such that there can be little doubt that the function of the chalky deposit is to fill in rapidly grooves, hollows, and other spaces, which are inimical to efficient functioning in the changing needs of the individual.

In *O. edulis* of medium age large deposits occur regularly in the shell adjacent to the exhalent chamber and smaller ones on the border of the shell in the region of the inhalent chamber. The hypothesis is advanced that these regular deposits can be explained in the same way as those more easily understood by assuming that in a high percentage of shells of medium age, the contour of the shell in the region of the exhalent chamber and other parts is such that rapid extension and contraction of the mantle cannot be effected; deposition of chalky shell-material modifies this contour of the shell with certainty in some cases, but hypothetically in others, so that the mantle can be extended and retracted with a maximum of efficiency.

Sections of shells of *O. edulis* show that more than one layer of nacreous shell-material may be laid down in one growing season, and general field observations indicate that the normal number of nacreous layers deposited may be two or more in certain parts of the shell each growing season.

Two main periods of shell growth, i.e. growth of shell at the periphery of the left valve, were observed in the Fal Estuary in 1926; one in spring and one in autumn.

Observations are given which indicate that crystalline calcareous depositions cease in *O. edulis* at a temperature not less than and probably slightly above 52° F.

Conchyolin depositions on the internal faces of both valves in the form of extensive thin sheets are found in a very high percentage of shells

of *O. edulis* in the Fal Estuary, and in small areas in a fair percentage of shells from West Mersea.

A theory is advanced to explain these conchyolin deposits. Conchyolin can therefore be produced and deposited by the whole of the mantle lining the shell in *O. edulis*, as well as by the specialised cells at the edge of the mantle.

Black pigmentation has been observed on the visceral mass of thin-shelled *O. edulis*, a phenomenon apparently due to actinic rays penetrating the thin shell.

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A Note on the Chemical Composition of "Chalky" Deposits on the Shells of *O. edulis*.

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The "chalky" deposit consists of a white, impalpable powder. Microscopic examination showed that it was mainly exceedingly fine crystalline matter, and did not appear to be a precipitated substance. Its general composition is shown in the following table. The analysis was made on a mixed sample of the "chalky" deposit taken from four separate left

valves of *O. edulis* from the Fal Estuary, October, 1926. The approximate composition* is as follows :—

	%
$CaCO_3$	78·5
Water and organic matter . . .	19·2
Undetermined, including MgO, Na_2O, P_2O_5, SiO_2, So_3, Cl, and S. . .	2·3
	100·0

It is hoped, at a later date, to make detailed comparative analyses of the "crystalline" and "chalky" deposits of shells from different localities.

* The (water+organic matter) represents the loss on gentle ignition at a temperature below that causing decomposition of the $CaCO_3$, and weighed to a constant weight. Lime was determined in the usual way by precipitation as oxalate, weighed as CaO, and the result calculated to $CaCO_3$.

The Adsorption of Ions from Sea-Water by Sand.

By

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THE surface adsorption of molecules and ions of electrolytes by solid matter in a fine state of subdivision is a phenomenon of widespread and common occurrence in Nature, and its study an extremely important one. It plays a fundamental rôle in agricultural problems, the character of a soil being to a large extent governed by its adsorbing power for salts and non-electrolytes dissolved in the water which permeates it. From a technical point of view, its applications are numerous. The use of charcoal as a purifying agent is due to its high adsorptive power for impurities. The precipitation of colloids takes place through the adsorption of ions by them and the neutralisation of the electric charge they carry. The study of adsorption and its effects is a field in itself, and in the present paper only a brief résumé will be given, in introduction, of the subject of adsorption from solution.

Owing to the fact that adsorption is necessarily allied with surface effect, the study of adsorption phenomena is more or less confined to that branch of chemistry which deals with the physical and chemical effects of surface as opposed to mass. If any substance exists in a highly subdivided state, the surface presented is very large compared with the mass, and the laws governing the properties of surfaces come into play. All solids tend to condense or adsorb on their surface any gases, vapours, or ions in solution with which they may come into contact. Hence, when the surface of solid exposed is large compared with its mass, the tendency to adsorption, or surface condensation, is also very large. In the case of adsorption from solution, the possibility of adsorption of solvent must also be taken into account. If the adsorption of solute is greater than that of solvent, the adsorption is positive, the solution of necessity becoming more dilute; and, vice versa, negative adsorption results in a more concentrated solution, through preferential adsorption of solvent. When positive adsorption takes place from a solution containing more than one entity (such as a number of ions), the point arises as to what extent the adsorption is specific to each entity in the solution, that is, the extent to which the adsorption is selective. During research on the adsorption of various salts by blood charcoal, Osaka (1) found that the adsorption of

anions with the same base decreased in the order $I > NO_3 > Br > Cl > SO_4$. Rona and Michaelis (**2**) state the order of adsorption of anions by charcoal to be $OH > CNS > I > NO_3 > Br > Cl > HPO_4 > SO_4$, and of cations $H > Al > Ca > Zn > Mg > NH_4 > K, Na$. It should be mentioned that this adsorption order has been adversely criticised by Loeb (**3**), in his researches on protein adsorption, in which combination probably takes place according to the ordinary laws of primary and secondary valency. In the work of Rona and Michaelis, however, and in the present investigation, we are dealing with a simple inorganic adsorbing agent, and not a complex protein. Consequently, the adsorption depends on the mobility of the ion and the position in the electrolytic potential series, as well as on the valency (**4**).

Apart from the purely physical effects following upon adsorption, selective adsorption always connotes the possibility of chemical decomposition as a result of that adsorption. For example, if a substance adsorbs a base in preference to an acid, there will be a tendency for the salt of that base and acid to hydrolyse, the base then being adsorbed to a greater extent than the acid (**5**). Fuller's earth adsorbs the base from sodium chloride solution, rendering the filtrate acid to litmus. The well-known Permutit system of water softening is due to a chemical replacement of magnesium and calcium by sodium on filtration through specially prepared sands of the zeolite type.

Sea-water is a relatively complex solution containing the metallic ions sodium, potassium, magnesium, and calcium, and the anions sulphate, chloride and carbonate in more or less invariant proportions. It is a matter of interest, therefore, to investigate from the point of view of adsorption, the effect on the chemical and physical properties of such a solution, of percolation through and continued contact with sand, especially as the ions of calcium and magnesium, which are of recognised biological importance, are present in sea-water in a state of delicate equilibrium, so far as they exist as carbonate and bicarbonate, and, as shown by Atkins (**6**), require a relatively small alteration in pH to cause their partial precipitation.

Investigations of the salinity at various points in the circulation of the Zoological Society's Aquarium had revealed the interesting fact that a concentration of the saline constituents of the sea-water took place in the sand of the filter beds, where the water passes slowly through fine sand. The salinity in the filter beds (which was determined by carefully draining off a known volume of water from the sand and estimating the total solids at 180° C.), was 37·35 per mille. The average salinity of the water in circulation at the time was 33·7 per mille.

A weighed amount of the wet sand was next dried in a steam oven, and the water driven off estimated by weight. Knowing the normal

salinity of the water in use, it is easy to calculate the weight of solid matter which should be associated with it. The sand was then thoroughly washed with distilled water, and the total solids in the washings determined. In every case an increase in concentration was observed over the calculated normal value, due to positive adsorption by the sand particles. One instance is cited :—

From 116·423 grammes of wet sand, 17·4435 grammes of water were expelled. With this weight of water should be associated 0·6081 grammes of saline matter. Evaporation of the washings and estimation of the latter, however, indicated the presence of 0·7840 grammes of solid. This represents an increase in concentration of over 25 per cent. The point was further investigated by the author, and from the results of analysis, which are appended below, the conclusion was arrived at that this concentration was due to positive adsorption, brought about by the large surface exposed to the water by the sand particles.

Specific Adsorption of the Constituent Ions of Sea-water.

In the following experiments different varieties* of sand were used, but in order as far as possible to render the conditions of experimental procedure uniform, similar weights of each sand were employed in each experiment, and equal volumes of sea-water. The sand was treated with hydrochloric acid to dissolve small fragments of shell and carbonate particles, and finally washed free from chlorides with distilled water and dried in an air oven.

The first method adopted was to allow a known volume of sea-water to stand in contact with the sand for twenty-four hours, with regular shaking at intervals, and the supernatant liquid was subsequently withdrawn and analysed. The method, however, gave no conclusive results, as the adsorption was either practically nil, or else water and saline matter were adsorbed in equivalent proportions. This was probably due to the fact that relatively large volumes of water must be used in comparison with the quantity of sand. A percolation method was next employed, which at once gave evidence of positive adsorption of solute. The samples of clean dry sand were contained in glass jars provided with

* Experiments I and II were conducted with the original sample of sand from the Aquarium filter beds. This is a river sand from Leighton Buzzard, which has been in continuous contact with the sea-water for over two years. The sample in Experiment III was a marine sand collected in June, 1926, from the low tidal area of Port Erin bay, I.O.M. Experiment IV was undertaken with a fine silver sand on the high-water mark of Douglas beach, I.O.M., collected in June, 1926. Experiments were also conducted, the results of which are not given here, as they simply confirm the present ones, on another marine sand, the exact locality of which is not known, and on a fine silver sand from Bedfordshire. Unfortunately no samples have been obtained from the ocean bed, but it is unlikely that the results would differ appreciably from the samples studied, save perhaps in the extent of adsorption.

suitable outlets at the base, and sea-water allowed to spray over the surface at the rate of approximately 250 c.c. per hour. The filtrate was collected in fractions of 100 c.c., and submitted to analysis. Since the accurate estimation of calcium in the presence of magnesium is somewhat difficult, owing to the occlusion of magnesium in the calcium precipitate on separation, double precipitation of the calcium was carried out in the presence of ammonium citrate, according to the method employed by the author (**7**) in previous analyses. The estimation of the remaining constituents was carried out by the ordinary methods of inorganic analysis.

In all the cases investigated, percolation through sand was found to bring about a positive adsorption of solute, though the extent in many cases varied considerably with the sample of sand, and the volume of water filtered. Taken as a whole, the extent of the adsorption could not be termed very large, save in two cases, which are cited below (Tables III and IV). Though the amount of total adsorption differed, however, in every case, the individual adsorption of the constituent ions was specific, and was found to be a factor of the concentration, with the exception of the calcium and magnesium ions, which exhibited an abnormality which could only be accounted for by a chemical interaction and exchange of ions with the " active " adsorbing agent. A few representative experiments are given below.

Experiment I.

Sea-water of salinity 34·71 per mille was allowed to percolate through sand, and the first 500 c.c. of percolate collected and analysed. The pH before the experiment was 8·1.* and after percolation 7·9.

TABLE I.

Ion Constituent.	Sample before treatment.	Sample after percolation.
Sodium and Potassium	10·91	10·47
Magnesium	1·392	1·221
Calcium	0·4002	0·4100
Sulphate	2·632	2·463
Bicarbonate	0·1500	0·1460
Chloride	19·23	18·04
	34·71(00)	32·75(00)

It will be observed that although the total adsorption is not large, all the constituent ions have undergone a more or less proportional individual adsorption, with the exception of calcium and magnesium, which exhibit abnormality, the concentration of calcium in the percolate,

* Corrected for salt error

in fact, being greater than in the original solution. The abnormality is more clearly brought out in Table II, which is a comparison of the actual results obtained, with those calculated on the basis of an adsorption of each constituent ion in the proportion equivalent to the total adsorption, i.e.

$$C_{calc.} = \text{Original concentration} \times \left(\frac{32{\cdot}75}{34{\cdot}71}\right)$$

TABLE II.

Constituent Ion.	$C_{calc.}$	$C_{observed.}$
Sodium and Potassium .	10.29	10·47
Magnesium . . .	1·313	1·221
Calcium	0·3779	0·4100
Sulphate . . .	2·4840	2·4630
Chloride . . .	18·13	18·04
Bicarbonate . . .	0·1420	0·1460
	32·74(00)	32·75(00)

Experiment II.

The rate of percolation and other conditions of experiment were unaltered, but only the first 100 c.c. of the percolate were collected and analysed. The pH remained practically unaltered throughout the experiment.

TABLE III.

Ion Constituent.	Sample before treatment.	Percolate.	$C_{calc.}$
Sodium and Potassium .	10·91	9·51	9·22
Magnesium . . .	1·392	1·070	1·176
Calcium . . .	0·4002	0·3921	0·3382
Chloride . . .	19·23	15·96	16·25
Sulphate . . .	2·632	2·270	2·224
Bicarbonate . . .	0·1500	0·1260	0·1270
	34·71(00)	29·33(00)	29·33(00)

In the present case the extent of total adsorption is over 15 per cent. Each constituent ion has been adsorbed, and the agreement between $C_{observed}$ and $C_{calc.}$ is fairly good in the case of sodium and potassium, sulphate, chloride and bicarbonate ions; but differs appreciably for calcium and magnesium, the observed value for the former being much too high, and the latter apparently having undergone a greater adsorption than the remaining ions.

Experiment III.

A sample of fine marine sand was employed, and sea-water of a slightly lower salinity was allowed to percolate through at the rate of about 250 c.c. per hour. The first 100 c.c. were submitted to analysis.

TABLE IV.

Ion Constituent.	Sample before treatment.	Percolate.	$C_{calc.}$
Sodium, Potassium	10·45	9·47	9·30
Magnesium	1·333	1·085	1·185
Calcium	0·3834	0·3736	0·3409
Sulphate	2·521	2·300	2·242
Chloride	18·42	16·20	16·38
Bicarbonate	0·1440	0·1320	0·1280
	33·25(00)	29·56(00)	29·57(00)

The results offer a close parallel with those obtaining in the previous experiment. The pH altered from 8·0 to 7·7, indicating a trifle more acidity.

Experiment IV.

The same procedure was adopted as in the previous experiments, but the sample of sand employed adsorbed very little of the constituent electrolytes in the water. The results of analysis are important, however, as the same phenomenon was observable in the case of calcium and magnesium as in the previous cases, the concentration of calcium in the percolate, in fact, being higher than in the original solution.

TABLE V.

Ion Constituent.	Sample before treatment.	Percolate.	$C_{calc.}$
Sodium, Potassium	10·41	10·29	10·20
Magnesium	1·330	1·150	1·303
Calcium	0·3820	0·4070	0·3741
Sulphate	2·5140	2·470	2·462
Chloride	18·40	18·04	18·02
Bicarbonate	0·1440	0·1420	0·1410
	33·18(00)	32·50(00)	32·50(00)

DISCUSSION OF RESULTS.

In the preceding tables, a comparison between the concentrations of each constituent ion after percolation and the concentrations calculated on the basis of a proportional adsorption of each ion, that is, between C_{actual} and $C_{calc.}$ indicates the comparative normality in the adsorption of sodium and potassium, sulphate and chloride ions, the discrepancy apparently lying between the ions of calcium and magnesium. Since the concentrations of the respective ions in sea-water are widely divergent, it is unlikely that the order of physical adsorption of the ions (in the absence of chemical interaction with an *active* adsorbing agent) will more than approximate to that of Rona and Michaelis (loc. cit.). If, however, the adsorption be purely physical, it is dependent on *a* the concentration of the adsorbed ion, *b* the nature and amount of the adsorbing agent, *c* the temperature, and *d* the rate of percolation; *b*, *c*, and *d* are constant throughout each experiment. Hence it is possible by dividing the amount of adsorption, *x*, of each constituent ion, by its concentration, *c*, to obtain a rough measure of the order of adsorption of the ions in sea-water, and to compare the order obtained with that of Michaelis and Rona. The ratio x/a is given in the following table.

TABLE VI.

Ion Constituent.	Expt. I x/a.	Expt. II x/a.	Expt. III x/a.	Expt. IV x/a.
Magnesium . .	0·123	0·23	0·188	0·134
Sodium, Potassium .	0·040	0·13	0·094	0·012
Calcium . . .	—0·024	0·02	0·026	—0·060
Chloride . . .	0·062	0·17	0·120	0·019
Sulphate . . .	(0·064)	0·14	0·087	0·016
Bicarbonate . .	(0·027)	0·16	0·083	0·014

It is apparent from the above table that the order of adsorption is the same in each case, viz. $Mg > Na,K > Ca$, and $Cl > SO_4, HCO_3$. For the anions, this is in agreement with the observations of Rona and Michaelis (loc. cit.) on the adsorption by charcoal of anions attached to the same cation. The rule breaks down with the cations, however; Rona and Michaelis finding the order $Ca > Zn > Mg > NH_4 > K,Na$. We find in the present case that the calcium ion is adsorbed to a far less extent than magnesium ion. In sea-water, both these ions exist in combination with the same anions—chloride and carbonate—and, to a less extent, with sulphate ion, hence the rule of Rona and Michaelis should hold, if the adsorbing agent were inert.

It must be remembered, however, that the work of Rona and Michaelis was undertaken with charcoal as the adsorbing agent. Charcoal may

be termed inert, in so far as it is incapable of discharging any ions into the solution in contact with it. Many adsorbing agents, it is well known, are active, and can discharge into solution either anions or cations. In this case ionic adsorption and interchange take place. As an example may be cited the absorption of methylene blue hydrochloride by silicates :—

Calcium silicate+methylene blue hydrochloride=methylene blue silicate +calcium chloride,

the net result being the replacement of one base by another and the passage into solution of calcium as calcium chloride. The interaction between Fuller's earth and neutral sodium chloride solution, already mentioned, is also relevant, on account of the alternative theory of Bancroft (**8**) to the hypothesis of ionic interchange. The sodium ions in the solution adsorbed by the Fuller's earth have, according to Michaelis, been replaced by hydrogen ions from the earth, as the indirect result of the liberation of calcium ions. According to Bancroft, if a salt undergo hydrolysis in solution, according to the equation :—

$$M'+X'+H_2O \rightleftharpoons M'+OH'+X'+H',$$

and the acid H'X' is selectively adsorbed, hydrolysis will proceed until equilibrium is attained. In the case of Fuller's earth, the hydrochloric acid formed is adsorbed, and an alkaline solution of sodium hydroxide left. The two hypotheses are consequently at variance. Rona and Michaelis (loc. cit.), after examination of various cases of adsorption, came to the conclusion that the mechanism was simply one of ionic interchange and not of promoted hydrolysis.

In the present case we are dealing not with compounds consisting of an organic acid or base combined with a simple electrolytic anion or cation, such as methylene blue hydrochloride, but with the adsorption of simple electrolytes ; and all the evidence points to the fact that the adsorbing medium is not in all probability an inert one, and if Bancroft's theory is correct, the possibility remains of a promoted hydrolysis in sea-water following adsorption. On the other hand, the mechanism may be one of adsorption accompanied by simple ionic exchange.

It is obvious from the results that whereas the remainder of the ions in the sea-water have undergone simple physical adsorption, the calcium and magnesium have entered into a chemical reaction. Promoted hydrolysis has evidently not taken place, as the liberated H' ions or OH' ions would render the fact apparent by the change of acidity of the percolate. The pH of the solution, however, has not changed sufficiently to warrant the conclusion that hydrolysis is appreciable. It seems certain, therefore, that the relatively small adsorption of calcium ion from the sea-water is due to ionic exchange between magnesium and the calcium salts contained in the sand (**7**). In order to investigate the mechanism more closely

experiments were carried out on the adsorption of each constituent ion from separate solutions containing the ion in the absence of the remainder. Each solution was made up of such a strength that the ion under investigation was present in roughly the same concentration as in sea-water. The first 100 c.c. of the solution was collected after percolation under the same conditions as before.

Sodium and Chloride Ions.

Since these ions form by far the largest portion of the ionic constituents of sea-water, and exist in it as sodium chloride, a solution of the latter was used of strength 26·66 grammes per litre. The total solids were estimated before and after percolation, the chloride ion determined by titration with standard silver nitrate solution, and the sodium by conversion into sulphate. Analysis also showed the presence of calcium in the percolate.

Constituent.	Concn. in gm. per litre before percolation.	Concn. in gm. per litre after treatment.	$C_{calc.}$
Sodium . .	10·48	8·63	8·62
Chloride . .	16·17	13·24	13·30
Calcium . .	—	0·065	—
Total Solid .	26·65	21·935	21·92

Magnesium.

A solution of magnesium sulphate was employed containing a concentration of magnesium ions of 1·412 grammes (approx.) per litre of solution, and submitted to treatment. The concentrations of magnesium ions before and after the experiment were respectively 1·413 and 1·139 grammes per litre. A positive adsorption had consequently taken place of 0·274 grammes per litre. Calcium was also found in the percolate in the concentration of 0·0725 grammes per litre.

Sulphate Ion.

Magnesium sulphate solution was again employed, of such strength that the sulphate concentration was 2·632 grammes per litre. After percolation the concentration was 2·213 grammes per litre, indicating a positive adsorption of 0·419 grammes per litre of solution.

Calcium Ion.

A solution of calcium chloride containing 0·403 grammes of calcium per litre was submitted to percolation. The calcium ion concentration by analysis before and after the experiment was estimated as 0·401 grammes and 0·383 grammes per litre respectively. Positive adsorption therefore takes place from a solution of pure calcium chloride.

Bicarbonate Ion.

Since practically all the excess base in sea-water exists as bicarbonate, the results in the preceding tables have been expressed as such, the actual carbonate ion being negligible. It is somewhat difficult to reproduce in individual solution the delicate balance of calcium and magnesium bicarbonates as they exist in sea-water; but by making up a solution of magnesium sulphate, calcium chloride, and a few drops of sodium carbonate, saturating with carbon dioxide gas, and, finally, removing the excess of the latter by blowing air through the solution, a medium of pH 7·7 was obtained. The bicarbonate was estimated before and after percolation by titration with 0·01 *N* hydrochloric acid, using bromocresol purple as indicator, and the concentrations found to be 0·1606 and 0·1411 grammes per litre respectively.

The ratio x/a has been calculated for the adsorption from individual solution, and the order of adsorption agrees with that found for sea-water viz. Mg(0·19)>Na,K(0·13)>Ca(0·045); and Cl(0·18)>SO_4(0·16)>HCO_3 (0·12). From the experimental data it is seen that individual solutions containing sodium and magnesium carry down with them calcium ion, the larger proportion being attributable to the magnesium. On account of the relatively high concentration of sodium chloride in sea-water, the small exchange with sodium is scarcely noticeable from the alteration in the concentration of sodium ion, but is easily detectable in the case of magnesium. If the amount of calcium brought down with sodium and magnesium be subtracted from the concentration of calcium found in the percolate, calcium assumes its proper position in the adsorption order of Rona and Michaelis. The cases cited above are representative of a number of experiments carried out on various sands; in every sample examined the concentration of calcium ion in the percolate was decidedly in excess of the calculated value; in fact, where the adsorption of the remaining ions was practically nil, the concentration of calcium ion was in excess of that in the original sea-water sample. Magnesium was invariably low. This exchange does not cease when the adsorption of the remaining salts has reached a limit. It cannot be due to the solution of particles of calcium carbonate in the sand, as the preliminary treatment of the sand with acid removes these. Sands, however, contain a certain quantity of silicates and alumino-silicates of calcium (**9**), and it is extremely probable that it is with these radicles that the exchange takes place, after the following manner:—

Calcium ortho-silicate
Calcium meta-silicate
Calcium alumino-silicate } + sodium chloride = { Sodium ortho-silicate
Sodium meta-silicate
Sodium alumino-silicate } + calcium chloride.

Calcium ortho-silicate
Calcium meta-silicate
Calcium alumino-silicate
} + magnesium chloride = { Magnesium o-silicate
Magnesium m-silicate
Magnesium al-silicate
+ calcium chloride.

Calcium o-silicate
Calcium m-silicate
Calcium al-silicate
} + magnesium bicarbonate = { Magnesium o-silicate
Magnesium m-silicate
Magnesium al-silicate
+ calcium bicarbonate.

The hydrolysis of the calcium chloride formed is very slight, and the quantity brought down small, hence the alteration in pH of the solution is also very slight, especially as the buffer action of sea-water is large on account of its bicarbonate content.

Summarising, the results show that the adsorption of the electrolytic constituents of sea-water by sand is small, and is perfectly normal, with the exception of a small basic exchange between calcium and magnesium. Though the results perhaps have more interest from a chemical point of view than a biological one, they have doubtless a slight bearing on the delicate calcium-magnesium-bicarbonate ratio in sea-water, which constitutes the alkaline reserve, and may be one of the contributory causes of the deposition of calcium carbonate by inorganic processes, as opposed to biological. Just as the addition of carbonate ion to a saturated solution of calcium carbonate in presence of solid calcium carbonate will precipitate the latter, the addition of calcium ion will have the same effect. This will be seen by the following line of argument :—

By the Law of Mass Action $\frac{[Ca]\,[CO_3]}{[CaCO_3]} = K$

Since in presence of solid calcium carbonate $[CaCO_3]$ is a constant,

$$[Ca]\,[CO_3] = K_1.$$

Any addition of calcium ion to the solution will cause a corresponding depression in the concentration of CO_3 ion, in order to keep the solubility product constant. This can only be effected by the precipitation of calcium carbonate. In tropical waters, for example, where the pH is high, and calcium carbonate is already present as coral or other calcareous deposit, a very slight increase in calcium ion concentration of the water by contact with and constant percolation through sand will cause a corresponding amount of precipitation of calcium carbonate from the water. The amount precipitated in this manner may be very small, but it is probably one of the indirect causes of inorganic deposition of calcium carbonate. In temperate zones, however, for large bulks of water, the adsorption and exchange is too small to cause any appreciable difference in the concentrations of calcium and magnesium in the water, and certainly does not promote sufficient hydrolysis to alter the pH of the medium unduly.

The adsorption of small variable constituents such as silicate and

phosphate is of importance, as the concentrations of these ions in ocean waters may be correlated with the seasonal variations in diatom and plankton crops (**10**). The work is at present under investigation.

In conclusion, the author wishes to express his indebtedness to Dr. P. Chalmers Mitchell, Secretary of the Zoological Society, for helpful suggestions and advice on the subject.

SUMMARY.

1. The ions present in sea-water are normally adsorbed by sand.

2. Percolation of sea-water through sand causes a slight abnormality in the concentrations of calcium and magnesium ions, due to the fact that sand is not an inert adsorbing agent, but is capable of discharging calcium ions into the water in exchange for magnesium and sodium.

3. The extent of adsorption and exchange is insufficient to cause hydrolysis and alteration in pH if the bulk of the sea-water is large.

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Observations and Experiments on Sex-Change in the European Oyster (*O. edulis.*)

Part I. The Change from Female to Male.

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With 4 Figures in the Text.

CONTENTS.

SECTION A. INTRODUCTION.

Observations indicating a change of sex in the European oyster (*O. edulis*) from female to male have been made by many naturalists in the past, and especially by Davaine, Möbius, and Hoek. The latter states (1883, p. 235) that individuals after spawning as females begin to produce sperm. Later Hoek (1902, Table 7, p. 175) gave details of the microscopic examination of the gonad of eight individuals which were carrying larvæ in the mantle cavity, and although in some of these cases Hoek found only scattered clumps of germ-cells, while in others abundant sperm, he confirmed his previous opinion that sperm-production begins after an individual has spawned as a female. Möbius (1877, p. 11, and 1883, p. 693) also found ripe sperm in blacksick oysters, but no sperm in whitesick ones. As both Hoek and Möbius held the view that individual oysters (*O. edulis*) function after the manner of one sex or the other at the moment of spawning, they concluded that a change of sex occurred from female to male at some time after the act of spawning as a female.

Other naturalists, of whom Lacaze-Dathiers may be cited, had observed hermaphrodite individuals, and disagreed with those who contended the general unisexuality of individuals, while Hoek himself, in a later work (1902, p. 174), records fairly high percentages of hermaphrodites; thus considerable confusion occurred in the literature as to what are the actual sex-phenomena in this species. This confusion persisted down to recent years, and is well brought out by Spärck in a recent review of the literature (1924).

The present writer was attracted to this problem by noticing the rapidity with which an oyster which had recently spawned as a female attained a condition—with the gonoducts full of ripe sperm—ready to spawn again as a male (1921), and from a review of the conflicting views found in the literature arrived at the conclusion that nothing less than a collection of facts and definite experimental results would offer critical evidence of the sex-conditions existing in *O. edulis*. A change of sex from male to female was inferred by many workers, and Hoek (1883, p. 235) states that in his opinion a class of individuals function as males, and afterwards—but only in the following year—function as females, and at once remarks, "toutefois nous n'avons point la preuve que cela doive nécessairement arriver." In 1921 (loc. cit.), the present writer began experiments to obtain the proof which Hoek saw was necessary, and later (1924) was able to give a preliminary report of experiments which proved the change of sex from male to female in a small proportion of cases. At about the same time Spärck (1924), who had been

experimenting on similar lines, was also able to report the observation of a change of sex from male to female in three individuals.

A change of sex from male to female in all young individuals, i.e. protandry, has also been a popular conception for many years, but the writer has shown (1922) that the evidence for this view is not satisfactory, and will be difficult to obtain, nor has the matter been advanced critically by Spärck's recent work in the Limfjord (1924). These subjects may be discussed later, when the data accumulated have been presented.

In order to obtain definite information on the problems of sex-change in the oyster it was decided :—

(*a*) To examine the living tissues, or if necessary in some cases microscopic sections also, of 1000 female-functioning oysters, at about the time of spawning and at various periods afterwards, from as many different localities as possible, and to note the condition of the gonad with regard to the production of sex-elements.

During the years 1920–26 more than 1000 such individuals have been examined, and the results are given and discussed herein, but an extended discussion of various aspects of the work is necessary before the results obtained can be approached in a logical manner.

(*b*) To isolate in cages in the sea individuals proved to be males at the instant of examination—by tapping the gonad through a boring in the shell—and to re-examine the same oysters at successive periods for female spawning and ripe female individuals, which must therefore have undergone sex-change from male to female.

A number of experiments on these lines have been carried out, and will be discussed later in Part II of this work.

(*c*) To isolate in cages in the sea female-functioning individuals carrying spawn with a view to their examination at later dates, for

(1) individuals which might again be found carrying eggs, embryos, or larvæ, and

(2) the state of the gonad at a definite epoch in the (presumed) sex-cycle.

Experiments in this category are noted in Table IV, but will be discussed later in Part II.

Material and Methods.

Oysters in spawn have been obtained from most of the beds in the South of England (see below) through the courtesy of the owners and managers of the beds. The opportunity of thanking the owners and their assistants given in the following list is here gladly taken.

Owners of Beds.	Assistants.
Tollesbury and Mersea Native Oyster Co., R. Blackwater	Mr. Louis French.
Corporation Oyster Committee, Truro Beds, Fal River and Estuary	Mr. E. Searle.
Corporation Oyster Committee, Falmouth Beds, Fal Estuary	Mr. C. May.
Seasalter and Ham Oyster Co., Whitstable, Thames Estuary	Mr. E. Luckhurst.
Duchy Oyster Farm, Helford River, Cornwall	Mr. S. Hodges.
Oyster Beds, Burnham River, by courtesy of	Mr. E. Luckhurst.
Yealm Oyster Fisheries, River Yealm, near Plymouth	Mr. J. Kingcome.
*Saltash Oyster Beds, River Tamar, near Plymouth	—
*Public Beds off Swansea, S. Wales	—
*Public Beds, Isle of Wight	—

A good deal of the valuable material examined on the beds at West Mersea was obtained when carrying out experiments subsidised by a Government grant from the Royal Society. Without this grant the earlier experiments on sex-change herein recorded could not have been carried out.

Oysters in spawn were obtained in various ways: from samples sent by post; individuals found "sick" on the beds and forwarded to Plymouth; from the examination of thousands of individuals in the Tollesbury and Mersea Company's stores; from the examination of samples on the shore adjacent to the working oyster-dredgermen, especially at Falmouth, in order to open the oysters with the least possible delay after their capture. In this way were obtained oysters carrying embryos from the unsegmented—but mitotically dividing—egg, through a great variety of stages of development to the fully formed shelled larva ready for independent life in the sea. The age of embryos and larvæ in various stages has been determined approximately by observation and experiment. Since a series of individuals was obtained carrying a graded series of spawn with regard to age, so also was obtained from the parent a series of gonads with regard to age, reckoned from the time of the act of spawning as a female. In such a series of gonads of approximately known age (as defined) the condition of the sex-elements, and especially the male elements, was carefully noted in each individual and recorded in tabular form, as shown in Tables IV and IX, pp. 999 and 1025. In this way the age of the gonad—reckoned from the time of the last female-spawning

* I am indebted to Mr. F. S. Wright as the representative of the Ministry of Agriculture and Fisheries, London, for samples from these beds.

act—is determined from the (approximately) known age of the embryos or larvæ carried by an individual, and can be correlated with the state of development of the male sex-elements. It will be seen from the results discussed later that there is a general progressive development of sperm from the first day of the female-spawning act.

Spermatogenesis.

In order to determine the condition of the gonad with regard to the development of male-elements, sperm, it is necessary to know the major details of spermatogenesis. The complete details of spermatogenesis in the oyster are badly needed and not yet known, and would well repay study. Hoek, however, as long ago as 1883, followed the main divisions of the sperm-mother cell to the production of a sperm-ball or sperm-morula. In an abstract of Hoek's paper, Bourne (1890) translates that "the minute mother-cells of the spermatozoa have a diameter of scarcely 8μ, they stain deeply with alum carmine and have dark granular contents and a small nucleus. The spermatozoa are developed from them as follows. In each cell after the division of the nucleus, the cell-body divides into two portions. Of these one is destined to give rise to numerous spermatozoa, the other seems to serve only as a provisional connexion between the developing spermatozoa and the wall of the follicle. The former cell grows rapidly, and the nucleus subdivides rapidly and repeatedly until a large cell is formed 25–30μ, containing 40 to 50 nuclei. Each nucleus is about 4μ in length. At this stage the whole structure looks like a club of which the swollen part is formed by the other derivative of the primitive cell. At this stage the multi-nuclear cell becomes separated from its peduncle. Its nuclei continue to subdivide, and become darker and more opaque. Finally, the mother-cell becomes entirely developed into spermatozoa derived from the subdivided nucleus, but one cannot explain precisely the steps by which the smallest nuclei are transformed into spermatozoa."

In contradistinction to the characters of the sperm-mother cell, Bourne, in the same abstract, shows that "in the youngest stage observed the ovum of the oyster is a little cell 20–24μ in diameter, flattened on the side of the canal wall and rounded on its free surface. The protoplasm of the cell-body is feebly granular; the nucleus is large, spherical, and has a highly refringent single nucleolus of moderate size. The youngest ovules pass by insensible gradations into the more advanced, and those again into the mature ova."

Hoek therefore shows that from a very early stage developing spermatogonial aggregates can easily be distinguished from a young ovum, since even the youngest ovum seen by Hoek at 20–24μ had a well-marked nucleus and nucleolus, while a sperm mother-cell begins to divide when

only about 8μ, and contains 40 to 80 nuclei when 25–30μ at a size a little bigger than the smallest ovum seen by Hoek.

It will be noted that Hoek does not give any final limit to the size of the ripe sperm-morula, that is, the stage at which all the spermatozoa in one subspherical mass are fully developed and have tails. The reason is simple ; there is great variation in size of the ripe sperm-morula from subspherical masses 50 or 60 to 80μ in diameter to irregular cylindrical masses up to 110μ long by 40μ or more in diameter. It is not improbable that the masses developed from different mother-cells may fuse in groups of two or more.

In the fresh condition it is easy to distinguish young spermatogonial aggregates when about 20μ in diameter and containing about 10 cells, and identification is only difficult when there are only about 4 to 8 daughter-nuclei at sizes of about 10μ to 14μ. In these latter cases microscopic sections are necessary to confirm observations on the freshly teased gonad. There is, however, an outstanding appearance of living developing sperm-morulæ, which makes it a very simple matter to distinguish them under the microscope from ripe sperm-morulæ, namely, the clear translucent appearance of the former up to the stage in which the tails of the spermatozoa may occasionally appear, and the dark granular appearance of the sperm-morula with fully developed spermatozoa with active tails. There is a very sharp differentiation into clear translucent, unripe, and opaque ripe sperm-masses. It would seem that the granular appearance arises at about the time when the spermatids are transformed into spermatozoa, and that this phase occurs in a very short space of time.

In practice developing sperm-masses from 20 to about 60μ are easily distinguished by their general appearance and translucency, and there are no other tissues in the oyster with which these can be confused ; the ripe sperm-masses are opaque, of characteristic appearance with actively vibrating tails radiating outwards from the surface of the mass ; moreover, it was found that sperm develop so rapidly that only in relatively few cases were they so little developed that identification in the fresh material required to be supplemented by prepared microscopical sections.

It may be observed that in Hoek's account of the early development of the sperm-mass he describes that one of the cells derived from the first division " seems to serve as a provisional connexion between the developing spermatozoa and the wall of the follicle." There can be little doubt that this provisional connexion forms the channel of nourishment for the developing spermatozoa, and also develops into the protoplasmic strands visible in the freshly teased ripe sperm-morula (see Orton, 1924, Plate IX). When living ripe sperm-morulæ are obtained on a slide, and when a little sea-water has been added to the body fluid, the sperm become more and more active until first a few and, finally, all wriggle away from the

residual matrix, a tenuous reticular mass, which is probably also partly the remains of the original provisional connexion noted by Hoek.

It is an interesting observation that sea-water needs to be added to ripe sperm-morulæ, in order to induce the sperm to segregate; in the first place separate sperm are not found normally in the gonoducts, as they are, for example, in the Portuguese oyster, or in sea-urchins and numerous similar cases. In case of doubt, therefore, the condition of the ripe sperm serves as a character to distinguish the Portuguese from the European oyster. Among the thousands of male European oysters examined by the writer, only one or two cases of the occurrence of separate sperm in the gonoducts have been met with, and in these cases the oysters were either dead or dying, and doubtless sea-water had entered the relaxed ducts and induced segregation of the sperm. As ripe sperm-morulæ do not disintegrate in the ducts, they must either pass into sea-water or some medium, which probably needs to be—like sea-water—slightly alkaline, before the sperm are set free to effect fertilisation of the ova, a fact which indicates—but does not prove—an adaptation to cross-fertilisation in the species. As ripe sperm-morulæ disintegrate in sea-water, it is suggested that sperm are normally distributed through the water where the sperm-morulæ are spawned, and it may therefore be inferred that sperm are collected by female-functioning oysters (as Hoek and Mobius believed) in the region of the reproductive apertures for the purpose of effecting cross-fertilisation. Further investigations are required on these matters, and are being carried out.

On Spawning.

Sperm-spawning.

In *O. edulis* a class of individuals with a well-developed gonad containing millions of ripe sperm-morulæ undoubtedly occurs, but there are few—if any—records of the observation of spawning males. In the writer's experience probably not more than six individual males have been under observation during the spawning act. In one well-marked case, a male spawned millions of ripe sperm-morulæ into a petrie dish, the spawn having a greyish white appearance which might easily have been mistaken by the unwary for embryos or larvæ in the mass. Similar less complete spawnings have been seen, and in a very large number of cases ripe sperm-morulæ are found in the liquor obtained when the oyster is opened; but as in these latter cases the frail gonoducts on the surface of the body are generally broken, it is more probable that these sperm-morulæ have escaped from the broken ducts than that they have been naturally spawned.

Although sperm-spawning individuals have rarely been met with, it is quite possible for the inexperienced observer to mistake a spawning

male for a spawning female, especially when the spawn is extruded from the edge of the shell in an oyster out of water, but a glance at the spawn rinsed into water is sufficient to discriminate between them. The spawning of the males is an important phase in the general course of reproduction in the oyster, and as yet little attention has been given to the subject. The writer will be able to give figures later which prove that there is a big spawning of males at the beginning of the breeding season at about the time the earliest females are found in spawn, and probably the oyster is seasonally protandrous; at the same time observations (see pp. 1025 to 1034) made in summer on individuals at various times after these have spawned as females—earlier in the same year—show that there must also occur a considerable amount of sperm-spawning in summer also. It is highly probable that the spawning of the males is correlated in some way with that of the females, but the manner of this correlation (if any) is not known. It is possible, for instance, that a female with ripe ova may retain its ova until a sufficiency of sperm has been accumulated (assuming for the time that self-fertilisation does not occur), for it is rare to find unfertilised eggs in the mantle cavity of a female which has spawned naturally.

It will be convenient at times to refer to sperm-spawning as andro-spawning when the term is used in the sense of spawning as a male, and in the same manner ovum-spawning may be referred to as gyne-spawning to imply the act of spawning as a female.

Egg-spawning and the Fate of Unspawned Eggs.

It is normal in *O. edulis* for the whole of the eggs to ripen at the same time, and for the ripe female to extrude the whole of the ova contained in the gonad and gonoducts in one act. The ova are fertilised normally at some instant of their passage from the gonoducts to the exterior. In many cases, however, a portion—which may be small or great—of the ova may remain behind in the gonad after the spawning act has taken place. A glance at the column reserved in Table IV, pp. 999 to 1021, for remarks on such ova left in the gonad after the spawning act, will show that it is quite common for isolated small or large patches of ova to remain unspawned. Such ova may either be retained in the gonad and degenerate and become absorbed, or they may be included in egg-cysts and extruded in masses and excreted *en bloc* on to the internal face of the shell and covered over with nacreous or horny matter in the form of an excretion blister. From a study of the records of the gonad condition given in Table IX, pp. 1025 to 1034, it seems probable that relict ova may also be extruded later through the reproductive aperture, and in a small percentage of cases, where a large part of the gonad retained its eggs, it would certainly seem possible that a second spawning act of one set of

eggs may occur. If such a second batch of eggs is fertilised then the individual will appear to have spawned twice as a female within a very short time, although the two spawnings are made from one batch of eggs. This possibility is believed to have been a probability *in a few cases* out of the large number observed; it is a serious handicap to some experiments on sex-change, and necessitates the demonstration of sex-change in a significant number of individuals to render the results free from doubt. Thus *isolated* experimental cases of change of sex from male to female or from female to female again must always be regarded with a reasonable amount of suspicion, and the factor of the proportion of individuals showing sex-change in any experiment is an important one. From examination of weekly samples of oysters from the Falmouth Oyster Beds in 1925 (Orton, 1926)—confirmed in 1926—the writer was able to show that the largest proportion of ripe females occurs in a population at the beginning of the summer and gradually diminishes throughout the summer until at the end of the breeding season, only a few ripe females remain. The proportion of ripe females remaining unspent at the end of the summer was found to be from 0 to 5% in 1925 and 1926 in the Fal Estuary and in 1926 in the Blackwater Beds. The proportion of females ripe at the beginning of the breeding season is a variable factor, not yet sufficiently known; it undoubtedly varies with age, and for samples of mixed ages, which were *estimated* at mainly 4 to 5 years, the proportion on the Truro Beds in the Fal Estuary at the beginning of the breeding season in 1925 was about 50% (Orton, 1926, p. 205). (See also Table I, p. 979). On other beds in other years it is probable that smaller percentages of ripe females occur, but fresh observations in the light of recent work are required to obtain comparable figures extending over a number of years.

Hermaphrodite Individuals and other Sex-categories.

The examination of the gonad of a large number of individuals carrying embryos or larvæ—detailed in Table IV, pp. 999 to 1021—has shown that a fair proportion of individuals do not spawn all their eggs at the gyne-spawning act, and as it will be shown later that the gonad becomes actively sperm-producing at about the time of the egg-spawning, the appearance of such a gonad with ripe eggs and developing, or later, fully developed sperm may be essentially that of a hermaphrodite individual. Nevertheless such individuals are not hermaphrodite (in a strict sense which will be defined later). In spite of the occurrence of such incompletely spawned females, it is certain that true hermaphrodite individuals also occur in fair proportion. True hermaphrodites are defined as individuals with ripe ova and ripe sperm developed generally evenly throughout the

gonad. These hermaphrodite individuals resemble females in the appearance of the body to the naked eye when the sex-elements are ripe, and statistical observations indicate that such individuals do actually spawn as females and extrude normally the whole of their genital products at the same time, and further that such individuals hatch a batch of larvæ. Direct proof of this should be obtained, however, by the examination of the whole of the sex-elements of a number of individuals—apparently female—caught in the act of spawning, but it is a very difficult matter to catch individuals in this phase. One such case is, however, recorded in Table IV, individual No. 614, p. 1016. (See note 15, p. 1021.)

In the case of hermaphrodite individuals as defined above, the occurrence of *developing* sperm-morulæ with ripe ova has very rarely been observed, and in only a very small percentage of the hermaphrodites examined. This observation may probably be important.

It was noticed during the course of the investigations that hermaphrodite individuals have varying proportions of *ripe* spermatozoa in relation to the number of ova in the gonad, so that in an effort to compare individuals of one population with those of another, it became necessary to adopt arbitrary categories for oysters with abundant ripe eggs, but with a varying amount of ripe sperm-morulæ. The conditions are not dissimilar to those described in Crepidula (Orton, 1909), but there the gradation occurs in relation to both primary and secondary sexual characters, whereas in the European oyster, as is well known, there are no morphological secondary sexual characters visible to the naked eye.

In the oyster the arbitrary categories adopted are :—

1. Hermaphrodite, ♀, individuals with a large quantity of ripe spermatozoa and abundant ripe ova.

2. Hermaphrodite female, ♀(♀), individuals with fewer ripe sperm-morulæ than the foregoing category and abundant ripe ova.

3. Female with a trace of maleness, ♀(♂), with a gonad filled with ripe ova, but where a few ripe sperm-morulæ may also be found.

All these three categories are regarded, however, as essentially functional females. In addition to these, two other categories of mixed sexes are recognised.

4. Male with a trace of femaleness, ♂(♀), (A), individuals in which ripe and occasionally also developing sperm-morulæ occur in predominant proportion in a well-developed gonad along with numerous though relatively few large ova.

This category, which may consist of two or three different kinds of individuals, is not properly understood, and has been marked down for a separate research. Successive weekly statistical examinations of

samples at the beginning of the breeding season indicate that this category may consist of hermaphrodite forms in which maleness is well advanced or fully developed, while femaleness is not quite fully developed. This view is supported to some extent by an examination of the fresh gonad ; the eggs, although large, have not the resilience of ripe ova and burst with the slightest pressure, but the contents of the egg have not the same appearance as obviously degenerating ova left behind in the gonad of an incompletely spawned female. It is, however, possible that some individuals in this category may be either well-fished (i.e. with large stores of reserve products) males which have retained and are absorbing unspent ova, or may even be abortive females.

Male with a trace of female, ♂(♀) B, individuals in which the gonad is not usually well developed and contains ripe or ripe and developing sperm-morulæ and also a small or fair number of degenerating and obviously relict ova ; these individuals are obviously and undoubtedly in a functional male stage.

5. Female-like ♂'s, individuals which in the living condition have the appearance of and are indistinguishable with certainty by the naked eye from pure females, but whose sex-elements consist entirely of sperm-morulæ, ripe or ripening in a matrix of granular reserve products. It is difficult to resist the impression that this category is derived from individuals in which ova have been absorbed, and in which the resultant nutriment of the ova is being transformed into viable metabolic products, but there is no other sex-designation of the category possible than simply males. It is not impossible, however, that the reserve products in these individuals may be an expression of imminent female potentialities coexisting with well-developed maleness.

To complete the sex-categories of individuals it is necessary to add :—

6. Pure ♂'s, individuals with a well-developed ramifying gonad full of ripe or in addition ripening sperm-morulæ and in the spawning condition with the gonoducts on the surface of the body crammed full of ripe sperm-morulæ ready to be shot out.

This kind of male is quite a different individual—or perhaps phase—from the male phase, into which the ripe female passes after spawning. Indeed, it is not impossible that there are two kinds of male in the oyster—and perhaps other molluscs—but this subject may be discussed more fully later.

7. Pure ♀'s, individuals whose gonad, when ripe, contains entirely and only ripe ova. The appearance of ripe ♀'s to the naked eye is similar to that of the ♂(♀), ♀(♂), and ♂ like ♀'s, all of which can easily be distinguished from the great variety of male and neuter phases which occur—at a glance.

In the ripe ♀ and ripe ♀-like forms the body has an opaque somewhat yellowish chalky and creamy appearance, in contrast with the white to grey creamy and more translucent appearance of the pure males and the post-sick male phases.

8. Other categories. In addition to the categories mentioned above, all of which have ripe or ripening sex-elements of some kind in the gonad, a number of definable phases in the sperm-producing gonad of the post-sick oyster have been recognised, as well as certain neuter phases, but so far the effort to discriminate the post-spawning phases of the *pure* male has failed. A discussion of these matters is reserved for a later communication, when it is hoped to describe the microscopical character of the gonads of the different kinds of male categories recognised herein, and the neuter and young female stages which follow the male phase attained after a previous spawning as a female.

Examples of the Constitution of an Oyster Population at the Beginning of the Breeding Season.

The proportion in which the individuals of the foregoing sex-conditions occur in an oyster population is a matter of importance in the problem under investigation, and in order to give some indication of their relative frequency the following analyses in Table I of several samples may be given :—

The first six samples given in Table I, p. 979, were examined at the beginning of the breeding season (in 1926), when the proportion of the different kinds of egg-bearing individuals can best be determined, for it has been shown (Orton, 1926) that the proportion of females—and it may be added egg-bearing individuals—gradually diminishes during the breeding season.

The last two examples in Table I were examined after the breeding season had begun in 1922 and 1923, when some of each kind of egg-bearing category might already have spawned ; it may be noticed that there is a reduced percentage of the mixed sexes as compared with the samples examined at the beginning of the breeding season in 1926.

Preliminary Discussion on the Significance of Mixed Sexes.

It has been mentioned above that both Hoek and Möbius considered the oyster as essentially a bisexual species with regard to spawning. The figures given in Table I, p. 979, lend support to this view, but the relatively high proportion of mixed sexes (hermaphrodites of various categories) justifies the view maintained by Lacaze-Duthiers that the gonad of this oyster appears to be " sometimes male, sometimes female, and sometimes hermaphrodite.

TABLE I.

FREQUENCIES OF DIFFERENT SEX-TYPES IN DIFFERENT POPULATIONS OF OYSTERS AT THE BEGINNING OF THE BREEDING SEASON, 1926.

Date.	Locality.	Total examined.	Pure Male.			Impure. ♂'s with eggs unspawned.	Neuter.	Mixed sexes.			Female		Total. Functional ♀ and ripe ♀	Total. With eggs.	Total. Pure ♂'s	Total. Mixed sexes.
			Ripe ♂'s	Fair* ♂'s	Indifferent ♂'s			♂♀	♀♂ (♀)	♀♂ (♂)	Pure ripe ♀	With embryos and larvæ.				
1926.	FAL ESTUARY BEDS.															
June 9	Turnaware Bar	174	53	23	21	22	6	9	4	6	28+1†	1	48	71	97	19
			(30·5)	(13·2)	(12·1)	(12·7)	(3·4)	(5·2)	(2·3)	(3·4)	(16·1)	(0·5)	(27·6)	(40·8)	(55 8)	(10·9)
,, 22	East Bank	151	41	30	17	15	3	13	2	4	24	2‡	45	60	88	19
			(27·2)	(20)	(11 3)	(10)	(2)	(8·6)	(1·3)	(2·6)	(15·9)	(1·3)	(29·8)	(39·8)	(58·3)	(12·6)
,, 23	Turnaware Bar	100	30	5	5	12	4	6	4	6	28	0	44	56	40	16
	Totals	425	124	58	43	49	13	28	10	16	80†1	3	137	187	225	54
	Percentages		(29·2)	(13·6)	(10·1)	(11·5)	(3)	(6·6)	(2·3)	(3·7)	(18·8)	(0·7)	(32·2)	(44)	(53)	(12·7)
1926.	WEST MERSEA BEDS.															
June 10	Thornfleet	107	45	6	10	19	3	6	3	2	9	4	24	43	61	11
,, 16	do.	103	24	15	14	5	1	4	3	5	17	15	44	49	53	12
,, 23	do.	100	3	45§	4	4	1	2	3	3	8	27	43	47	52	8
	Totals	310	72	66	28	28	5	12	9	10	34	46	111	139	166	31
	Percentages		(23·3)	(21·4)	(9)	(9)	(1·6)	(3·9)	(2·9)	(3·2)	(11·1)	(14·9)	(36)	(45)	(53·8)	(10)
June 28–29, 1922		105‖	—	—	—	15	4	5	0	3	18	7‖	33	48	53	8
July 24, 1923		156‖	—	—	—	19	12	5	1	0	16	10‖	32	51	93	6

NOTES TO TABLE I.—Percentages where necessary are given in brackets, all other figures give the number of each sex-type found.

* Includes individuals which may be partly spent and others probably completing development of maleness.

† One individual was a young female.

‡ Two individuals which probably spawned prematurely as a result of being dredged.

§ Includes an unknown proportion of indifferent males.

‖ Percentages are not given for these samples, because some spawning females may have been taken from them before they were examined microscopically; and the pure males are not classified into ripe, fair and indifferent groups. These samples are given merely to show the reduced proportion of mixed sexes at a period after the beginning of the breeding season.

Hoek also held that cross-fertilisation always or mostly occurred in this species inasmuch as (1) the eggs are extruded in a fertilised condition (Hoek quotes and infers that the eggs are always extruded in a segmenting condition, but this incorrect view is only a minor point), and (2) Hoek found and figured discrete spermatozoa aggregated in the region of the external opening of the oviduct (gonoduct). The views of Hoek and Möbius may be accepted with regard to pure females and pure males without at present admitting that cross-fertilisation necessarily occurs in all cases. There is, however, at present no information about the mode of fertilisation in the mixed sexes, and the mode of spawning of these can only at present be inferred from (1) statistical studies of the seasonal variation in the proportion of the various sex-categories in an oyster population, and (2) the condition of the gonad immediately after a gyne-spawning. It is important at this point to recall the observation that hermaphrodite forms with ripe ova have in only an insignificant number of cases developing sperm in the gonad in addition to ripe sperm. Thus if a hermaphrodite form did not spawn completely, some eggs and some ripe sperm-morulæ would remain behind in the gonad, but very rarely would *developing* sperm from the pre-spawning period be left. Proof will be given later that sex-change does occur from female to male and from male to female and from female back to female again: such changes indicate the control of sex by some kind of factor. These facts are probably sufficient for the moment to explain a proportion of mixed sexes in an oyster population, since a slight deviation from a presumed normal sequence of sex-changes may be sufficient to cause an overlapping in the manifestations of the sex-causative factors—whatever these may be—and result in a mixed sex. Further discussion on sex in this species may be deferred until the data herein presented have been examined.

SECTION B. RESULTS OF EXAMINING THE GONAD IN 702 (♀) "SICK" OYSTERS.

It has already been noted that many observers (especially Hoek, 1883) have in the past recorded the occurrence of ripe or developing sperm in the gonads of oysters carrying embryos or larvæ in the mantle cavity, but no systematic examination has been made to determine whether such a condition is always the case, or whether only a certain proportion of individuals show ripe sperm in the gonad after spawning as females. For the establishment of a specific rhythmic sex-change it is not sufficient to know that sex-change occurs in some cases, hence the need for a systematic examination of the gonad of individuals carrying embryos or larvæ in as great a variety of conditions of development as can be obtained.

The condition of the sex-cells in the gonad of individuals which have recently or within a known time spawned as females may be represented in most cases by one of the following ten categories. A gonad which does not fall into one of these categories will be noted specially.

TABLE II.

Categories of Gonad Condition in ♀ "Sick" and ♀ "Post-Sick" Individuals.

	Sex-cells Present in the Gonad.		
	Ripe sperm-morulæ.	Developing sperm-morulæ.	Ripe unspawned ova.
Category I	none	none	none or a variable no.
,, II	none	some doubtful	do.
,, III	none	a few to ∞ young up to 40 μ	do.
,, IV	none	f ∞ or ∞ over 40 μ	do.
,, V	few or occasional	∞	do.
,, VI	f ∞ or ∞	f ∞ or ∞	do.
,, VII	∞	few to fair no.	do.
,, VIII	f ∞ or ∞	none	do.
,, IX	few to fair no.	none	do.
,, X	none	none	none or a variable no.

NOTES ON TABLE II.

The abbreviations used in Table II have the following meanings :—

∞ = numerous. f ∞ = fairly numerous.

The final stage or category, X, is indistinguishable from the first stage, but in view of the results obtained there is justification for using the figure X in the case of individuals which have long ago evacuated their young.

Ripe sperm-morulæ have a dark granular appearance in the fresh condition, and when transferred to sea-water at ordinary room-temperature break up into active sperm ; they may vary in size and shape from about 50 μ spherical to 80 μ or more elongate cylindrical (see Plate V, Hoek, 1883 ; and Plate IX, Orton, 1924).

Developing sperm-morulæ are translucent agglomerations of cells arising from spermatogonia, and vary in size in the fresh condition from about 10 μ in the 4-celled stage, 14 μ in the 7- or 8-celled stage, 19 μ in the 10-celled stage to as much as 80 μ in the penultimate stage, when the tails of the sperm may just be beginning to be developed, but even at this last stage the cytoplasm of the mass remains translucent.

Normally all ova are extruded in the spawning act, but in a not inconsiderable number of cases tiny or large isolated patches of ripe—and occasionally some unripe—eggs may remain in the gonad after the spawning act ; in a smaller proportion of cases considerable irregular areas may remain undischarged. Rare cases have been observed where one gonad —the right—was spent, and the other remained full of ripe ova.

Young ova become recognisable in the fresh tissues at a size of about 40 to 50 μ, but only a few gonads with young ova were encountered and recorded ; it was not, therefore, necessary to retain a column in this Table for developing ova.

The Age of Arbitrary Progressive Periods in the Development of the Oyster Embryo and Larva.

As the condition of the gonad of individuals carrying embryos or larvæ may vary directly with the period which has elapsed since the instant of spawning, it is important to know what this period is approximately in hours or days in the case of each gonad examined. Although no direct observation of this period is possible a close approximation can be made from the stage of development of the embryos or larvæ, since the rate of development has been observed in sufficient cases to give such an approximation. The rate of development of embryos and larvæ will undoubtedly vary with the conditions and especially with temperature, but conditions which retard or hasten embryonic development may not unreasonably be regarded as having generally a similar effect on sperm-development. Therefore the stage of development of embryos or larvæ may be more closely related to sperm-development in the gonad of the adult carrying them than to the actual time which has elapsed after the spawning act, if it is a fact that sperm-development does begin normally after the spawning act. In Table IV, p. 999, are given details of the stages of development of the embryos and larvæ, but the variety of these stages renders it necessary to group them into successive time-periods in order to obtain a perspective view of the successive changes in the sex-condition of the adults as their eggs develop into larvæ.

Accordingly the whole range of development from the time the egg is fertilised to the time the larvæ is set free from the parent has been divided up into six periods as shown in Table III on page 983,

Correlation between the Age of the Gonad—reckoned from the instant of Egg-spawning—and the Development of Maleness in the same Gonad.

By the use of Tables II and III it will now be possible to summarise the whole of the observations made on embryos and larvæ and gonad condition; for with the categories of gonad-condition—which are arranged in successive stages of development of maleness—in Table II, and the periods of development of embryos and larvæ—which give the age of the post-spawned gonad of individuals carrying the young—it is possible to show in a correlation table and in graphs the results of examining hundreds of individuals for both these sets of characters.

The detailed results of the examination of 702 oysters carrying embryos or larvæ are set out in Table IV, pp. 999 to 1021. It will be observed that " sick " oysters have been obtained from a good number of different beds in the southern part of England during the years 1920–1926, while

the results obtained show that there is an essential similarity in behaviour of all oysters from all the beds examined throughout at least the main part of the breeding season. Remarks on various anomalies and other points of interest are made in the notes and discussion on the Table on p. 1019 onwards.

TABLE III.

DEFINITIONS OF SUCCESSIVE ARBITRARY PERIODS OF DEVELOPMENT OF THE EMBRYO AND LARVA OF *O. EDULIS*.

	Age.	State of development.
Period A.	0 to about 4½ hours.	0 to mainly 4-celled stages.
	Fertilised unsegmented eggs have on several occasions been found in the mantle cavity, evidence of fertilisation existing in the occurrence of mitotic spindles in the egg, and in subsequent segmentation.	
Period B.	About 8½ to about 20 hours.	8 to about 32–celled stage.
	Some caution must be exercised in dealing with embryos in this group in which arrested development may have occurred. Many samples of oysters have necessarily had to be examined the day after they were dredged, and also after being out of water for about a day. Under these conditions—in summer—the liquid in the mantle cavity becomes more or less fouled. In such samples embryos in the 16- to 32-celled condition have so often been met with, that it is highly probable that development may have been arrested at these stages owing to the unfavourable conditions. In some cases therefore the embryos may be a little older than this state of development indicates, and it follows that in such cases the age of the gonad—reckoned from the gyne-spawning—would also be a little older than is indicated by the stage of development of the embryos.	
Period C.	About 30 hours to 2½ days.	More than 32 blastomeres to the elongate heart-shaped but unciliated embryo.
Period D.	3 to 4 days.	Elongate heart-shaped but now ciliated embryo, with or without a mere rudiment of the larval shell.
Period E.	4 to 5 days.	White to grey ciliated embryos with a growing larval shell ranging in length from 50 to about 150μ.
Period F.	6 to 10 (or 12 days) normally, but may be older at the end of the breeding season, or under cold conditions.	Coloured fully-shelled larvæ, that is, lilac, slate or blue, black or purplish-black larvæ, with shells ranging in length from 150 to 200μ usually — and rarely 210 to 220μ.

Table IV is summarised in Table V, which faces p. 984, in order to show the *frequencies* of occurrence of the different sex-conditions of the post-spawned gonad correlated with the different periods of development of the embryos or larvæ. Table V is in turn again summarised to give the

correlation table, shown on p. 985 as Table VI. From Table VI, with its accompanying graphs, Fig. 1, p. 991, it is possible to see at a glance the relation between the condition of the sex-elements in the gonad of individuals and the age of the gonad—reckoned from the recent gyne-spawning—as inferred from the age of the embryos or larvæ carried by the same individuals.

A glance at the correlation table, Table VI, on p. 985, shows that :—

1. The youngest gonad (reckoned from the instant of the recent spawning) has the youngest male sex-elements—or none at all—and has no ripe male elements.

2. As the gonad increases in age (as defined above), so the ripe male-elements increase and the unripe ones decrease. Exception to these statements occurs but so rarely as to be non-significant.

3. There is a clear correlation between increasing ripeness of male products and increasing age of gonad (as defined).

4. As the period of age of the gonad increases so also advances the progressive development of maleness in the gonad.

5. The occurrence of eight gonads with no maleness in the F period is contrary to the general trend of the table (see below).

6. The mean stage of development of maleness shows a progressive increase in correlation with the progressive ages of gonads, and this fact along with the progressive distribution of the categories with 50 % of individuals or more in each period, is proof of a positive correlation.

The frequencies of the different kinds of sex-condition in the gonad of individuals carrying embryos or larvæ in each of the periods A to F are plotted (as percentages) to give the series of graphs shown in Fig. 1, p. 991. These graphs show clearly the points noted above, and bring out the fact that about 50% of the individuals contain few or a great number of ripe sperm in the gonad already at the D period, that is, at an age of three or four days. For the periods earlier than D, the stage of development of maleness is retrogressively less advanced, and beyond D the development of maleness is successively greater. In stages E and F the percentage of individuals with *only* developing sperm dwindles to about 22% in the E stage (four to five days), and 3 to 6% in the F stage (six to twelve days). In the F period eight individuals (3 to 13%) had no sex-elements at all in the gonad ; it is highly probable that these eight individuals are abnormal, and some possibly pathological ; but it is certainly significant that six of these individuals occurred amongst the

TABLE V.

Summary of Sex-categories, 1 to 8 (see Table II, p. 981), found in Gonads belonging to Oysters carrying Embryos or Larvæ in the successive Periods of Development, A to F (see Table III, p. 983).

Group No. and No. of oysters examined.		Date dredged.	Date examined.	Locality.	0 to 4½ hours. A					8½ to 20 hours. B						30 hours to 2½ days. C							3 to 4 days. D							4 to 5 or more days. E							6 to 10 to 12 or more days. F						
					1	2	3	4	5	1	2	3	4	5	6	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7	8
1.	1	1920	July 30	Yealm.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2.	1	1921	June 15	Whitstable	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
3.	2	—	July 6	Cowes.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–
4.	1	—	,, 7	Yealm.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
5.	1	—	,, 13	Plymouth Sound.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
6.	1	26.7.21	Aug. 4	Whitstable.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7.	1	—	Sept. 12	Swansea.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
8.	2	—	June 19	West Mersea.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
		1922																																									
9.	3	June 21	June 22	Yealm.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10.	4	,, 28	,, 28–29	Deeps. W. Mersea.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11.	4	,, 29	,, 29–30	Thornfleet, W. M.	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
12.	3	July 3	July 4	Var. Grnds., W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
13.	3	,, 4	,, 5	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
14.	9	,, 8	,, 9	,, ,,	–	–	1	–	–	–	–	1	–	–	–	–	–	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
15.	2	,, 12	,, 13	Helford River.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–
16.	1	,, 21	,, 23	Whitstable.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
17.	5	,, 27	,, 31	,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	3	–	–
18.	9	,, 31	Aug. 1	Port Navas, H. R.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	2	–	–	–	–	–	4	2	–	–
19.	6	Aug. 1	,, 2	Whitstable.	–	–	–	–	–	–	–	1	–	–	–	–	–	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
20.	6	,, 3	,, 4	,,	–	–	–	–	–	–	–	–	–	–	–	1	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
21.	5	,, 3	,, 4	West Mersea.	–	–	–	–	–	–	–	1	–	–	–	–	–	1	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
22.	1	,, 16	,, 17	Helford River.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
23.	2	,, 23	,, 24	Yealm River.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
24.	3	,, 30	,, 31-31.9	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
		1923																																									
25.	1	Aug. 3	Aug. 6	West Mersea.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
26.	1	—	,, 31	Yealm.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
27.	1	—	Sept. 4	,, Cage.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
28.	1	July 18	July 18	Thornfleet, W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
29.	1	,, 25	,, 26	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
30.	2	,, 26	,, 27	Noss End, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–
31.	2	,, 27	,, 28	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
32.	2	,, 30	,, 31	Thornfleet, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–
33.	1	Aug. 2	Aug. 3	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		1924																																									
34.	3	June 3	June 7–8	Var. Grnds., W. M.	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35.	1	,, 3	,, 7	Burnham River	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
36.	2	,, 12	,, 13	Var. Grnds., W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
37.	21	30	July 1	Back of Noss ,,	–	–	–	–	–	–	–	2	–	–	–	–	–	1	5	1	–	–	–	–	–	–	2	3	–	–	–	–	–	–	2	–	–	–	–	–	–	3	2	–
		1924 (*contin ed*)—																																									
38.	6	July 1	July 2	Var. Grnds. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
39.	3	,, 2	,, 3	South Shore ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–
40.	2	,, 4	,, 5–7	Var. Grnds. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
41.	2	—	,, 16	Yealm Cage.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
42.	3	—	Aug. 8	,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–
43.	3	Aug. 15	,, 18–23	Perceil R., Fal. Est.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–
44.	3		,, 28	Yealm Cage Expts.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–
45.	8	—	July 1–8	West Mersea Cage.	–	–	–	–	–	–	1	–	–	–	–	–	–	1	3	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–
		1925																																									
46.	15	July 1	July 2–4	East Bank, F. E.	–	–	–	–	–	–	–	1	–	1	–	–	–	1	3	–	–	–	–	–	1	1	1	–	–	–	3	1	2	–	–	–	–	–	–	–	–	–	–	–
47.	10	,, 8	,, 11	Turnaware ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	2	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–
48.	9	,, 15	,, 18	East Bank ,,	–	–	–	–	–	–	–	–	–	–	–	–	1	3	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2	–	–
49.	26	,, 22	,, 24	E. & Mylor B. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	2	7	–	2	–	–	–	–	3	5	–	–	–	–	–	–	1	4	–	–
50.	18	,, 30	,, 31 & Aug. 2	Turnaware ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	2	–	–	–	–	–	2	1	7	–	–	–	–	–	–	3	–	–
51.	13	Aug. 5	Aug. 6	,, & E. Edge ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	–	–	–	–	2	1	–	1	–	–	–	–	–	5	–	–
52.	30	,, 10	,, 12	Fal. N. Bk. ,,	–	–	–	–	–	–	1	2	–	–	–	–	–	–	6	2	–	–	–	–	–	–	–	–	–	–	–	1	4	–	–	–	–	–	1	13	–	–
53.	24	,, 11	,, 13	East Edge ,,	1	1	3	–	–	1	–	–	–	–	–	–	–	–	1	–	–	–	–	–	3	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	11	–	–
54.	22	,, 18	,, 20	Mylor Bank ,,				–	–	–	–	1	–	–	–	–	–	–	4	–	–	–	–	–	4	3	1	–	–	–	–	1	1	5	–	–	–	–	–	–	2	–	–
55.	26	,, 26	,, 28	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1	–	–	–	–	–	–	2	–	–	–	–	–	1	5	13	2	–
56.	29	Sept. 3	Sept. 5	Turnaware B. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	3	9	3	2	–	–	–	1	–	2	1	–	–	–	–	–	2	–	–	–	–	1	1	4	–	–
57.	35	,, 9	,, 11	East Edge ,,	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	8	–	–	–	–	1	2	16	1	2
58.	11	,, 16	,, 18	Turnaware Pt. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	1	–	–	–	1	7	–	–
59.	2	,, 23	,, 24	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–
60.	10	,, 30–Nov. 5	,, 30–Nov. 5	Var. Grnds. ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	3	–	–	2	1	–	–	1
61.	8	July 10	July 11	Var. Grnds., W. M.	–	–	1	2	–	–	–	1	1	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
62.	7	,, 21	,, 21	South Shore ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	1	1	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–
63.	7	,, 2	,, 3–14	Exptl. Cage ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
		1926																																									
64.	4	June 2	June 3	Turnaware B., F. E.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
65.	5	,, 9–16	,, 9–17	,, ,,	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–
66.	4	,, 22–23	,, 22–25	,, E. Bank ,,	–	–	–	–	–	–	–	1	–	–	–	–	–	–	2	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
67.	27	,, 23	,, 24	Thornfleet, W. M.	1	–	–	–	–	–	–	–	–	–	–	–	–	1	7	1	–	–	–	–	–	1	2	2	–	–	–	–	–	1	–	–	–	–	–	–	–	11	–	–
68.	27	,, 28	,, 28–9	Turnaware B., F. E.	–	–	–	–	–	–	–	5	3	–	–	–	–	–	6	1	1	–	–	–	1	–	3	–	–	–	–	1	–	3	–	–	–	–	–	–	–	3	–	–
69.	4	,, 29	,, 29	Mylor Bank ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
70.	20	,, 30	30, July 1	East Bank ,,	–	–	–	–	1	–	–	–	3	–	–	–	–	–	7	1	–	–	–	–	–	2	1	2	–	–	–	–	–	1	–	–	–	–	–	–	–	2	–	–
71.	25	,, 30	,,	Turnaware B. ,,	–	–	2	–	–	–	–	1	1	–	–	–	–	2	7	1	1	–	–	–	–	1	1	1	–	–	–	–	–	1	–	–	–	–	–	1	5	–	–	–
72.	2	July 5	July 7	South Shore, W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–
73.	13	,, 7	,, 7	Thornfleet ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	1	–	–	–	1	–	2	–	–	–	–	–	–	5	–	–
74.	12	,, 7	,, 8	South Shore ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	4	–	–	–	–	–	–	5	–	–
75.	29	,, 6	,, 9	Turnaware B., F. E.	1	1	3	–	–	–	1	5	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	5	1	2	–	–	–	–	–	–	7	–	–
76.	13	,, 10	,, 10	Noss End, W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1	3	–	–	–	–	–	–	7	–	–
77.	16	,, 12	,, 12	,, ,,	–	–	–	–	–	–	–	2	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	–	–	–	1	5	–	–	–
78.	4	Aug. 4	,, 5	Thornfleet ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	3	–	–	–
79.	14	,, 10	,, 10	Mylor Bank, F. E.	1	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	1	–	–	–	–	–	3	3	–	–	–
80.	16	,, 10	,, 10	East Bank ,,	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	3	–	1	–	–	–	2	–	–	–	–	–	6	1	–	–
81.	1	Sept. 1	Sept. 2	Thornfleet, W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
82.	16	Sept.-Oct.	Sept.-Oct.	Var. Grnds., F. E.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	4	2	1	–	–	–	–	1	5	2	–	–
83.	3	Sept. 29	Sept. 29	Exptl. Cages ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
702				Totals	5	2	*12*	5	0	1	4	*25*	19	1	1	1	1	26	*83*	14	5	0	0	1	12	*39*	*33*	26	0	1	0	3	25	27	*74*	0	8	0	0	6	31	*197*	11	3
				Total in each period			24					51						130							111						130							256						

last spawners at the end of the breeding season : one in September and three in October, 1925, and two on September 29, 1926.

Experiments on the Rate of Development of Sperm-morulæ.

When the examination of the gonad of a large number of " sick " oysters had shown that maleness is developed at once in nearly all individuals at or soon after egg-spawning, an experiment was carried out in order to obtain additional information and data.

On July 14, 1925, a sample of 3,700 oysters of various ages, from three years upwards, was examined, and nine blacksick and eleven whitesick individuals picked out of the pile by simple inspection of the whole individuals ; the sample was dredged on the previous day, and had lain in a pile in the store overnight. Amongst the eleven whitesick individuals were nine in which the embryos were found to be in very early segmentation stages, ranging from 0 to the 8-celled condition. Particulars of the eleven individuals are as follows :—

	Length in mms.	Depth in mms.	1925 shoot in mms.	State of embryos.
1	61	69	4	2 to 4-celled.
2	64	66	11	2 to 8 ,,
3	52	57	?	Unsegmented eggs only.
4	57	62	9	2 to 6-celled.
5	53	56	2	0 to 2 ,,
6	56	56	12	0 to 2 ,,
7	66	60	19	0 to 8 ,,
8	63	59	17	0 to 2 ,,
9	52	57	4	4 to 8 ,,
10	53	59	11	ca. 16 ,,
11	65	61	15	Morulæ.

Ten of the whitesick individuals (excluding No. 11) were chosen for the experiment ; one was opened and examined microscopically on July 14th and the others at successive intervals of one or two days, after being put back in the sea at a depth of about one fathom, in a stramin bag attached to the stern of an old store-vessel, which was moored in midstream in 2½ fathoms of water at low water, in Thornfleet, West Mersea. The results of the several examinations appear in Table VII, p. 987.

TABLE VI.

Correlation between the Progressive Development of Maleness and the Progressive Age of the Gonad—reckoned from the instant of Egg-spawning—in 702 Oysters carrying Embryos or Larvæ

Mean age of gonads in each period.	A to F, progressive periods of age of gonads inferred from age of embryos or larvæ.	Numbers and percentages (in brackets) of Categories I to X, progressive stages in the development of maleness observed in gonads at each period.										Total No. of individuals examined in each period.	Mean stage of development of maleness.
		I	II	III	IV	V	VI	VII	VIII	IX	X		
2¼ hours	A period	5 (20·9)	2 (16·6)	12 (50)	5 (20·9)	0	0	0	0	0	0	24	2·71
14 hours	B do.	1 (1·97)	4 (7·85)	25 (49·1)	19 (37·3)	1 (1·97)	1 (1·97)	0	0	0	0	51	3·26
45 hours	C do.	1 (0·77)	1 (0·77)	26 (20·1)	83 (63·9)	14 (10·8)	5 (3·85)	0	0	0	0	130	3·95
3½ days	D do.	0	1 (0·9)	12 (10·9)	39 (35·2)	33 (29·8)	26 (23·5)	0	0	0	0	111	4·65
4½ days	E do.	1 (0·77)	0	3 (2·31)	25 (19·3)	27 (20·8)	74 (57·1	0	0	0	0	130	5·31
8½ days	F do.	8 (3·12)	0	0	6 (2·34)	31 (12·1)	197 (76·9)	11 (4·29)	3 (1·17)	0	0	256	5·73
Total no. in each category of maleness . . .		**16**	**8**	**78**	**177**	**106**	**303**	**11**	**3**	**0**	**0**	**702**	
Total per cent in each category of maleness . . .		(2·28)	(1·14)	(11·1)	(25·2)	(15·1)	(43·1)	(1·56)	(0·4)				

NOTES ON TABLE VI.

In the A category only 24 individuals were examined and recorded, owing partly to the relative scarcity of this type, but also to the reluctance and inability to spare the time for the long examination often necessary in these cases to prove a negative. In a number of additional cases a partial examination was made, but the results not recorded as it was felt that a longer period of examination than could be afforded on the beds would be necessary before a correct description of the gonad could be recorded with certainty. In these unrecorded cases the gonad would fall in one of the first two categories of sex-condition, that is, either no maleness, or doubtfully developing very young spermatogonia. For these reasons it is probable that the mean state of development of maleness in the gonad of this category, namely, 2·69, is slightly too high. Although the total number of individuals recorded in this category is small, it is sufficient for the purposes of the present problem, and a special investigation of this particular period of the gonad will be worth while later to determine more nearly the limits of the beginning of the development of maleness. It is interesting that the largest number of individuals in this category should just show definite signs of early developing maleness.

In the B category 88 per cent of the individuals show early signs of the acquisition of maleness, and two individuals show well advanced maleness. In view of the general character of the correlation table these latter individuals cannot be regarded as having developed their maleness wholly since the last gyne-spawning.

In the C category the highest percentage of individuals has maleness obviously developing, while in the D group more than 50 per cent have now few or abundant ripe male-elements.

In the E group all individuals are definitely male in some stage of development except one neuter individual, with a maximum percentage, 57, with abundant ripe sperm-morulæ.

In the F group there is a still bigger percentage with abundant ripe sperm-morulæ, 77, and a few individuals show a waning in the development of maleness, or absence of developing sperm. The waning of the production of sperm in this group is confirmed by the examination of the gonad of individuals which have extruded their larvæ (see p. 1025). It has already been noted that of the eight neuter individuals in this group six were found at the tail-end of the breeding season, and demand special consideration.

The end columns in this table give respectively the mean age of the arbitrary progressive periods of development of embryos or larvæ in hours or days, and the mean stage of development of maleness in the gonads of the adults carrying the young of the corresponding periods. The stage of development of maleness is obtained by dividing the total number of individuals in each category into the sum of the products of the number at each stage and the number denoting that stage. These two *means* can be used to plot a graph depicting the average rate of development of maleness (see **Fig. 2**, p. 993).

TABLE VII.

EXPERIMENT ON THE RATE OF DEVELOPMENT OF SPERM-MORULÆ *IN SITU* IN THE GONAD.

Approximate age of post-sick gonad.	Date.	Serial number of oyster.	Elements in gonad. Ripe sperm-morulæ.	Unripe sperm-morulæ.	Ripe ova left in gonad.	Stage* of development of maleness. A	B
6 hours	July 14	1	none	few about 30μ	fair no.	3	3·0
2¼ days	,, 16	2	none	f ∞ up to 40μ	few; rounded off	3	3·5
do.	,, 16	3	∞	∞	few	6	6·0
3¼ days	,, 17	4	none	∞ large up to 60μ some nearly ripe	do.	4	4·0
do.	,, 17	5	few	f ∞	do.	5	5·0
5¼ days	,, 19	6	fair no.	∞ up to 70μ and 60μ spherical	do.	6	5·5
do.	,, 19	7	do.	∞ up to 80μ	few patches	6	5·5
6¼ days	,, 20	8	few	∞ full size and nearly ripe	rare	5	5·0
8¼ days	,, 22	9	f ∞	∞	few	6	5·75
—	,, 22	10	dead	—	—	–	—

* In column A are given numerical figures corresponding to those given in Tables IV, V, and VI; in column B are given figures to show smaller differences in the stages of development of sperm-morulæ.

The variation in the temperature conditions on the site of the experiment on the rate of development of sperm-morulæ in the oyster is very nearly shown by the following readings, taken at a depth of 1 foot with a certificated Calderara thermometer. Where only one observation was made on one day on the site of the experiment—S.V. Frolic, in mid-Channel, Thornfleet, West Mersea—additional observations from other similar thermal situations are given for comparison. These readings were generally taken at about the time of high and low water as indicated.

1925.	Time.	Approx. state of tide.	Temperature, °F.	Position.
July 13	7 a.m.	H.W.	65	Thornfleet.
,, 13	1 p.m.	L.W.	67	do.
,, 14	8 a.m.	H.W.	65	do.
,, 14	2 p.m.	L.W.	67	do.
,, 14	8 p.m.	ca. H.W.	66	do.
,, 15	9 a.m.	H.W.	67	do.
,, 15	3 p.m.	L.W.	69	Dan's Moorings.*
,, 15	6 p.m.	—	67	Thornfleet.
,, 16	6 a.m.	2 hrs. after L.W.	69	Dan's Moorings.
,, 16	10 a.m.	H.W.	69	Off Mell Pier.
,, 16	8 p.m.	—	69	Thornfleet.
,, 17	6 a.m.	1 hr. after L.W.	70	Dan's Moorings.
,, 17	11 a.m.	H.W.	67	Mell Pier.
,, 17	8 p.m.	—	71	Thornfleet.
,, 18	6 a.m.	ca. L.W.	68	Dan's Moorings.
,, 18	12 noon	ca. H.W.	67	Thornfleet.
,, 18	8 p.m.	—	70	do.
,, 20	6 a.m.	ca. L.W.	67	Dan's Moorings.
,, 20	12 noon	ca. H.W.	67	South Shore.
,, 21	7 a.m.	L.W.	68	Thornfleet.
,, 21	1 p.m.	H.W.	67	Mell Pier.
,, 22	8 a.m.	L.W.	68	Thornfleet.
,, 22	2 p.m.	H.W.	69	Mell Pier.

An inspection of Table VII shows that—excepting No. 3 oyster—there was a gradual increase in size of the developing sperm-morulæ, and a gradual production of ripe tailed sperm-morulæ in the series of oysters examined: indeed, except for numbers 3 and 8, the individuals form a surprisingly good graded series, considering that individual variation does occur in the rate of development of maleness (see Table VI).

* m.b. Dan's moorings are in 1½ fathoms of water at L.W. in Salcot Creek. All readings are in mid-Channel except off Mell Pier and South Shore.

Since all these individuals spawned on July 13th or a few hours later, the following deductions can now be drawn. Within one day after spawning, a few sperm-morulæ developed and attained a size of 30μ, and within three days after spawning numerous sperm-morulæ were developed to a size of 40μ. (No. 3 oyster is omitted for the moment.) Within four days after spawning, numerous sperm-morulæ were now developed to a size of 60μ in one individual, and in another the first ripe sperm-morulæ are now fully developed.

In the sixth day the number of ripe sperm-morulæ is increasing, and ripening morulæ have a size now of 70 to 80μ. The individual examined on the seventh day is lagging, and is no further advanced than the more advanced one examined on the fourth day. On the ninth day ripe sperm are now found in greater quantity than in any of the ones previously examined—excepting No. 3. The latter individual is an aberrant one, and it may be seen from Table VI that similar individuals occurred very rarely even in Periods A to C. In Periods A and B only 2 such individuals occurred among 75 examined, and in Period C only 5 occurred in 130 examined, so that in Periods A to C only 7 such individuals occurred in 205 examined.

It is not possible to state whether No. 3 had developed maleness unusually quickly, or, as is possible, was previously hermaphrodite and did not extrude all its gonadial products at the last spawning. It may be noted from Table VII that a few ova were left behind in this gonad after spawning, but at the time of the examination no observation was made as to whether ripe sperm-morulæ were confined to the portion of the gonad where the eggs occurred. Although No. 3 oyster in the experiment breaks the graded series of results obtained, it draws attention to the fact that individuals—in small proportion—may have ripe sperm-morulæ in their gonad on the third day after gyne-spawning.

Although the number of individuals made use of in this experiment is small, it may be noted that they were picked out of a sample 3,700. A similar experiment carried out with a larger number of individuals should be repeated, and with our increased knowledge of spawning epochs in this species, such an experiment may be possible in the near future.

The following additional observations have also been made. An oyster proved to be male in July, 1923, and kept afterwards in a cage in the sea, extruded ciliated larvæ on July 1, 1924, after the cage was hauled. The gonad was examined by tapping the gonad with a fine pipette through the reperforated shell on July 2, 1924. The oyster was then replaced in the sea—in an oyster pit—and opened and examined on July 8, 1924, with the following results, which show a rather slower than average rate of development of ripe sperm. Temperatures were

not taken on this occasion. The rather slow rate of development of ripe sperm in this case was probably partly due to an injury, as the rectum was perforated when tapping the gonad on July 2nd.

July 2, 1924.	No ripe sperm-morulæ.	Fair no. of young sperm-morulæ.	Fair no. of unspawned ova.	Male category = No. III.
July 8, 1924.	A few ripe sperm.	f ∞ large developing sperm-morulæ.	Fair no. of ova in spots.	do. = No. V.

General Remarks on the Sex-condition following Egg-spawning.

The results of the examination of the sex-condition of oysters at various periods after egg-spawning given in Table VI, p. 985, and shown in the series of graphs in Fig. 1, p. 991, may now be reviewed along with the information obtained from the experiments on the rate of development of sperm. The correlation between increase of age of gonad after egg-spawning and increase in maleness is clear, in spite of the slight weakness in the evidence due to the small numbers of individuals examined in Periods A and B. It is therefore a fact that the gonad of an oyster changes at once to sperm-producing at some very early period after the egg-spawning act, and very quickly develops fair quantities of freshly formed ripe sperm-morulæ. The change of the gonad to a purely sperm-producing phase occurs generally, but not always, within at least a few hours after the spawning act has taken place. In a small percentage of cases observed, this change did not occur apparently up to twelve days or more after the egg-spawning, but it has been noted that a good proportion of these abnormal gonads occurred amongst individuals which spawned late in the season. Although the sperm-producing phase usually begins within a few hours after spawning and continues at a quick average rate a small proportion of individuals show lagging on this general rate. The average rate of development of maleness can be obtained by plotting the mean age of the gonads—after egg-spawning—in each period, against the mean stage of development of maleness in the same gonads, the figures for which are given in Table VI, p. 985. The graph obtained from these data is given in Fig. 2 on p. 993. It will be seen that Fig. 2 is a common form of growth curve, showing a very rapid growth on the average during the first three days and thereafter slowing down considerably; growth indeed would appear to be approaching a maximum even in the period under consideration, that is, on the average $8\frac{1}{2}$ days, but covering a period up to 10 to 12 days. Thus the development of maleness is very rapid, and serves as an example of the difficulties which have to be overcome in observing sex-changes. It is necessary at this point to draw attention to the fact that the growth curve in Fig. 2 is more qualitative than quantitative; it is probable that a quantitative curve—such as

might be obtainable by a possible modification of Manoiloff's sex-reaction —would show a similar sharp rise, but a continuance of the rise over a longer period. Further, there is no doubt whatever that an imaginary

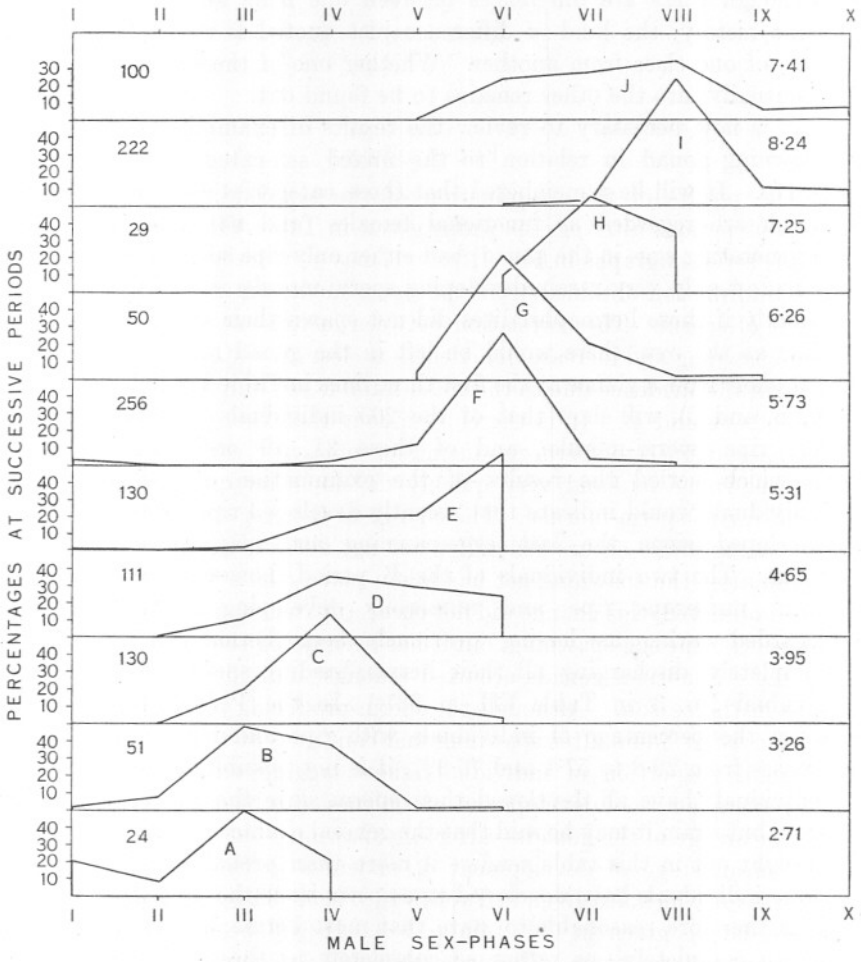

FIG. 1.—The series of graphs A to J show the percentage frequencies of different male sex-phases of *O. edulis*, in relation to the progressive ages A to J of the gonad—reckoned from the instant of the last egg-spawning.

The graphs A to F are constructed from data derived from oysters actually carrying embryos or larvæ at the time of examination; graphs G to J from individuals which, after being found with young, had been isolated in tanks or in experimental cages in the sea.

I to X are sex-phases defined on p. 981; the figures on the right-hand side of each graph give the mean sex-condition in each period.

A to J are periods defined on pp. 983 and 1022; the numbers on the left-hand side of each graph give the total number of individuals examined in each period.

quantitative determination of maleness in the well-fished pure males, which one finds especially at the beginning of the breeding season, would give numerical results estimated fiftyfold of those obtainable from the males which develop immediately from the recently spawned females. Although there are differences between one male and another of the same history, the kind of difference just quoted is regarded rather as that of one class from another. Whether one of these classes develops eventually into the other remains to be found out.

It is now necessary to review the results of examining the post-egg-spawning gonad in relation to the mixed sex-categories recorded on p. 976. It will be remembered that those categories of hermaphrodites, which are regarded as functional females (and not individuals with degenerating eggs in the gonad) had either only ripe sperm-morulæ in the gonad or only very rarely developing sperm-morulæ in addition. Consequently if these hermaphrodites did not spawn their sperm at the same time as the ova, there would be left in the gonad mainly *ripe* sperm-morulæ. Now a glance at the first three lines in Table VI, p. 985 (Periods A, B, and C), will show that of the 205 individuals examined only 21 had ripe sperm-morulæ, and of these 21, 19 occur in Period C, in which period the results of the examination of the B and D individuals would indicate that recently developed ripe sperm-morulæ—developed since the last egg-spawning act—may be expected to occur. The two individuals of the B period, however, which showed both numerous ripe and numerous developing sperm, must be regarded rather as having previously been hermaphrodite without completely discharging all their hermaphroditic sperm. (Compare individual No. 3 in Table VII, p. 987.) In the Periods D, E, and F, when the percentage of individuals with ripe and ripening sperm increases from 29·8 to 57·1 and 76·9%, it is not possible to say that these individuals have all developed their sperm since the last egg-spawning act ; but again it may be said that the general character of the correlation brought out in this table renders it more than probable that nearly all these individuals have developed ripe sperm since the last egg-spawning. It is therefore reasonable to state that most hermaphrodite individuals spawn completely—or rather as completely as the pure females—and that only in those cases where an incomplete spawning occurs will ripe sperm-morulæ be left behind in the gonad after the spawning act. Therefore the views of Hoek and Möbius—that individuals of *O. edulis* spawn essentially as males or females—are justified by the results described above.

When the results obtained in this work are looked at as a whole—after making allowance for the non-development of maleness in some individuals, and for other small deviations, which may be pathological or abnormal—it is clear that the instant an oyster spawns as a female a

distinct point is reached in the sexual rhythm in the species. It will therefore now be possible to work towards this fixed point and forward from it in order to unravel systematically the sex-phenomena in the species. It is possible, therefore, to state categorically that—excepting a small percentage of abnormal or pathological individuals, among which are included the spawners at the end of the season—all female

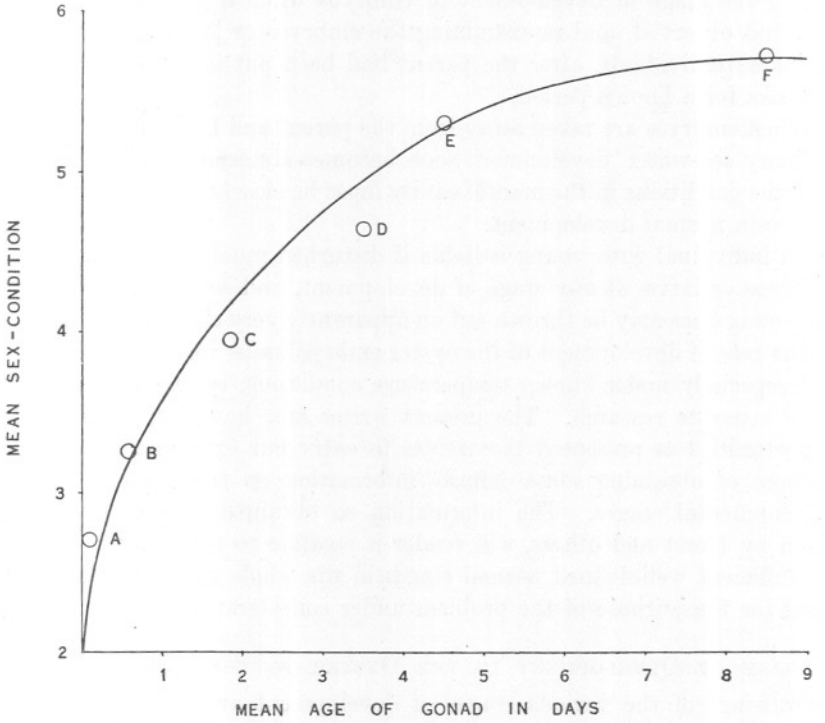

FIG. 2.—Graph showing rate of development of maleness in 702 oysters which were carrying young at the time of examination.
A to F are mean periods of age of the post egg-spawning gonad in groups of individuals with gonads of progressively increasing age as defined on p. 983.

oysters (*O. edulis*) normally change their sex at, or within, a few hours after spawning, and develop ripe sperm, generally in abundance, before their larvæ are normally set free in the water.

EXPERIMENTS AND OBSERVATIONS ON THE RATE OF DEVELOPMENT OF THE OYSTER EMBRYO AND LARVA.

A good general account of the development of the oyster larva (*O. edulis*) is given by Horst (1883), who, like preceding workers, found it impossible to rear the larvæ outside the body of the oyster from the segmentation stages, or, indeed, from later stages. The course of the development

was therefore determined by observing overlapping sectional periods of differentiation. Artificial fertilisation cannot be performed at present in the case of *O. edulis* with much chance of obtaining a normal rate of development, therefore Horst's method of finding the age of embryos and larvæ at different stages of development has been used mainly by the present writer, but some stages have in addition been followed by noting the stage of development of embryos when a gravid individual was first observed, and re-examining the embryos or larvæ given off by the same individuals, after the parent had been put back in the sea or in tanks for a known period.

When embryos are taken away from the parent and kept in unchanged ordinary sea-water, development soon becomes abnormal, and it is clear that the conditions in the mantle cavity must be closely imitated in order to obtain normal development.

An individual with young is liable if disturbed much to throw out its embryos or larvæ at any stage of development, and sometimes in tanks the young ones may be thrown out on apparently very slight provocation.

The rate of development of the oyster embryo under known conditions, and especially under known temperature conditions, is still a fit subject for a separate research. The present writer has, however, taken such opportunities as presented themselves to carry out experiments for the purpose of obtaining some definite information on the age of various developmental stages. The information so obtained, along with that given by Horst and others, will render it possible to fix an average age for sufficient well-defined normal stages in the whole course of development for the purpose of the problem under consideration.

Outline of Development in the Oyster to the Larval Stage.

Drawings of the various stages of development are given by Horst (loc. cit. Plate VI). In the mantle cavity of an oyster all stages in development may be found from the unsegmented—but generally fertilised egg as is denoted by the presence of two nuclei with or without a spindle—to the fully formed pigmented and fully shelled larvæ.

In the early segmentation stages embryos with any number from one to eight blastomeres may be found, but regular division at least into two and afterwards into four blastomeres is more common. In stages later than eight to sixteen blastomeres it becomes difficult to see at a glance how many blastomeres occur, and it is safer to count the nuclei by compressing the embryo, in order to obtain information from the fresh object. From the 16-celled to the 32-celled stage the embryo often takes on the appearance of a morula, that is, a sphere made up of small spheres, whose outlines stand out on the periphery of the larger sphere. In the 32-celled stage, and a little later, the embryo attains a good

spherical shape, and with a slight depression at one place marking the beginning of the blastoporal invagination. At about the 64-celled stage the blastopore is well developed, and the depression noted above is well-marked. At about the 100 nucleated condition the embryo lengthens, and a new depression (the shell anlage) appears to give an elongated heart-shaped embryo. At this stage the embryo becomes ciliated, and a shell rudiment appears in the new depression noted and gradually extends over the embryo, while at the same time the original band of cilia develops into the velum. Finally, the shell completely covers the embryo, and the velum can be retracted entirely within the larval shell. At this stage the larva leaves the parent.

The colour of the embryos from the early stages to the ciliated heart-shaped larva is white, and an individual carrying such embryos is said to be whitesick. From the early stage of development of the shell to the stage when the shell is about 150μ long, the colour of the larvæ is white in bulk, but appears more and more grey as the shell develops when the larvæ are seen dispersed in a little water. When the shell is about 160μ long the larvæ have first a grey appearance in bulk, and then with very slight increase in length of the shell begin to acquire colour, due to pigment appearing in the digestive gland. The grey larvæ pass successively through shades of lavender-grey, heliotrope, light slate, dark slate, to a purplish black, and in some cases to quite a good black colour when seen in bulk as the pigment increases in the digestive gland. Individuals found with grey-coloured larvæ are called greysick, and others black-sick when carrying any of the definitely coloured larvæ. The length of the shell in the coloured larvæ increases with the pigmentation from about 170μ to about 190 to 200μ. Occasionally larvæ are found in the mantle cavity with shells 210μ long and rarely 220μ, but the purplish black larva generally has a shell ranging from 180 to about 200μ, and undoubtedly varies in size at equivalent stages of differentiation. Indications have been obtained that the shell is developed more rapidly at high temperatures (e.g. over 70° F.) and retarded in growth at low temperatures (e.g. about 60° F.). It is probable that larvæ develop somewhat differently, and are emitted in slightly different conditions at different seasons, and places.

Generally all the embryos or larvæ of an individual are developed to the same stage, but occasional instances have been noted of slightly different early stages in one mantle cavity, and rather more frequently, but not commonly, two sizes of coloured larvæ; the latter cases have seemed to be more common in dumpy oysters.

Experiment 1.

On June 23, 1926, a sample of oysters was dredged at Turnaware Bar, Fal Estuary, and brought at once to the beach for examination. The

oysters were opened rapidly, and at 11.55 a.m. an individual which had just spawned was discovered. The history of the development of this batch of eggs is as follows :—

			Approximate age of embryos.
June 23	11.55 a.m.	Eggs just extruded, entire, with 2 nuclei, transferred to sea-water : estimated that egg-extrusion occurred at about 11.30 a.m.	
	2.40 p.m.	Practically all in 2-celled stage, one 3-celled stage seen	3 hours.
	2.50 p.m.	4 nuclei showing clearly . . .	
	4.30 p.m.	4-celled stages now distinct . .	5 hours.
	8.45 p.m.	Small proportion 8-celled and a few with 16 nuclei	9¼ hours.
	midnight	16-celled stages common ; no 32-celled stages seen	12½ hours.
June 24	1.30 a.m.	do.	
	2.30 a.m.	16-celled beginning to pass to 32-celled stage ; a few 20 to 21 nucleated stages seen	15 hours.
	9.30 a.m.	32-celled stages common, good spherical embryos in morula and early blastopore stages ; one 50-nucleated stage seen	22 hours.
	3 p.m.	32 to 64 nuclei present, but embryos mostly still in 32-celled stage and of good spherical shape . . .	27½ hours.
	6.25 p.m.	Mostly 40 to 50 nuclei ; 64 nuclei rare .	
June 25	10.25 a.m.	Beginning of heart-shaped stage, but 50 to 64 nuclei only (cold overnight). The embryos could not be examined afterwards	47 hours.

The temperature conditions could not be determined accurately in this —partly a field—experiment ; the water in the vessel used was, however, probably 65° to 70° F. from June 23 to 2.30 a.m. June 24, and thereafter colder, and falling to below 60° F. in the night of June 24–25.

When the individual used for Experiment 1 was obtained, the dredging was continued at the same place as before, from 11.30 a.m. to 2 p.m., and a sample of oysters obtained which was not opened until 10.40 to 11 a.m. on

June 25th. One individual in this sample was found with young embryos, which may not unreasonably (see Table I, p. 979) be regarded as a control on Experiment 1. At about 11 a.m. on June 25 the embryos of this oyster were found to be mainly 32-celled in good morula stages with a fair number of 50-to 64-celled stages. These embryos were therefore in almost exactly the same stage at the same time as the experimental embryos, and since natural spawning had not begun on the beds on June 23, it is reasonable to suppose that spawning had been precipitated in both these cases by the act of dredging, and that therefore the embryos were about the same age.

Experiment 2.

A sample of oysters were dredged, June 30, 11.30 a.m. to about noon (East Bank, Fal Estuary), and when examined later the following sick oysters were found :—

1926.		No. 1.	No. 2.	Approximate age* of embryos. 1.	2.
June 30	3.50 p.m.	Embryos in 2- and 3-celled stages .		4 hrs.	
	4.15 p.m.		Embryos in 2-celled stages .		$4\frac{1}{4}$ hrs.
		transferred samples of embryos to water.			
July 1	1.15 a.m.	Embryos in 7-celled stages . .		$13\frac{1}{2}$ hrs.	
	1.25 a.m.		Embryos in 16-celled stages .		$13\frac{1}{2}$ hrs.
	10.15 a.m.	16 passing to 32-celled stages, 20 nuclei seen . .		$22\frac{1}{2}$ hrs.	
	10.20 a.m.		16 passing to 32-celled stages, 24 nuclei seen		$22\frac{1}{2}$ hrs.
			Embryos of good spherical shape, odd ones showing beginning of blastopore invagination.		

In this experiment the room temperature remained fairly constant between 65·5° F. and 66·5° F.

* Assuming that spawning occurred about 11.45 a.m.

Experiments 1 and 2, confirmed by other similar observations, suffice to enable the approximate times of the attainment of definite early segmentation stages to be fixed as follows :—

No. of blastomeres.	2	4	8	16	32, morula and early blastopore stage.
Age	2–2½ hrs.	4½ hrs.	8½–9 hrs.	11–12 hrs.	about 20 hrs.

64, early heart-shaped not ciliated embryo, about 46 hours.

From this information can safely be extracted the data required for the purposes of determining the early periods of development, namely,

(A) that the 0 to 4-celled stage is attained in 0 to about 4½ hours, and

(B) that the 8 to 32-celled stages is attained in about 8½ to 20 hours.

A number of experiments designed to obtain information on the succeeding stages of development can be summarised as follows :—

Expt.	Date.	Approximate age. 12 to 20 hrs.	1½ to 2 days.	2½ to 3 days.	3½ to 4 days.
III.	July 6–7, 1924.	Morulæ at 7 p.m.	Heart-shaped, not ciliated.	—	—
IV.	July 6–8, 1924.	do.	—	Heart-shaped, not ciliated.	—
V.	June 4–5, 1926.	Early blastopore.	Heart-shaped, not ciliated.	—	—
VI.	June 3–7, 1926.	Morula at 7.30 p.m.	Early heart-shape.	Good heart-shaped, not ciliated.	Ciliated at 11 a.m., 7th, trace of shell.
VII.	June 3–5, 1926.	Morula at 7.20 p.m.	—	Heart-shaped and just ciliated.	—

The experiments just recorded, confirmed by many similar ones, enable us to fix the next period of development required for the purposes of the present paper, namely, that

(C) the 40-nucleated stage to the elongated heart-shaped, but not ciliated, stage is reached in from 30 hours to 2½ days.

(D) The elongate heart-shaped and ciliated stage with or without a trace of the larval shell is attained in from 3 to 4 days.

Some experiments on the rate of development to the coloured and fully-shelled larva have already been recorded (Orton, 1926, p. 217), showing that this stage was attained in temperatures mainly 62·5° to 64·0° F. in 6 to 7 days. Spärck (1924, pp. 31 and 46) has made similar observations. It is now possible, therefore, to complete the definition of periods of development as follows :—

(E) The incompletely shelled larva with a shell varying in length from about 40 to 150μ—or rarely to 170μ—is normally developed in from 4 to 5 days.

(F) The coloured and fully-shelled larva is developed normally in 6 and retained normally to 10 or 12 days (see Orton, 1926, p. 216), and has an average length of shell ranging from 170μ to 200μ.

It has been found, however, that at temperatures of about 60° F., the grey-shelled period may be prolonged to as long as 12 days, and in a similar way coloured larvæ may be retained in isolated cases for a long period in cold weather, and especially towards the end of the breeding season.

TABLE IV.

DETAILED RESULTS OF THE EXAMINATION OF THE EMBRYOS AND LARVÆ, THE GONAD, AND OTHER CHARACTERS OF 702 OYSTERS IN SPAWN.

1	Gonad of adult.			Embryos and larvæ.		7	8
	2	3	4	5	6		
Serial Numbers.	Ripe sperm-morulæ.	Unripe sperm-morulæ.	Ripe unspawned. ova.	Colour.	Stage of development.	Period of development of embryos and category of gonad.	Remarks.
1. 1920. DREDGED YEALM, JULY 17; KEPT IN PLYMOUTH TANKS, EXAMINED JULY 30.							
1	none	∞	some	White	heart shaped	C4	
2. 1921. A WHITSTABLE OYSTER KEPT IN THE TANKS AT PLYMOUTH, JUNE 15.							
2	∞	∞	—	Black	Not Observed.	F6	
3. A COWES OYSTER KEPT IN TANKS AT PLYMOUTH, JULY 6.							
3	few	∞	—	Bl.	N.O.	F5	
4	∞	∞	—	do.		F6	
4. YEALM OYSTERS KEPT IN TANKS AT PLYMOUTH, NUMBER 5, WHITESICK, JULY 4; ALL EXAMINED JULY 7.							
5	some	some	—	Wh.	N.O.	—	
6	none	∞	—	Wh.	N.O.	—	
7	some	∞	—	Grey	N.O.	E5	
5. HAND-COLLECTED, GREAT WESTERN WHARF, PLYMOUTH, JULY 12; EXAMINED JULY 13.							
8	none	some	a few	Wh.	early segm. stages	B3–4	
6. WHITSTABLE OYSTER, DREDGED JULY 26; EXAMINED AUGUST 4.							
9	—	∞ young	∞	Wh.	heart shaped ciliated	D3	
7. SWANSEA OYSTER KEPT IN TANKS AT PLYMOUTH; EXAMINED SEPTEMBER 12, 1921.							
10	none	∞	—	Wh.	heart shaped ciliated	D4	
8. 1922. DREDGED WEST MERSEA, JUNE 15; EXAMINED JUNE 19.							
11	∞	∞	—	Bl.		F6	
12	none	a few	some	Wh.	N.O.	—	
13	fair no.	fair no.	some	Bl.		F6	
14	none	a few	∞	Wh.	N.O.	—	

1	2	6	4	5	6	7	8
			9. DREDGED YEALM, JUNE 21; EXAMINED JUNE 22.				
15	a few	∞	occ.	Wh.	ciliated	D5	
16	none	fair no.	none	do.	do.	D4	
17	none	a few	∞	do.	do.	D4	
			10. DREDGED IN DEEPS, WEST MERSEA, JUNE 28; EXAMINED JUNE 28 AND 29.				
18	none	a few	—	Wh.	ciliated	D4	
19	a few	∞	none	do.	do.	D5	
20	none	a few	do.	do.	do.	D4	
21	none	fair no.	∞ relict	do.	morula	B4	
			11. DREDGED THORNFLEET, WEST MERSEA, JUNE 29; EXAMINED 29 AND 30.				
22	fair no.	∞	none	Bl.		F6	
23	none	fair no.	∞	Wh.	1–4 celled	A4	inc. sp.
24	fair no.	∞	none	Bl.		F6	
25	none	a few	—	Wh.	1–5 celled	A4	
			12. DREDGED VARIOUS GROUNDS, WEST MERSEA, JULY 3; EXAMINED JULY 4				
26	∞	∞	none	Bl.		F6	
27	∞	∞	none	do.		F6	
28	∞	∞	none	do.		F6	
			13. DREDGED VARIOUS GROUNDS, WEST MERSEA, JULY 4; EXAMINED JULY 5.				
29	f ∞	∞	none	Bl.		F6	
30	∞	∞	do.	do.		F6	
31	f ∞	∞	do.	do.		F6	
			14. DREDGED JULY 8 VARIOUS GROUNDS, WEST MERSEA; EXAMINED JULY 9.				
32	none	fair no. young	fair no.	Wh.	N.O.	—	
33	do.	do.	do.	do.	segn. stages	B3	
34	do.	few very young	do.	do.	heart shaped	C3	
35	do.	f ∞ young	a few	do.	late segn. stages	C3	
36	do.	∞	none	do.	do.	C4	
37	do.	∞	fair no.	do.	do.	C4	
38	a few	∞	a few	Wh.-gr.	small shells	E5	
39	none	few young large number	some very young?	Wh.	1–3 celled	A3	
40	none	∞ young	a few	do.	late segn. stages	C3	
41	do.	do.	do.	do.	N.O.	—	
42	do.	∞	some	do.	late segn. stages	C4	
			15. DREDGED HELFORD RIVER, JULY 12/22; EXAMINED JULY 13.				
43	rare	∞	none	Bl.		F5	
44	∞	∞	none	do.		F6	V, 162
			16. DREDGED WHITSTABLE 21.7.22; EXAMINED 23.7.22.				
45	a few	∞	a few	Bl.		F5	
			17. DREDGED WHITSTABLE, 27.7.22; EXAMINED 31.7.22.				
46	fair no.	∞	N.O.	Wh.	early shelled stage	E6	V, 178
47	fair no.	∞	∞ relict	Wh.	ciliated	D6	
48	do.	do.	few	Bl.		F6	
49	f ∞	f ∞	a few	do.		F6	
50	fair no.	∞	none	Bl.		F6	

1	2	3	4	5	6	7	8
	18. DREDGED PORT NAVAS 31.7.22; EXAMINED 1.8.22.						
51	few	∞	few	Wh.	ciliated	D5	
52	f ∞	∞	few	Wh.	early shelled	E6	
53	rare	∞	none	Bl.		F5	
54	f ∞	∞	N.O.	Wh.	⅔ shelled	E6	
55	few	v. ∞	few	Bl.		F5	
56	few	few only	few	Bl.		F5	
57	f. no.	∞	none	do.		F6	
58	few	∞	few	do.		F5	
59	f ∞	∞	few	do.		F6	
	19. DREDGED WHITSTABLE, 1.8.22; EXAMINED 2.8.22.						
60	f no	∞	none	W.	late segn. stages	C6	
61	few	∞	few	do.	just ciliated	D5	
62	none	∞	none	do	heart shaped	C4	
63	rare	∞	fair no.	do.	late segn. stages	C5	
64	none	∞ young	few	do.	late segn. stages	C3	
65	do.	∞ young	fair no.	do.	middle segn. stages	B3	
	20. DREDGED WHITSTABLE, 3.8.22; EXAMINED 4.8.22.						
66	none	few to fair no.	good no.	Wh.	∞ unsegmented to late segn. stages	C4	
67	∞	∞	none	Bl.		F6	
68	none	fair no.	few	Wh.	∞ unsegmented to late segn. stages	C4	spotty
69	none	none	∞	do.	do.	C1	Note 1
70	none	fair no.	few	do.	do.	C4	
71	none	few	few	do.	do.	C4	
	21. DREDGED WEST MERSEA, 3.8.22, EXAMINED 4.8.22 (BROOD OYSTERS, 33 TO 40 MMS. LONG).						
72	none	few young	few	Wh.	morula stage	B3	
73	few	few	N.O.	Bl.		F5	
74	— none	few	∞	Wh.	late segn. stages	C4	
75	none	∞ v. young	few	do.	do.	C3	
76	few	∞	few	do.	just ciliated	D5	
	22. DREDGED, HELFORD RIVER, 16.8.22; EXAMINED 17.8.22.						
77	f ∞	f ∞	some	Bl.		F6	
	23. DREDGED, RIVER YEALM, 23.8.22; EXAMINED 24.8.22.						
78	few	∞	none	Wh.	early shelled stage	E5	
79	do.	f ∞	do.	do.	do.	E5	
	24. DREDGED, RIVER YEALM, 30.8.22; EXAMINED 31.8.22 AND 1.9.22.						
80	f ∞	f ∞	none	Bl.		F6	
81	f ∞	f ∞	none	do.		F6	
82	v ∞	v ∞	none	do.		F6	

1	2	3	4	5	6	7	8
25. 1923. DREDGED WEST MERSEA, AUGUST 3; EXAMINED AUGUST 6/23 (1921 SPAT).							
83	few	∞	none	Wh.	shelled	E5	
26. YEALM OYSTER, KEPT IN PLYMOUTH TANKS; EXAMINED AUGUST 31/23.							
84	∞	∞	none	Bl.		F6	
27. YEALM CAGE OYSTER ♂, JULY 9/23; EXAMINED FOR EMBRYOS 31.8.23, FOR SEX-CONDITION 4.9.23.							
85	a few	∞	none	Bl.	mainly 170μ	F5	
28. DREDGED THORNFLEET, WEST MERSEA, 18.7.23; EXAMINED 18.7.23.							
86	∞	∞	—	Sl.	180μ	F6	
29. DREDGED THORNFLEET, WEST MERSEA, 25.7.23; EXAMINED 26.7.23.							
87	none	f ∞	∞	Wh.	early shelled	E4	patchy
30. DREDGED NOSS END, WEST MERSEA, 26.7.23; EXAMINED 27.7 23							
88	fair no.	∞	none	Bl.	170μ	F6	
89	none	a few very young	—	Wh.	early shelled	E3	
31. DREDGED NOSS END, WEST MERSEA, 27.7.23; EXAMINED 28.7.23.							
90	none	fair no. v. young, a few nearly ripe 70μ	few	Wh.	early shelled	D4	
91	a few	fair no.	none	Gr.		E5	
32. DREDGED THORNFLEET, WEST MERSEA, 30.7.23; EXAMINED 31.7.23 (ESTIMATED 1921 SPAT).							
92	∞	∞	none	Bl.		F6	
93	∞	∞	none	Wh.	early shelled	E6	
33. SAME, 2.8.23; EXAMINED 3.8.23.							
94	none	f ∞ young	some	do.	late segn. stages	C3	
34. 1924. DREDGED JUNE 3, 1924, VARIOUS GROUNDS, WEST MERSEA EXAMINED 7–8.6.24.							
95	none	f ∞ young	some	Wh.	unsegmented	A3	
96	—	some very young	few	Wh.	N.O.	—	
97	—	∞young	none	do.	N.O.	—	
98	—	∞ large with 500 subdivisions	none	do.	just ciliated	D4	
99	none	few young 8–30 cells, a few bigger	few	do.	late segn. stages	C3	
35. DREDGED BURNHAM RIVER BEDS, 3.6.24; EXAMINED 7.6.24.							
100	none	∞ young	—	Gr.-Wh.	shell young	E3	
101	∞	∞	—	Wh.	N.O.	—	
102	some	fair no.	—	do.	N.O.	—	

1	2	3	4	5	6	7	8
36. DREDGED THURSLEET AND NOSS END, WEST MERSEA, 12.6.24; EXAMINED 13.6.24.							
103	∞	∞	none	Bl.	N.O.	F6	
104	∞	∞	none	do.	N.O.	F6	
37. DREDGED BACK OF NOSS, WEST MERSEA, 30.6.24; EXAMINED 1.7.24.							Colour of digestive organ.
105	f ∞	a few	none	Lilac Grey		F7	— Note 2
106	∞	a few	do.	Bl.		F7	fawny brown
107	∞	∞	do.	do.		F6	do.
108	∞	∞	few spots	Bl.		F6	do.
109	fair no.	fair no.	fair no.	Wh.	trace of shell	D6	—
110	∞	∞	few spots	Bl.		F6	fawny brown
111	none	fair no. v. young	few spots	Wh.	early segn. stages	B3	brown
112	none	do.	do.	do.	do.	B3	do.
113	∞	∞	do.	do.	ciliated with shell rudiment	D6	yellow
114	none	∞	few	do.	late segn. stages	C4	fawny brown
115	f ∞	∞	one spot	do.	½ shelled	E6	yellow-brown
116	none	∞	few	do.	late segn. stages	C4	choc. brown
117	fair no.	∞	few	do.	just ciliated	D6	yellow-brown
118	none	f ∞	few	do.	late segn. stages	C4	light choc. brown
119	few	∞	few	do.	ciliated	D5	yellow
120	none	∞	few	do.	late segn. stages	C4	choc. brown
121	∞	∞	do.	Gr.	shelled	E6	yellow-brown
122	one seen	∞	fair no.	Wh.	late segn. stages	C5	choc. brown
123	none	f ∞ v.young	few	do.	do.	C3	do.
124	few	∞	few	do.	shell rudiment	D5	yellow-brown
125	none	fair no.	few	do.	late segn. stages	C4	light choc. brown
38. DREDGED VARIOUS GROUNDS, WEST MERSEA, 1.7.24; EXAMINED 2.7.24.							
126	∞	fair no. large	none	Bl.		F6	N.O.
127	∞	do.	do.	do.		F6	N.O.
128	∞	do.	do.	do.		F6	yellow-brown
129	rare	∞	do.	Wh.	late segn. stages	C5	choc. brown
130	none	f ∞ young	do.	do.	do.	C3	N.O.
131	few	v ∞	few spots	do.	do.	C5	light choc. brown
39. DREDGED SOUTH SHORE, WEST MERSEA, 2.7.24; EXAMINED 3.7.24.							
132	few	∞	few spots	Wh.	heart shaped	C5	choc. brown
133	∞	few	none	Bl.		F7	yellow-brown
134	f ∞	∞	few	Gr.	½ shelled	E6	fawny colour
40. DREDGED VARIOUS GROUNDS, WEST MERSEA, 4-6-7.24; EXAMINED 5-7-7.24.							
135	f ∞	∞	few	Bl.		F6	brown
136	∞	∞	none	do.		F6	good chocolate

1	2	3	4	5	6	7	8
41. YEALM CAGE EXPERIMENT OYSTERS "SICK," 1923, AND "SICK" AGAIN 16.7.24; EXAMINED FOR SEX 18.7.24.							
137	none	f ∞ to 40μ	none	Wh.	ciliated	D3	
138	none	a few to 40μ	fair no.	Wh.	do.	D3	
42. YEALM CAGE EXPERIMENT OYSTERS ♂ 1923, AND "SICK," 8.8.24.							
139	f ∞	∞	a few	Sl.	160–175μ	F6	
140	∞	∞	none	Bl.	170–180μ	F6	
YEALM CAGE EXPERIMENT OYSTER "SICK," 1923, AND "SICK" AGAIN 8.8.24.							
141	fair no.	∞	none	Sl.	180–190μ	F6	
43. DREDGED PERCUIL RIVER, FAL ESTUARY, 15.8.24; EXAMINED 18.8.24 FOR EMBRYOS, 23.8.24 FOR SEX.							
142	∞	fair no.	none	Gr.	170μ	E6	
143	∞	f ∞	none	Wh.	ciliated	D6	Note 3
144	fair no.	∞	none	Sl.		F6	
44. YEALM CAGE 3 OYSTERS, MALE 1923; SPAWNED 27/28–8.24; EXAMINED 28.8.24.							
145	f ∞	f ∞	none	Sl.	170μ	F6	
146	f ∞	a few	none	do.	170μ	F7	
147	f ∞	f ∞	few	do.	N.O.	F6	
45. EXPERIMENTAL OYSTERS FROM CAGE KEPT IN THE SEA AT WEST MERSEA, CAGE HAULED JUNE 30, OYSTERS EXAMINED JULY 1ST TO 8TH 1924.							
148	N.O.	N.O.	N.O.	Wh.	ciliated	—	♂ in July, 1923,* (July 1, 1924.)
149	none	fair no. young	fair no.	N.O.		D3	♂ in July, 1923, (July 2, 1924.)
150	few	f ∞ large	do.	N.O.		F5	♂ in July, 1923, (July 8, 1924.)
151	none	∞ 110 × 30.μ	few spots	Wh.	heart shaped	C4	♂ in July, 1923, (July 7, 1924.)
152	none	∞ tailed and nearly ripe	fair no.	do.	do.	C4	♀ in July 1923, (July 8, 1924.)
153	none	∞	few	do.	morula stages on the 6th	C4	♀ in July, 1923, (July 8, 1924.)
154	f ∞	∞	none	Sl.		F6	♂ in July, 1922 (July 1, 1924.)
155	none	f ∞ young	f. ∞ relict	Wh.	morula stages on 6th	C3	♂ in July, 1922. (July 8 1924.)
156	none	a few very young ?	v. ∞ relict	do.	segmentation stages	B2	♀ in July, 1922, (July 6, 1924.) ¼ spent.
46. DREDGED EAST BANK (WATERING), FAL ESTUARY, 1.7.25; EXAMINED 2.7.25.							
157	none	f ∞ to 60μ	few groups	Wh.	heart shaped	C4	
158	a few	do.	do.	do.	do.	C4	
159	f ∞	f ∞	none	do.	trace of shell	D6	
160	none	f ∞ to ca 60μ	∞ patches	do.	heart shaped	C4	
161	none	few full size	f ∞	do.	ciliated	D4	d
162	do.	do.	∞	do.	stage doubtful	—	d
163	f ∞	∞	none	do.	½ shelled	E6	d
164	rare	f ∞	few	do.	do.	E5	d
165	none	few young	few	do.	morula	B3	d
166	rare	fair no.	few patches	do.	do.	B5	d

* The dates of examination of individuals in lot 45 are given in brackets.

1	2	3	4	5	6	7	8
			THE SAME LOT EXAMINED 4.7.25.				
167	rare	f ∞	none	do.	ciliated	D5	
168	none	few small	fair no.	do.	heart shaped	C3	
169	fair no.	f ∞	few patches	Gr.	early shelled	E6	
170	none	f ∞	do.	do.	do.	E4	
171	do.	fair no.	do.	do.	do.	E4	d
172	do.	fair no. medium size	none	do.	do.	E4	d
			47. DREDGED TURNAWARE BAR, FAL ESTUARY, 8.7.24; EXAMINED 11.7.25.				
173	none	∞ to 50μ	few patches	Wh.	ciliated	D4	11.7.25
174	few	∞	do.	do.	do.	D5	do.
175	none	few very young	do.	do.	late segn. stages	C3	do.
176	do.	∞ to 80μ	—	do.	just shelled	C4	12.7.25
177	do.	f ∞ nearly ripe	few	do.	ciliated	C4	do.
178	f ∞	∞	—	do.	early shelled	D6	do.
179	rare	∞	few	do.	ciliated	D5	do.
180	∞	∞	few patches	Bl.		F6	do.
181	∞	some	none	do.		F7	do. d
182	none	few	—	Wh.	ciliated	D4	do. d
			48. DREDGED EAST BANK, 15.7.25; EXAMINED 18.7.25.				
183	none	few very young	few	Wh.	spherical	C3	
184	do.	∞ to 30μ	do.	do.	do.	C3	
185	few	f ∞ to 70μ	f ∞	Bl.		F5	
186	none	∞ to 70μ	none	do.		F4	
187	f ∞	∞	few	do.		F6	
188	fair no.	f ∞	few	do.		F6	
189	none	∞ v. young?	some	Wh.	just shelled	D2	
190	do.	∞ to 30μ	few	do.	spherical	C3	
191	do.	∞ v. young?	fair no.	do.	do.	C2	
			49. DREDGED EAST BANK (WATERING) AND MYLOR BANK, 22.7.25; EXAMINED 24.7.25.				
192	none	∞	few patches	Gr.	little shell	D4	
193	∞	∞	—	Bl.		F6	
194	∞	f ∞	∞	do.		F6	
195	few	f ∞	few patches	Gr.	some shell	E5	
196	∞	∞	none	Bl.		F6	
197	∞	f ∞	do.	Wh.	trace of shell	D6	
198	none	f ∞ to 30μ	do.	Wh.	do.	D3	
199	f ∞	∞	few patches	do.	ciliated	D6	
200	none	∞ to 70μ	do.	do.	trace of shell	D4	
201	f ∞	∞	do.	do.	¼ shelled	E6	
202	few	∞	none	Bl.		F5	
203	none	f ∞ small	few patches	Wh.	trace of shell	D3	d
204	do.	f ∞	∞ patches	do.	ciliated	D4	d
205	do.	∞	few patches	do.	do.	D4	d
206	do.	few	do.	do.	trace of shell	D4	d
207	∞	∞	few patches	Wh.	½ shelled	E6	d
208	fair no.	f ∞	one patch	do.	nearly fully shelled	E6	d
209	rare	∞	few patches	Gr.	¾ shelled	E5	d
210	none	few	∞ patches	Wh.	late segn. stages	C4	d
211	do.	∞	few patches	do.	trace of shell	D4	sl. d
212	rare	very rare	none	do.	½ shelled	E5	d
213	fair no.	∞	∞ patches	do.	¾ shelled	E6	d

1	2	3	4	5	6	7	8
214	v ∞	v ∞	few patches	Gr.	170μ	E6	sl. d
215	v ∞	fair no.	none	Bl.		F6	d
216	none	rare	few patches	Wh.	trace of shell	D4	d
217	do.	f ∞ small	—	do.	heart shaped	C3	d

50. DREDGED 30.7.25, TURNAWARE BAR; EXAMINED 31.7.25.

218	none	v ∞ to 60μ	one patch	Wh.	late segn. stages	C4	d Note 4.
219	fair no.	∞	occ. patches	Gr.	fully shelled	E6	d
220	f ∞	∞	—	do.	do.	E6	
221	f ∞	v ∞	—	Bl.	190μ	F6	d
222	v ∞	f ∞	—	Gr.	fully shelled	E6	
223	f ∞	∞	—	Bl.		F6	sl. d.
224	none	∞	∞ patches	Wh.	late segn. stages	C4	Examined 2.8.25
225	∞	∞	few patches	Gr.	150μ	E6	
226	∞	∞	one patch	Gr.	150μ	E6	
227	none	f ∞ to 50μ	several patches	Wh.	late segn. stages	C4	
228	do.	∞	nearly ripe few patches	Gr.	150μ	E4	
229	do.	∞ do.	occ.	do.	do.	E4	sl. d
230	v ∞	v ∞	do.	do.	do.	E6	d
231	few	∞	∞ patches	do.	do.	E5	d
232	none	∞	occ.	Wh.	ciliated trace of shell	D4	sl. d
233	∞	∞	none	do.	½ shelled	E6	sl. d
234	none	∞	occ. patches	do.	heart shaped	C4	d
235	fair no.	v. ∞	do.	Lilac-grey		F6	sl. d.

51. DREDGED TURNAWARE POINT AND EAST EDGE, 5.8.25; EXAMINED 6.8.25.

236	f ∞	∞	none	Grey-white	150μ	E6	sl. d
237	∞	f ∞	do.	Bl	200μ	F6	d
238	none	∞	nearly ripe rare patches	Wh.	ciliated trace of shell	D4	d
239	none	none	none	Bl.	180μ	F1 or 10	Note 5. d
240	few	f ∞	fair no. of patches	Gr.	½ shelled	E5	
241	none	∞	none	Grey-white	ciliated trace of shell	D4	
242	∞	∞	none	Bl.	180μ	F6	
243	v ∞	f ∞ large	do.	do.		F6	
244	∞	∞	do.	do.	180μ	F6	
245	fair no.	f ∞	do.	Wh.	ciliated trace of shell	D6	d
246	none	f ∞ to 50μ	few	do.	do.	D4	d
247	few	∞ full size	—	White-grey	⅔ shelled	E5	d
248	∞	∞	few patches	Bl.	200μ	F6	sl. d

52. DREDGED FALMOUTH NORTH BANK 10.8.25; EXAMINED 12.8.25.

249	none	∞ up to 50μ	few patches	Wh.	spherical	C4	d
250	∞	∞	none	Bl.	200μ	F6	d
251	rare	∞	few	Wh.	heart shaped	C5	
252	∞	∞	none	White-grey	⅔ shelled	E6	d
253	f ∞	∞	do.	Bl.	180–190μ	F6	
254	none	∞	few	Wh.	late segn. stages	C4	
255	∞	∞	few patches	Grey-white	½ shelled	E6	Examined 13.8.25
256	fair no.	v ∞	none	Bl.	190μ	F6	
257	none	∞	occ.	Wh.	late segn. stages	C4	
258	few	∞	few	Bl.	180μ	F5	sl. d

1	2	3	4	5	6	7	8
259	f ∞	∞	few patches	Purplish-grey	170μ	F6	
260	∞	∞	∞ patches	Bl.	200μ	F6	d
261	∞	∞	none	do.	190μ	F6	d
262	∞	f ∞	—	Bl.	200μ	F6	N
263	few	few	few patches	Gr.	170μ	E5	N
264	none	v ∞	2 do.	Wh.	late segn. stages	C4	d
265	f ∞	v ∞	2 do.	Gr.	150μ	E6	sl. d
266	f ∞	∞	—	Bl.	180μ	F6	d
267	fair no.	∞	—	Gr.	170μ	E6	d
268	f ∞	f ∞	few patches	Bl.		F6	sl. d
269	none	rare probably ∞ v. small	few patches	Wh.	4–32-celled	B3	
270	none	probably some v. small	∞	do.	heart shaped	B2	½ spent
271	do.	a few young	few	do.	early segn. stages	B3	
272	fair no.	∞	fair no. in patches	do.	heart shaped	C5	
273	none	few to 50μ	few patches	do.	late segn. stages	C4	
274	f ∞	∞	occ. patches	Purplish-grey	180μ	F6	
275	v ∞	v ∞	none	do.	160μ	F6	
276	none	few	few patches	Wh.	late segn. stages	C4	
277	∞	∞	none	Bl.		F6	
278	f ∞	∞	none	Purplish-grey	170μ	F6	

53. DREDGED EAST EDGE, FAL ESTUARY, 11.8.25; EXAMINED 13.8.25.

279	none	none	∞ small patches	Wh.	4–16-celled	B1	d
280	∞	∞	none	Bl.	170μ	F6	d
281	none	∞ small	do.	Wh.	0–4-celled	A3	N
282	do.	probably ∞ v. young	few patches	do.	0–4-celled	A2	N
283	f ∞	∞	occ. patches	do.	ciliated	D6	Sl. d
284	few	∞	—	do.	do.	D5	N
285	none	∞ large	few patches	do.	do.	D4	N
286	few	∞	one patch	Grey-white	ciliated trace of shell	D5	N
287	none	few small	∞ patches	Wh.	0–4-celled	A3	sl. d
288	∞	∞	one patch	Bl.	200μ	F6	N
289	f ∞	∞	none	do.	180μ	F6	sl. d
290	none	none	3 or 4 patches	Wh.	0–4-celled	A1	N
291	none	∞	fair no. of patches	White-grey	ciliated trace of shell	D4	N
292	do.	occ. young	∞	Wh.	0–4-celled	A3	N
293	do.	∞ 50μ	2 patches	do.	heart shaped	C4	N
294	do.	∞	∞ patches	do.	ciliated	D4	N
295	f ∞	∞	few patches	Bl.	190μ	F6	N
296	f ∞	∞	none	do.		F6	N
297	∞	∞	none	Bl.	160–180μ	F6	N
298	∞	∞	do.	do.	200μ	F6	N
299	∞	f ∞	—	do.	160–180μ	F6	N
300	f ∞	f ∞	1 patch	do.	180μ	F6	N Examined 14.8.25
301	f ∞	∞	none	do.	180μ	F6	N
302	∞	∞	—	do.	180μ	F6	sl. d

1	2	3	4	5	6	7	8
54. DREDGED EAST END MYLOR BANK, FAL ESTUARY, 18.8.25; EXAMINED 20.8.25.							
303	∞	f ∞	few patches	Bl.	200μ	F6	sl. d
304	few	∞	many do.	Grey-white	ciliated	D5	d
305	few	∞	none	Gr.	½ shelled	E6	d
306	none	f ∞ small	one patch	Wh.	to 16-celled	B3	N
307	none	∞ to 80μ	1 big patch	do.	heart shaped	C4	N
308	few	∞ full size	∞ scattered	do.	ciliated	D5	d
309	none	v ∞ full size	few	do.	do.	D4	sl. d
310	fair no.	∞	few	do.	do.	D6	N
311	do.	∞	few spots	White-grey	½ shelled	E6	N
312	none	∞	fair no. of patches	Wh.	ciliated	D4	d
313	∞	∞	none	Grey-white	shells 150μ	E6	d
314	f ∞	∞	occ. patches	Gr.	150μ	E6	N
315	few	∞	do.	Wh.	ciliated	D5	N
316	f ∞	∞	do.	Grey-white	½ shelled	E6	N
317	∞	∞	none	Bl.	200μ	F6	N
318	∞	v ∞	few patches	Gr.	150μ	E6	sl. d
319	none	∞	fair no.	Wh.	½ shelled	E4	d
320	do.	∞	occ. patches	Wh.	heart shaped	C4	d
321	do.	f ∞	many patches	do.	do.	C4	sl. d
322	do.	∞	occ. patches	do.	ciliated	D4	sl. d
323	do.	f ∞	fair no.	do.	heart shaped	C4	sl. d
324	do.	∞	∞ patches	do.	ciliated	D4	sl. d
55. DREDGED MYLOR BANK, FAL ESTUARY, 26.8.25; EXAMINED 28.8.25.							
325	∞	fair no.	none	Bl.	180–190μ	F6	d
326	∞	f ∞	do.	do.	do.	F6	d
327	∞	do.	do.	do.	170–190μ	F6	d
328	∞	do.	do.	do.	190μ	F6	d
329	∞	do.	do.	do.	180–200μ	F6	d
330	f ∞	∞	do.	Grey-white	½ shelled	E6	d
331	f ∞	∞	do.	Bl.	180–190μ	F6	N
332	none	∞	do.	Bl.	mainly 180μ range 170–190μ	F4	N
333	none	∞ small	do.	Wh.	heart shaped	D3	d
334	few	∞	do.	Bl.	180μ	F5	N
335	∞	few only	none	Bl.	190–200μ	F7	N
336	rare	∞	none	do.	full size	F5	N
337	none	∞	∞ small patches	Wh.	heart shaped	C4	N
338	few	∞	none	Bl.	full size	F5	N
339	∞	∞	do.	do.		F6	N
340	∞	∞	1 or 2 patches	do.		F6	N
341	f ∞	∞	none	do.	180–200μ	F6	N
342	none	f ∞	few	do.	180μ	F4	N
343	v ∞	v ∞	few patches	Grey-white	½ shelled	E6	d
344	∞	∞	—	Bl.	180–190μ	F6	d
345	none	fair no.	none	Wh.	late segn. stages	C4	d
346	∞	∞	do.	Bl.	200μ	F6	d
347	∞	few	do.	do.	180μ	F7	d
348	few	∞	none	Purple-grey	160μ	F5	sl. d
349	f ∞	∞	do.	Bl.	180μ	F6	sl. d
350	∞	∞	—	do.	180μ	F6	sl. d

1	2	3	4	5	6	7	8
56.	DREDGED TURNAWARE BAR, FAL ESTUARY, 3.9.25; EXAMINED 5–6.9.25						
351	rare	∞	few patches	Gr.	ciliated trace of shell	D5	d
352	∞	fair no.	none	Bl.		F6	d
353	none	∞	∞ small patches	Wh.	heart shaped	C4	N
354	∞	∞	none	Grey-white	¼ shelled	E6	d
355	∞	∞	2 or 3 patches	Grey-wh.	trace of shell	D6	d
			EXAMINED 6.9.25.				
356	∞	fair no.	none	Bl.	160–170μ	F6	d
357	none	few	few patches	Wh.	heart shaped	C4	d
358	do.	∞	none	do.	do.	C4	d
359	fair no.	∞	few patches	do.	¼ shelled	E6	sl. d
360	few	f ∞	none	Bl.	180μ	F5	d
361	∞	∞	1 or 2 patches	do.	full size	F6	d
362	rare	∞	none	Wh.	ciliated	D5	d
363	none	∞	1 or 2 patches	do.	heart shaped	C4	d
364	do.	fair no. young	few patches	do.	ciliated	C3	sl. d
365	do.	v ∞	none	Purplish-grey	150–160μ	F4	d
366	few	v ∞	few patches	Wh.	heart shaped	C5	sl. d
367	none	few	none	do.	do.	C4	sl. d
368	do.	∞ young	∞	do.	do.	C3	N
369	do.	do.	do.	do.	ciliated	D3	N
370	fair no.	v ∞	1 or 2 patches	do.	heart shaped	C6	N
371	none	∞	few patches	do.	late segn. stages	C4	N
372	few	∞	1 or 2 patches	Wh.	heart shaped	C5	N
373	fair no.	∞	1 patch	do.	ciliated	C6	N
374	none	∞	several patches	do.	heart shaped	C4	N
375	do.	∞	many	do.	ciliated	C4	N
376	do.	∞ nearly ripe	∞ patches	do.	heart shaped	C4	N
377	do.	fair no. young	some	do.	do.	C3	N
378	∞	∞	none	Bl.	170–180μ	F6	N
379	few	v ∞	few patches	Wh.	ciliated	C5	N
57.	DREDGED EAST EDGE, FAL ESTUARY, 9.9.25. EXAMINED 11–12.9.25.						
380	f ∞	f ∞	several big patches	Purplish grey	160μ	F6	d
381	none	v ∞	few patches	Wh.	late segn. stages	B4	d
382	fair no.	∞	none	Gr.	150μ	E6	d
383	∞	∞	none	Purplish grey	160μ	F6	d
384	f ∞	f ∞	fair no. in patches	Gr.	160μ	E6	d
385	∞	∞	few patches	Bl.	170μ	F6	d
386	∞	f ∞	none	do.	170μ	F6	d
387	∞	∞	occ. patches	do.	160–170μ	F6	d
388	∞	∞	none	Purplish grey	160μ	F6	d
389	none	∞ young a few to 60μ	few patches	Wh.	heart shaped	C4	d
390	∞	∞	fair no. of patches	Gr.	150μ	E6	d
391	∞	∞	—	Gr.	155μ	E6	sl. d
392	∞	∞	none	Bl.	—	F6	N
393	∞	f ∞	do.	Gr.	160μ	E6	N
394	∞	∞	few patches	Bl.	160μ	F6	N
395	f. no.	∞	∞ scattered	Gr.	160μ	E6	N

1	2	3	4	5	6	7	8
			EXAMINED 12.9.25.				
396	few	∞	1 or 2 patches	do.	160μ	E5	N
397	∞	none	none	Bl.		F8	N
398	∞	rare	do.	do.		F7 Note 6	N
399	?	some	∞	Purplish-grey	poor condition	—	N
400	∞	f ∞	∞	Bl.		F6	N
401	few	some	few	Gr.		E5	N
402	∞	none	several patches	Bl.		F8	N
403	∞	∞	none	do.		F6	N
404	none	few small	several large patches	Wh.	morula stage	B3	N
405	few	∞	none	Purplish grey	150μ	F5	sl. d
406	do.	∞	rare	do.	150μ	F5	N
407	∞	∞	none	do.	160μ	F6	N
408	∞	∞	do.	do.	160μ	F6	N
409	f ∞	f ∞	none	Purplish grey	160μ	F6	N
410	none	∞	few patches	do	do.	F4	N
411	∞	∞	none	do.	do.	F6	N
412	f ∞	f ∞	do.	Bl.	170μ	F6	N
413	∞	∞	rare patches	do.	180μ	F6	N
414	∞	∞	none	Gr.	150μ	E6	d
415	f ∞	f ∞	few patches	do.	160μ	E6	N
	58. DREDGED TURNAWARE POINT, 16.9.25; EXAMINED 18–19.9.25.						
416	∞	∞	none	Bl.	170–180μ	F6	N
417	∞	f ∞	rare patches	do	190–200μ	F6	N
418	none	∞	small and 1 large patch	Wh.	ciliated trace of shell	D4	N
419	do.	f ∞ young	few patches	Wh.	¼ to ½ shelled	E3	N Note 7
			EXAMINED 19.9.25.				
420	few	few	none	Bl.	170–180μ	F5	N
421	∞	∞	do.	do.	180–190μ	F6	N
422	none	none	none	do.	170–180μ	F1–10	d
423	∞	∞	none	do.	180–190μ	F6	d
424	v ∞	v ∞	do.	do.	180μ	F6	d
425	∞	∞	do.	do.	190–200μ	F6	sl. d
426	∞	∞	do.	do.	180μ	F6	sl. d
	59. DREDGED TURNAWARE POINT, 23.9.25; EXAMINED 24.9.25.						
427	f ∞	∞	few patches	Slate-grey	150–155μ	F6	
428	fair no.	∞	none	do.	160–170μ	F6	
	60. VARIOUS GROUNDS, FAL ESTUARY, OCTOBER, 1925.						
429	none	few v. young	few	Wh.	heart shaped	C3	Dredged and examined 30.9.25, Mylor Pool.
430	∞	none	none	Bl.	180–190μ	F8	do. 2.10.25, Turnaware Point. Note 8
431	few	few	do.	do.	170μ	F5	do. 7.10.25,
432	none	few young	none	Wh.	heart shaped	C3	do. 8.10.25, Mylor Pool.
433	do.	none	none	Bl.	190μ	F1–10	do. do.
434	none	none	none	do.	195–200μ	F1–10	do. 14.10.25, do. 15.10.25, Turnaware Point.

1	2	3	4	5	6	5	8
435	none	few to 50μ	none	Gr.	½ to ⅔ shelled	E4	Turnaware Point.
436	none	fair no. up to 50μ	none	Sl.	180μ	F4	Hand collected, Turnaware Point, 19.10.25.
437	none	a few large	few	Bl.	180μ	F4	Dredged 27th ; examined 29.10.25 ; Mylor Bank.
438	none	none	none	do.	190–200μ	F1–10	do. 3rd, do. 5.11.25, Turnaware Bar.

61. DREDGED VARIOUS GROUNDS, WEST MERSEA, 10.7.25 ; EXAMINED 11.7.25.

439	none	∞	few	Wh.	4 to 8-celled stages	B4	
440	do.	∞	—	do.	heart shaped	C4	
441	do.	few young	—	do.	do.	C3	
442	few	∞ full size	few	do.	do.	C5	
443	none	some probably ∞ very young	few	do.	2–3-celled stages	A3	
444	none	f ∞ to 50μ	patches	do.	0–4-celled stages	A4	
445	none	∞ v young few to 50μ	few	do.	0–2-celled stages	A4	
446	none	few to 30μ	fair no.	do.	4–8-celled stages	B3	Dredged 13th, examined 14.7.25

62. SAMPLE OF BROOD ESTIMATED IN SECOND AND THIRD SUMMER ; DREDGED SOUTH SHORE AND EXAMINED 21.7.25.

447	∞	∞	none	Wh.	½ shelled	E6	37	36	8
448	few	∞	few	do.	ciliated	D5	35	42	10–25
449	∞	∞	few	do.	do.	D6	39	43	4
450	none	∞ 40μ	—	do.	spherical	C3	37	38	6
451	do.	do.	—	do.	ciliated	D3	43	42	12
452	do.	∞	few patches	do.	spherical	C4	48	50	4
453	do.	∞	∞ patches	do.	partly shelled	E4	45	49	10

OYSTERS FROM EXPERIMENTAL CAGE SUNK IN DEEPS, WEST MERSEA ; CAGE HAULED 2.7.25.

63*a*. A. INDIVIDUALS WHITESICK 10.6.24 TO 9.7.24, NOW "SICK" AGAIN ; EXAMINED 3–13.7.25.

454	∞	∞	none	Bl.		F6
455	rare	f ∞ to 60μ	few patches	Wh.	ciliated	D5
456	none	∞	do.	do.	do.	D4

63*b*. B. INDIVIDUALS BLACKSICK 1–9.7.24, NOW "SICK" AGAIN ; EXAMINED 13–14.7.25.

457	few	few large fair no. very young	few	Wh.	ciliated	D5
458	f ∞	∞	none	Bl.		F6
459	none	f ∞ a few nearly ripe	none	Wh.	ciliated	D4
460	none	f ∞ to 35μ	few	do.	do.	D3

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64. DREDGED TURNAWARE BAR, FAL ESTUARY, JUNE 2, 11.30 A.M. TO 3 P.M. ; EXAMINED JUNE 3, 1926.

461	none	f ∞ 30μ a few 70μ	fair no. of small patches	Wh.	32 celled	B4

1	2	3	4	5	6	7	8
			EXAMINED JUNE 5, 11.0 A.M.				
462	none	∞ to 40–50μ	∞ in small patches	Wh.	heart shaped only	C4	
			EXAMINED JUNE 14.				
463	a few	f ∞	fair no. in patches	Grey-white	150–160μ	E5	
464	f ∞	∞	few patches	Gr.	160μ	E6	
	65. DREDGED TURNAWARE BAR, FAL ESTUARY, JUNE 9, ABOUT LOW-WATER MARK, 10 A.M.–1.15 P.M.; EXAMINED JUNE 9, 4.30 P.M.						
465	rare	v ∞	a few relict	Wh.	½ shelled	E5	
	65*a*. DREDGED TURNAWARE BAR, FAL ESTUARY, JUNE 16, 9.30–12 NOON; EXAMINED JUNE 17, 11.30 A.M.; TWO DUMPS EXAMINED JUNE 18 AT NOON.						
466	none	f ∞ 50μ	occ. patch	Wh.	morula stage 70 % unsegmented	B4	
467	f ∞	∞ large to 70μ	occ. spots	Wh.	½ to ⅔ shelled	E6	
468	none	∞ 50μ	few patches	Wh.	to morula stages 10 % unsegmented	B4	sl. d
469	none	∞ fo 50μ	one fair patch	Wh.	to 32-celled stages 15 % unsegmented	B4	sl. d
	66. DREDGED BROWN ROSE BAR, EAST BANK, FALMOUTH, JUNE 22, 9 A.M. ONWARDS, EXAMINED JUNE 22, 6.10–6.45 P.M.						
470	none	few to 30μ	few patches relict	Wh.	32 or a few more cells	B3	58 62 3
	DREDGED BELOW LOW-WATER MARK, TURNAWARE BAR, JUNE 23, 9–11.25 A.M.; EXAMINED JUNE 24, 6.20 P.M.						
471	none	∞	few	Wh.	40–50 nuclei, 64 rare	C4	
	DREDGED TURNAWARE BAR, JUNE 23, 11.30 A.M. TO 2 P.M.; EXAMINED JUNE 25, 10.40 TO 11.0 A.M.						
472	none	∞	none	Wh.	ciliated	D4	58 62 nil trs.
473	none	∞	∞	do.	up to 64 celled	C4	ca. ¼ spent
	67. DREDGED THORNFLEET, WEST MERSEA, JUNE 23, 7–8 A.M.; EXAMINED JUNE 24, NOON TO 3.45 P.M.						
474	f ∞	∞ large	small patches	Bl.	200μ	F6	Liver a little black, i.e. nearly choc.-brown; sl. curd.
475	∞	∞	few	Sl.	180μ	F6	Liver a little black, i.e. nearly choc.-brown
476	∞	∞	none	Slate-purple	190–200μ	F6	do.
477	f ∞	∞	do.	Sl.	200	F6	do.
478	f ∞	∞	f ∞ in spots	Sl.	200	F6	do. spotted
479	f ∞	∞	none	Purple-slate	190	F6	Liver a little black, i.e. nearly choc.-brown
480	f ∞	∞	none.	Sl.	200	F6	do.

1	2	3	4	5	6	7	8
481	f ∞	∞	few spots	Sl.	200× 160–170μ	F6	do. sq.
482	∞	∞	none	do.	do.	F6	do, trs.
483	f ∞	f ∞	do.	do.	do.	F6	do. trs. & sq.
484	f ∞	∞	few spots	Light slate	180–190	F6	do. Note 9. trs.
485	none	∞	fair no. of patches	Wh.	ca 64-celled	C4	trs. spotty
486	none	none	∞ patches	do.	unsegmented	A1	unspent
487	f ∞	∞	few patches	do.	just ciliated	D6	trs.
488	f ∞	∞	fair no. of patches	do.	do.	D6	trs.
489	none	∞	do.	do.	64-celled	C4	sq. and ¼ trs.
480	do.	f ∞ large	few patches	do.	do.	C4	trs.
491	none	few	very ∞ patches	do.	ciliated trace of shell	D4	Note 10 sl. curdled
492	do.	f ∞	few big patches	do.	ca 64-celled	C4	trs.
493	do.	∞	fair no. small patches	do.	do.	C4	trs.
494	do.	∞	few	do.	32–64-celled	C4	trs.
495	do.	∞	few	do.	do.	C4	trs.
496	∞	∞	none	do.	ca ½-shelled	E6	trs.
497	rare	few	∞ incompletely spawned	do.	just ciliated	D5	Note 10 ¼ spent
498	rare	∞	few	do.	ciliated trace of shell	D5	
499	rare	∞	none	do.	64 nuclei	C5	trs.
500	none	few young	few	do.	32–64 nuclei	C3	trs.

68*a*. A. COLLECTED AT L.W., TURNAWARE BAR, F. E. JUNE 28, 1.40–3 P.M., AND B. DREDGED BEFORE AND AFTER L.W. JUNE 28; EXAMINED JUNE 28, 6–10 P.M.

				A.			
501	rare	∞ 60μ	occ.	Wh.	just ciliated	D5	
502	few	∞ 80μ	few patches	do.	do.	D5	
503	rare	∞ 80μ	none	do.	heart shaped	C5	
504	none	∞ 80μ	∞	do.	do.	C4	¾ spent
505	none	∞ 80μ	fair no. of patches	do.	do.	C4	
506	none	∞ young 30μ	occ.	do.	50% just ciliated 50% unsegmented	D3	Note 11
507	none	∞ young	few patches	do.	32-celled	B3	
508	rare	∞	rare	do.	ciliated	D5	d Dumps
509	none	∞	occ.	do.	16–32 nuclei	B4	d
510	do.	few	∞	do.	64-celled	C4	Note 12 d ⅝ spent
511	f ∞	∞	few	do.	heart shaped	C6	d
512	f ∞	f ∞	few	do.	¾ shelled	E6	d
513	none	∞	∞	do.	heart shaped	C4	d
				B.			
514	none	∞ 60μ	few patches	do.	heart shaped	C4	
515	none	∞ young	none	do.	16–20 nuclei	B3	
516	∞	∞	none	Bl.	200μ, shells purplish	F6	
517	none	∞ 40–50μ	none	Wh.	16–32 nuclei 20% unsegmented	B4	d
518	∞	∞	none	Wh.	¾ shelled	E6	d

1	2	3	4	5	6	7	8
68*b*. DREDGED TURNAWARE BAR, F, 9.50–11 A.M. ON THE FLOOD TIDE, JUNE 28; EXAMINED JUNE 29, 9.45 A.M. (TWO DUMPS AT 8 P.M.).							
519	none	∞	fair no.	Wh.	32 nuclei	B4	
520	fair no.	∞	none	Sl.	150μ	E6	
521	none	∞	very ∞	Wh.	64-celled	C4	¼ spent
522	none	∞ young	∞	Wh.	16–32-celled 50% unsegmented	B3	¾ spent
523	none	∞ young	∞	Wh.	64 nuclei 20% unsegmented	B3	¾ spent
524	f ∞	∞	rare	Sl.	160μ	F6	
525	none	∞	∞	Wh.	¼ shelled	E4	¾ spent
526	∞	∞	none	Bl.	200μ	F6	d trs.
527	none	∞ young	none	Wh.	32 nuclei	B3	d
69. DREDGED MYLOR BANK, F, 11.30 A.M.–3.15 P.M., JUNE 29; EXAMINED 10 P.M. JUNE 29.							
528	a few	∞	∞	Wh.	ciliated trace of shell	D5	Note 13. ¼ spent
529	∞	∞	few	Wh.	do.	D6	
530	rare	∞	few patches	Wh.	do.	D5	d
531	none	∞	f ∞	Wh.	shells 100μ	E4	d spotty
70*a*. DREDGED EAST BANK, F, 11.30 TO ABOUT NOON; EXAMINED JULY 1, 1.0 A.M.							
532	none	∞	none	Wh.	16–32-celled	B4	d
533	do.	∞	none	do.	32–64-celled	C4	d
534	do.	few	∞	do.	heart shaped	C4	d patchy
535	do.	∞	none	do.	32-celled	B4	d
70*b*. DREDGED EAST BANK, F, ABOUT NOON TO 2.40 P.M., JUNE 30; EXAMINED 5.20 TO 8 P.M., JUNE 30.							
536	few	∞	none	Wh.	ciliated trace of shell	D5	60 63 3
537	none	f ∞	∞ patches	do.	heart shaped	C4	65 58 5
538	fair no.	∞	few	Wh.	do.	C6	60 61 7
539	none	f ∞	few	do.	32-celled	B4	55 55 5
540	do.	∞	none	do.	ciliated	D4	64 61 8
541	do.	∞	∞ relict	do.	do.	D4	64 73 3 ¾ spent
542	f ∞	∞	few patches	do.	do.	D6	60 60 5
543	∞	∞	f ∞ relict	do.	trace of shell	D6	61 62 0
544	none	∞	f ∞ relict	do.	4-celled stages	A4	61 67 8
545	do.	∞	do.	do.	heart shaped	C4	60 67 5
546	do.	∞	do.	do.	do.	C4	51 50 0
547	f ∞	∞	few	Sl.		F6	51 63 5 d
548	f ∞	∞	none	Bl.		F6	57 67 0 d
549	none	some	∞ relict	Wh.	heart shaped	C4	55 56 2 d
550	do.	some	∞ relict	do.	do.	C4	47 53 6 d
551	f ∞	∞	none	do.	¼ shelled	E6	55 66 0 d
71. DREDGED TURNAWARE BAR, BELOW L.W. MARK ON FLOOD TIDE JUNE 30, 3.15 TO 5.30 P.M.; EXAMINED JUNE 30, 8.42 P.M. TO 1.4 A.M. JULY 1.							
552	few	∞	f ∞	Wh.	heart shaped	C5	71 78 5–13
553	none	∞	none	do.	do. and ciliated	D4	57 58 4
554	f ∞	∞	few patches	do.	do.	D6	57 67 0–5
555	f ∞	∞	∞ relict	do.	heart shaped only	C6	53 53 4 ¾ spent

1	2	3	4	5	6	7	8			
556	none	few v. young	∞ Wh. heart shaped only		1–5-celled	A3	52	60	3	
557	none	∞	fair no.	do.	heart shaped	C4	53	60	6	
558	none	∞	v ∞	do.	do.	C4	64	60	10 ¼ spent	
559	f ∞	∞	none	Bl.	180–190μ	F6	58	62	5	
560	f ∞	∞	rare patches	do.	200μ	F6	55	60	4	
561	f ∞	∞	none	do.	190–200μ	F6	56	61	7	
562	f ∞	∞	none	do.	200μ	F6	60	57	10	
563	∞	∞	none	do.	190–200μ	F6	68	68	5	
564	none	∞	∞ patches	Wh.	heart shaped only	C4	65	74	7	spotty
565	f ∞	∞	f ∞ relict	do.	140μ ⅔ shelled	E6	62	61	4	do.
566	none	∞ young	few patches	do.	heart shaped only	C3	66	65	3	
567	none	few young	rare	do.	do.	C3	57	65	5	
568	none	∞	∞ in one large patch	do.	do.	C4	64	75	11	
569	none	v ∞	none	do.	do.	C4	58	67	4–8	
570	a few	∞	few patches	do.	do. and ciliated	D5	62	77	0	
571	none	∞ young	∞ in patches	do.	8-celled stages	B3	58	67	5	
572	none	∞ 50μ	few	do.	do.	B4	50	60	7	d
573	none	∞	rare	do.	64-celled	C4	57	63	2	d
574	none	∞	∞	do.	heart shaped only	C4	48	60	2 ⅓ spent	d
575	none	∞ v. young	none	do.	4-celled stages	A3	54	63	5	d
576	few	∞	none	Sl.	170μ	F5	45	57	4	d

72. DREDGED SOUTH SHORE, WEST MERSEA, JULY 5, 7 A.M. TO 2 P.M., EXAMINED JULY 7, 11.30 A.M. TO 1.40 P.M.

577	∞	∞	none	Sl.	180μ	F6				
578	f ∞	∞	occ. small patches	Gr.	140–150μ	E6	48	48	5	

73. DREDGED THORNFLEET, 7–8 A.M.; EXAMINED 12.30 P.M. JULY 7,

579	∞	∞	none	Bl.		F6			trs.	
580	∞	∞	do.	do.		F6			trs.	
581	∞	∞	few in ducts ?	do.		F6			trs. and sq.	
582	none	∞	few	Wh.	trace of shell 60μ	E4			trs.	
583	∞	∞	none	Bl.		F6			trs.	
584	∞	∞	none	Sl.	180μ	F6			trs. and sq.	
585	∞	∞	none	Gr.	150–160μ	E6			trs. and sq.	
586	few	∞	few	Wh.	trace of shell	D5			sq. and trs.	
587	f ∞	∞	none	do.	shell 50μ	E6			trs.	
588	rare	∞	occ.	do.	ciliated	D5			trs.	
589	few	∞	∞ in patches	do.	do.	D5			sq. and trs.	
590	rare	∞	∞ in patches	do.	shell ca 30μ	D5			⅚ spent	
591	f. no.	∞	f ∞ in small spots	do.	do.	D6			trs.	

74. DREDGED SOUTH SHORE, WEST MERSEA, JULY 7, 7.30–2.0 P.M. EXAMINED JULY 8, NOON TO 1 P.M.

592	∞	∞	none	Sl.	180μ	F6			trs;	
593	∞	∞	few small patches	Wh.	shells 100–120μ	E6			trs.	

1	2	3	4	5	6	7	8
594	f ∞	∞	none	Slate-grey	150–160μ	F6	trs.
595	f ∞	∞	do.	Gr.	150μ	E6	trs.
596	f ∞	∞	do.	do.	do.	E6	trs.
597	rare	∞	few patches	Wh.	trace of shell 60μ	E5	trs.
598	f ∞	f ∞	none	Bl.		F6	trs.
599	∞	∞	do.	Bl.	190μ	F6	trs.
600	∞	∞	do.	Sl.	180μ	F6	trs.
601	few	fair no.	none	Gr.	140–150μ	E5	trs. Note 14
602	f ∞	∞	few patches	do.	do.	E6	sq. and trs.
603	none	f ∞	none	Wh.	trace of shell 60μ	E4	trs.

75. DREDGED TURNAWARE BAR, FALMOUTH, JULY 6, 6 TO 7 A.M. EXAMINED JULY 9, 11 TO 11.40 A.M.

604	∞	∞	fair no. of small patches	Wh.	ciliated only	D6	trs.
605	none	f ∞ young	few	Wh.	16–32-celled	B3	trs.
606	do.	f ∞	few	do.	32-celled	B4	trs.
607	do.	some young?	∞ in small patches	do.	1–6, occ. 8-celled	B2	trs. and spotty
608	none	∞ young	few small patches	do.	1–8-celled	B3	trs. and sq.
609	none	f ∞ young	few small patches	do.	1–6 or 8	B3	trs.
610	none	?	∞ small patches	do.	4-celled	A2	$\frac{5}{6}$ spent
611	∞	∞	several patches	Gr.	170–180μ	E6	trs. spotty
612	f no.	∞	none	Slate-black	190μ	F6	sq. and trs.
613	none	f no. young	fair no. in small patches	Wh.	1–4-celled	A3	trs. spotty
614	f ∞ in ducts	f ∞ young	∞ ova in ducts	Wh.	heart shaped ciliated	D6	A spawning ♂ (♀). Note 15 $\frac{1}{4}$ spent
615	none	∞ young	∞ large patches	do.	1–16–32-celled	B3	trs. patchy
616	none	do.	do.	do.	16–32-celled	B3	$\frac{5}{6}$ spent
617	∞	∞	none	Sl.	170μ	F6	sq.
618	none	∞	occ. patches	Wh.	ciliated shells 120–130μ	E4	trs.
619	none	∞	occ.	Wh.	do.	E4	sq.
620	∞	∞	occ. patches	Bl.	200μ	F6	trs.
621	f ∞		one big patch	White-grey	120μ	E6	trs.
622	none	∞	occ. small patches	do.	110μ	E4	trs.
623	none	?	∞	Wh.	4-celled.	A1	ducts $\frac{1}{4}$ full of ova
624	∞	∞	none	Sl.	190μ	F6	trs.
625	none	f no. v. young	none	Wh.	1–5-celled	A3	trs.
626	none	few	∞ in small patches	Wh.	ciliated, shells 80–100μ	E4	trs. and sq.
627	none	f no. some nearly ripe	none	Wh.	do.	E4	sq.
628	f no.	∞	one patch	Slate Grey	180μ	F6	sq. and trs.
629	f no.	∞	several small patches	Sl.	180μ	F6	trs.
630	f no.	f ∞	f no.	Sl.	170μ	F6	sq.
631	none	∞ young	none	Wh.	1–4-celled	A3	trs
632	a few	∞	f no.	White-grey	shells 120μ	E5	sq. and trs.

1	2	3	4	5	6	7	8
76. DREDGED NOSS END, WEST MERSEA, JULY 10, EARLY MORNING; EXAMINED JULY 10, 1 TO 2.30 P.M.							
633	∞	∞	none	Bl.	200μ	F6	trs.
634	∞	f ∞	none	do.	200μ	F6	sq. and trs.
635	few	∞	fair no. of spots	Wh.	ciliated shell 50μ	E5	trs. spotty
636	f ∞	∞	occ.	Wh.	do.	E6	trs.
637	f ∞	∞	one patch	Wh.	do.	E6	trs.
638	none	∞	∞	Wh.	do.	E4	trs. and sq. and curdly
639	∞	∞	none	Bl.	210 × 200μ	F6	trs.
640	∞	f ∞	none	do.	210μ	F6	sq.
641	∞	∞	none	Black-slate	190μ	F6	trs.
642	f ∞	∞	none	Sl.	180 × 160μ and 190 × 170μ	F6	trs.
643	f ∞	∞	none	Slate-grey	180 × 150μ	F6	sq. and trs.
644	f ∞	∞	few spots	White-grey	130–140μ	E6	trs.
645	f no.	∞	occ. patches	Wh.	ciliated trace of shell	D6	trs. and sl. spotty
77. DREDGED NOSS END, WEST MERSEA, JULY 12, 7.30–2 P.M.; EXAMINED JULY 12, 4 TO 7.30 P.M.							
646	f ∞	∞	none	Wh.	shells 150–156μ	E6	trs.
647	none	f no.	one spot	Wh.	32-celled	B4	trs.
648	none	f no. young	none	Wh.	7–8-celled	B3	trs.
649	none	few v. young	none	do.	16–20-celled	B3	trs.
650	f no.	∞	one spot	Gr.	160–170μ	E6	trs.
651	none	none	none	Sl.	180μ relatively few	F1or10	sq. **sq.**
652	f no.	few only	none	Bl.	185μ	F7	
653	v ∞	∞	none	Bl.	220 × 200μ	F6	sq. and trs. Note 16.
654	f ∞	v ∞	none	Wh.	16-celled	B6	trs. Note 17.
655	none	few	one patch	do.	do.	B4	trs.
656	do.	f no.	∞ scattered	do.	do.	B4	trs. spotty
657	∞	f ∞	none	Gr.	160μ	E6	trs. and sq.
658	∞	∞	none	Bl.	205μ	F6	sq.
659	∞	∞	none	do.	200μ	F6	sq.
660	∞	∞	none	do.	195μ	F6	sq. and trs.
661	a few	∞	a few	Sl.	180–190μ	F5	sq.
78. DREDGED THORNFLEET, WEST MERSEA, AUGUST 4, 7–7.30 A.M.; EXAMINED AUGUST 5, 4 P.M.							
662	∞	∞	none	Sl.		F6	sq. and trs.
663	f no.	f ∞	∞	Slate-grey	160–170μ	F6	sq. and trs. spotty Note 18.
664	f no.	∞	none	Grey-slate	170μ	F6	sq. and trs.
665	∞	∞	none	Wh.	shells 130μ	E6	trs.
79. DREDGED MYLOR BANK, FALMOUTH, AUGUST 10, 11 A.M. TO 2 P.M.; EXAMINED FOR SEX, 10.40 P.M., FOR DEVELOPMENT 7 P.M. AUGUST 10.							
666	f ∞	∞	none	Slate-black	190μ	F6	sq. and trs.
667	f ∞	∞	do.	Slate-grey	170–180μ	F6	do.
668	none	f ∞	none	Gr.	170–180μ	E4	do.

1	2	3	4	5	6	7		8
669	few	∞	none	Gr.	170μ	E5		sq. and trs
670	few	few	none	Slate-grey	180μ	F5		do.
671	few	∞	none	do.	180μ	F5		trs.
672	f no.	∞	none	do.	170μ	F6		sq. and trs.
673	rare	∞	none	do.	160–170μ	F5		trs.
674	none	none	none	Wh.	4, a few 5-celled	A1		sq. and trs. inc. spent
675	none	occ. young	none	Wh.	4-celled	A3		sq. and trs.
676	rare	∞	none	Grey-white	ca 140μ	E5		sq. and trs.
677	none	∞	none	do.	ca 140μ	E4	d	do.
678	none	few young ?	∞ relict	Wh.	mainly unsegmented ca 10 % 32-celled	B2	d	do. and spotty
679	∞	∞	none	Gr.	ca 140μ	E6	d	sq. and trs.

80. DREDGED EAST BANK, FALMOUTH, AUGUST 10, 9 TO 11 A.M.; EXAMINED FOR DEVELOPMENT 8.30 TO 9.5 P.M., AND FOR SEX 10.50 TO 11.45 P.M. AUGUST 10.

680	∞	f no.	none	Bl.	190μ	F6		sq. and trs.
681	∞	∞	do.	do.	do.	F6		trs.
682	few	few	few	do.	180–190μ	F6		sq. and trs. and spotty
683	∞	∞	none	Wh.	ciliated shell ca 40μ	E6		sq. and trs.
684	few	∞	few spots	do.	ciliated	D5		trs.
685	∞	∞	none	do.	ciliated trace of shell	D6		trs.
686	f ∞	∞	none	do.	ciliated no shell	D6		sq. and trs.
687	rare	f no.	none	do.	do.	D5		do.
688	∞	∞	do.	do.	ciliated shell ca 40μ	E6		trs.
689	none	none	∞ relict	do.	do. 60μ	E1		sq. and trs. Note 19.
690	none	none	few	Wh.	2–4-celled	A1	d	sq. and trs. and spotty
691	f. no	∞	none	Wh.	ciliated trace of shell	D6	d	sq. and trs.
692	∞	rare	do.	Bl.	190μ	F7	d	do. Note 19.
693	∞	f ∞	do.	do.	190–200μ	F6	d	do.
694	f no.	∞	do.	do.	190μ	F6	d	do.
695	∞	∞	do.	Sl.	170–180μ	F6	d	do.

81. DREDGED THORNFLEET, WEST MERSEA, SEPTEMBER 1; EXAMINED SEPTEMBER 2, 12.30 P.M.

696	f no.	∞	none	White-grey	shell 80–90μ	E6		sq.

82*a*. DREDGED TURNAWARE BAR, FALMOUTH, SEPTEMBER 7, IN THE MORNING; EXAMINED SEPTEMBER 7, 7 P.M.

697	a few	∞	none	Gr.	shells ca 130μ	E5		sq. and trs.
698	none	∞	∞	do.	do. ca 60–70μ	E4		sq. and trs. and spotty

82*b*. DREDGED EAST BANK, FAL ESTUARY, SEPTEMBER 8, 12.30–3 P.M.; EXAMINED SEPTEMBER 8, 7–7.40 P.M.

699	none	v ∞	none	Gr.	150μ	E4		trs.
700	a few	∞	do.	Bl.	170–180μ	F5		trs.
701	none	a few	none	Gr.	150–160μ	E4	d	sq. and trs. Note 20.

1	2	3	4	5	6	7	8
				82*c*. DREDGED TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 9, 7–8.30 A.M.; EXAMINED SEPTEMBER 9, 6.15 P.M.			
702	f ∞	few	none	Purple-black	190–200μ	F7	sq. and trs. Note 20.
703	f ∞	fair no.	do.	Bl.	180μ	F6	trs. Note 20.
704	f ∞	fair no.	do.	Lilac-grey	160–170μ	F6	sq. and trs. Note 20.
705	f ∞	∞	do.	Sl.	170–180μ	F6	sq, and trs.
				82*d*. DREDGED TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 15; EXAMINED SEPTEMBER 16, 7.20 P.M.			
706	∞	a few	none	Bl.	190μ	F7	trs. Note 20.
707	none	few small	none	Wh.	ciliated no shell	D3	sq. and trs. Note 20
				82*e*. DREDGED TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 21, 9.30–11.0 A.M.; EXAMINED 7.17 P.M.			
708	few	f ∞	none	Gr.	170μ	E5	trs.
709	none	one large, one small seen	none	Gr.	160–170μ	E4 ?	trs. Note 20.
				82*f*. HAND-PICKED AT L.W., TURNAWARE BAR, FAL ESTUARY, SEPTEMBER 22, 12.30–1.30 P.M.; EXAMINED 7.30 P.M.			
710	∞	∞	none	Bl.	180–200μ	F6	sq. and trs.
				82*g*. DREDGED TURNAWARE BAR, FAL ESTUARY, 1.30–3 P.M.; EXAMINED 4.45 P.M. OCTOBER 1.			
711	f no.	f ∞	none	Gr.	160–170μ	E6	trs.
				82*h*. DREDGED FALMOUTH NORTH BANK, FAL ESTUARY, OCTOBER 7; EXAMINED OCTOBER 7, 1926.			
712	f no.	∞	none	Bl.	180–190μ	F6	sq. and trs.
				83. HAULED IN CAGES, FAL ESTUARY, SEPTEMBER 29/26; EXAMINED SEPT. 29/26.			
713	none	none	none	Bl.	190×170μ	F1–10 ?	trs. Note 20.
714	none	occ. ?	none	Bl.	180–190μ	F1–10 ?	sq. Note 20,
715	∞	∞	∞ young ?	Bl.		F6	sq. and trs.

NOTES ON TABLE IV.

The same abbreviations are used as in Tables II and III. Abbreviations used specially in describing sperm and eggs are as follows:—

∞ = numerous; f ∞ = fairly numerous; f. no. or fair no. = fair number; occ. = occasional; N.O. = not observed macro- or microscopically; v. = very.

The figures 1, 2, 3, 4, 5, 6 = sex-categories given in Table II, p. 981.

Abbreviations used in describing the colour of embryos and larvæ are:—

Wh. = white; Gr. = grey; Sl. = slate; Bl. = black.

The letters A, B, C, D, E, F denote the periods of development defined in Table III, p. 983.

Abbreviations used in describing the appearance of the gonad or tissues to the naked eye are:—

inc. sp. = incompletely spent, sl. curd. = slightly curdled in appearance with groups of unspawned ova. spotty = gonad spotty in appearance, with patches of unspawned ova.

trs. = tissues soft with a general translucent appearance.
sq. = tissues opaque with a consistency approaching—but not quite so firm as—that of the mantle wall of a squid ; hence the term " squiddy " or squid-like tissues.
sq. and trs. = tissues partly translucent and partly opaque as defined.

Abbreviations referring to the form of shell-growth are :—
N = normally- to well-grown shells.
d = dumpy or generally biconvex shells of stunted growth (see Orton, 1926).
sl. d. = slightly dumpy shells, or shells intermediate in growth characters between N and d.
L = length of shell in an antero-posterior direction.
D = depth of shell in a dorso-ventral direction.
sh = shoot, that is, the recent increment in growth in depth of the shell in the year of examination, measured in the median dorso-ventral line on the left valve.

Remarks on Special Individual Records and other matters in Table IV.

Note 1. No. 69 is an example of the delay in sperm-production not infrequently associated with the retention of numbers of eggs in the gonad.

Note 2. In Groups 37 to 40, Nos. 105 to 136, and at other times, the relation of the colour of the digestive gland to the state of development of the embryos and the state of development of sperm-morulæ was noted. It was found that in oysters carrying white embryos the frequency and occurrence of ripe-tailed sperm-morulæ could be predicted with good accuracy from the colour of the digestive gland. See also records of the colour of this gland in numbers 765 to 795, Table IX, p. 1026.

The series of stages observed are as follows :—

	Digestive gland.	Embryos.	ripe sperm mor.	unripe sperm mor.
a. Ripe ♀.	chocolate-brown.	—	—	—
b. Just spawned ♀.	light do.	segn. to early blastopore stages.	none	a few
c. Do. later.	yellow-brown.	heart shaped embryos.	a few	∞
d. Still later.	yellow tinged with brown.	early shelled stage.	∞	∞
e. Late blacksick stage.	brown.	fully developed larvæ.	∞	∞
f. A few days after extruding larvæ.	choc.-brown.	—	∞	∞

This loss of colour in the digestive gland after spawning is probably due to a break in the active feeding habits of the animal. As " sick " oysters, especially whitesick ones, are well known to be weak, this weakness and the loss of colour in the liver are probably due to the same cause. The normal colour, chocolate-brown, is also lost at the approach of winter and may then become brick-red ; in this case also the change in colour may be due solely to absence of active feeding (see Savage, 1925).

Note 3. Nos. 142 to 144 were examined for sex five days after the condition of the embryos were noted, therefore the gonad may be expected to show, as in No. 142, a state of development in advance of the average state associated with D embryos.

Note 4. In lots 47 and 50, one, two or three days elapsed between dredging and examining the samples. In such cases as these embryos and spent gonad may develop at slightly different rates, and the occurrence of low categories in period D in these samples might be due to a greater effect of exposure out of water on the adult than on the embryos.

Note 5. No. 239 is a rare case of absence of male elements in an oyster blacksick in the summer-time, namely, August 6.

Note 6. Lot 57, Nos. 397, 398, 399, 402, 410 are interesting in all showing unusual features with regard to sperm development in the month of September.

Note 7. Nos. 419, 420 and 422 show similar phenomena to those in Note 6.

Note 8. Nos. 431 to 438, found with spawn in October, 1925, are all peculiar and show a slowing down in sperm-production at this season of the year. This observation was confirmed in 1926 and may be important in its bearing on the conditions necessary for the proper development of maleness.

Note 9. No. 483 had very few larvæ which were obviously not fully developed. It was estimated that about 50,000 only were present in the mantle cavity : although it is probable that a large number may have been extruded, it is also possible that only a few eggs were spawned. As some ♂'s may function as females and extrude relatively few eggs, cases like this are worth recording.

Note 10. Nos. 490 and 496 are additional cases of arrest of sperm-development correlated with incomplete egg-spawning.

Note 11. No. 506 is interesting in carrying about 50% embryos advanced to the ciliated stage and 50% of unsegmented, and in this case almost certainly unfertilised eggs. Unfortunately no record was made of the nuclear condition of the eggs.

Note 12. No. 510 was only $\frac{5}{6}$ spent, and again there is the correlation of few—or delay in production of—developing sperm. See also the following numbers 521, 522, 523 and 525, 626, 638.

Note 13. No. 528 is a case where although the gonad was only $\frac{1}{4}$ spent yet sperm development is about normal.

Note 14. No. 601 is an example of a gonad with relatively few developing sperm, but the sequence, few ripe—fair no. developing, is normal. See also Nos. 670 and 682.

Note 15. No. 614 is interesting in proving that a heramphrodite-female individual can spawn as a female. In this case ripe sperm and ripe ova were found in the ducts and developing young sperm-morulæ in the gonad.

Note 16. No. 653 had remarkably large-shelled larvæ with shells 220μ long by 200μ deep.

Note 17. No. 654 is strikingly an abnormal case where ripe sperm are developed to a fairly numerous condition with embryos only in the 16-celled stage, and with a gonad emptied of eggs. The simplest explanation of this case is that prior to spawning it was hermaphrodite, but left behind fully developed sperm, but no eggs on egg-spawning.

Note 18. In No. 663 the sperm were found in a " squiddy " part of the gonad where there were no relict ova.

Note 19. Nos. 689 and 692 are unusual and occurred, it is noteworthy, in August, 1926.

Note 20. In Lot 82, samples dredged in September, 1926, again occur abnormal forms, namely : (1) blacksick individuals with ripe but few developing sperm, (2) blacksick individuals with no developing sperm, and (3) generally relatively little development of sperm in other late spawning individuals.

Two more blacksick individuals with no recognisable developing or developed sperm occur also in Lot 83 (September 29).

SECTION C. RESULTS OF EXAMINING THE GONAD IN 444 OYSTERS WHICH HAVE REARED AND EMITTED THEIR LARVÆ.

In addition to investigating the gonad of oysters which were actually carrying embryos or larvæ at the time of examination (see Table IV, pp. 999 to 1021), a large number of individuals have also been examined at various periods *after* they had extruded their young. In the latter cases the material was obtained experimentally by isolating in cages groups of individuals which had previously been found with embryos or larvæ in the mantle cavity. The detailed records of the examination of the material are given in Table IX, pp. 1025 to 1034, in a form exactly comparable with that of the " sick " individuals given in Table IV, p. 999. Table IX is summarised in Table X, which in turn provides the figures for the correlation table, Table XI, p. 1023, and for the graphs G, H, I, and J in Fig. 1, p. 991. In Table X, facing p. 1022, are given also the mean stage of development (now including waning) of the male phase, and the mean age of the gonad reckoned from the last egg-spawning. In defining the age of the post-" sick " gonad, the four periods given in the following table, Table VIII, are

recognised, and the notation is continued onwards from F, the final stage dealt with in Table VI, p. 985.

TABLE VIII.

DEFINITIONS OF PROGRESSIVE PERIODS OF AGE RECOGNISED IN THE EXAMINATION OF OYSTERS WHICH HAVE EXTRUDED LARVÆ.

Mean age of gonad* at each period.	Notation of progressive periods.	Range of period.
24 days	G	All individuals examined within 28 days after being observed "sick."
45·7 days	H	All individuals examined within 29 to 56 days after being observed "sick."
77·5 days	I	All individuals examined within 57 to 84 days after being observed "sick."
About 12 months	J	All individuals examined about 12 months after being observed "sick."

The results of the examination of these gonads can be discussed from a consideration of the summary given in Table X, opposite. From this table it is at once seen that the 50 per cent or more category of gonad lies in period G in VI; in H in VII; in I in VIII; and in J is contained in VII and VIII categories. There is thus a regular progression in the categories of the male phase in the periods G to I, which now include both waxing and waning phases of maleness. This progression is again reflected in the mean stage of development of maleness which from periods G to H increases through 6·39 to 8·2, but again falls to 7·43 in the J period. Table VI, p. 985, shows that the corresponding mean in the F period was 5·73. The increase in maleness developed in the gonad of oysters after spawning is therefore seen to be continued into our G period, that is, for about one month after spawning (mean age of gyne-spawned gonad=24 days); but thereafter the development of maleness wanes, since in the H period (one to two months after spawning) the categories VII and VIII become predominant. In these categories *developing* sperm become scarce in the former and are completely developed in the latter, which therefore marks the completion of the development of maleness. Category IX, which includes gonads with only a few ripe sperm, constitutes a definite stage in the decline of maleness which is completed in category X, in which the sex elements are in the primitive quiescent stage, that is, not developing. It may be remarked again that category X is the same as category I, but it is permissible in

* Reckoned from the average day when egg-spawning occurred.

TABLE X.

Summary of Sex-categories 4 to 10 (See Table II, p. 981), found in Gonads of Oysters at various successive periods after the emission of Larvæ.

Group No.	No. examined in each group.	Date found with embryos or larvæ.	Date gonad examined.	Post-"sick" period in days unless stated in months.	Locality of origin of oysters.	Period G 0 to 28 days. Categories of gonad.							Period H 29 to 56 days. Categories of gonad.						Period I 57 to 84 days. Catagories of gonad.						Period J About 12 months after wintering after "sickness" in previous summer. Categories of gonad.							Ripe ♀'s or ♀ functioning.
						4	5	6	7	8	9	10	5	6	7	8	9	10	5	6	7	8	9	10	4	5	6	7	8	9	10	
84.	1	1921, May 6	1921, July 7	62	Mylor Bank, Fal Estuary	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
85.	8	1922, June 8	1922, July 15	37	West Mersea	–	–	–	–	–	–	–	–	1	5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
86.	4	,, 23	,, 15	22	Whitstable	–	–	2	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
87.	2	,, 15	,, 15	30	West Mersea	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
88.	4	,, 16	,, 15	29	Whitstable	–	–	–	–	–	–	–	–	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
89.	2	,, 12	,, 15	33	,,	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
90.	2	,, 8	,, 15	37	,,	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
91.	5	,, 26	,, 15	19	Falmouth	–	–	4	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
92.	2	,, 17	,, 28	41	Helford	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
93.	6	,, 20–2	,, 28	36	Whitstable	–	–	–	–	–	–	–	–	–	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
94.	3	July 5	,, 18	13	,,	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
95.	3	,, 11	,, 18	7	,,	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
96.	1	,, 3	,, 28	25	No. 19, West Mersea	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
97.	1	1923, June 19	1923, July 3	14	Helford	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
98.	1	July 18	Sept. 3	50	Whitstable	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
99.	2	,, 25	,, 3	42	,,	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
100.	1	Aug. 7	Aug. 20	13	Yealm Cage	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
101.	13	1924, June end	July 3	ca. 7	West Mersea	–	–	12	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
102.	18	,, end	,, 4	ca. 7	,,	–	–	14	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
103.	1	,, 24	,, 16	22	Yealm Cage	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
104.	26	,, —	Aug. 25	>56	West Mersea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	0	0	–	–	–	–	–	–	–	–
105.	100	,, —	,, 28–9	>59	,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	93	3	4	–	–	–	–	–	–	–	–
106.	6	1922, June 28–July 7	1923, July 14	12 months	Cage Oysters, W. M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3	0	1	0	–	1
107.	2	1923, July end	Oct. 20	>81	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	0	1	–	–	–	–	–	–	–	–
108.	2	,,	1924, June 8	10¼ months	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–
109.	1	June	,, 24	12 ,,	,, Yealm	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
110.	18	,,	July 1–8	11¼ ,,	,, W.M.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	4	3	0	1	4
111.	38	1924, July 1–9	1925, July 13–15	12 ,,	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	10	9	3	0	5
112.	48	June 10–July 9	,, 3–16	12–13 ,,	,, ,,	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	13	21	3	5	3
113.	25	1925, July 21	1926, July 3–7	12 ,,	* ,,*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	(7*)	(4)	(3)	0	0	11
114.	58	1926, July 29	Sept. 29	63 days.	,, (River), F. E.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	4	28	11	12	–	–	–	–	–	–	–	2
115.	40	July 21	Sept. 30	72 ,,	,, Pole Rocks, F. E.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	4	16	12	4	–	–	–	–	–	–	–	3
	444				Totals	0	2	36	10	1	1	0	0	3	16	10	0	0	0	3	8	164	26	21	0	1	24	28	34	6	7	29
					Totals in each period	50							29						222+5♀=227						100+13♀=113							

* Fifty-seven oysters in this experiment, were not examined microscopically, therefore 14 ♂ individuals of this sample, which were examined microscopically, are not included in the totals for the J period.

TABLE XI

Correlation between Waxing and Waning of Maleness and the Age of the Post-"sick" Gonad in Individuals which have emitted their Larvæ.

Mean age of gonad* at each period.	Progressive periods of age of post-"sick" gonad.	Numbers and percentages (in concave brackets) of progressive stages (I to X) of maleness in post-"sick" oysters. I	II	III	IV	V	VI	VII	VIII	IX	X	Ripe ♀ or ♀ functioning.	Not observed.	Totals examined in each period.	Mean stage of development of maleness.
24 days	G	0	0	0	0	2 (4)	36 (72)	10 (20)	1 (2)	1 (2)	0	0	0	50	6·26
45·7 days	H	0	0	0	0	0	3 (10·4)	16 (55·2)	10 (34·5)	0	0	0	0	29	7·25
77·5 days	I	0	0	0	0	0	3 (1·35)	8 (3·61)	164 (73·9)	26 (11·7)	21 (9·46)	5	0	222+5	8·24†
ca. 12 months	J	0	0	0	0	1 (1)	24 [7] (24)	28 [4] (28)	34 [3] (34)	6 [0] (6)	7 [0] (7)	13 [11]‡	0 [57]‡	100+13 [82]‡	7·41§
Totals in each category		0	0	0	0	3	66	62	209	33	28	18+[11]		401+18 [82]	
Percentages	do.					(0·75)	(16·5)	(15·5)	(52·1)	(8·2)	(7)				

* Reckoned from the average date of the last act of spawning as a female.

† The mean stage of development of maleness in Period I gonads is calculated for the total number, male or neuter, that is, 222. If the five individuals found in a female condition or with larvæ be considered to have passed through stage X, the mean sex-condition for the whole sample becomes 8·28.

‡ Fourteen well-fished individuals in this sample were examined microscopically and are recorded in their categories in right-angled brackets, fifty-seven obviously indifferent males or neuter were not so examined, and eleven individuals were either ripe females or female-functioning forms, i.e. carrying embryos or larvæ at the time of examination.

§ In the J period the mean stage of development of maleness is calculated as in the I period. If the thirteen female-functioning individuals be considered to have passed through stage X, the mean stage works out at 7·71.

periods I and J to denote this stage by the figure X, rather than I, as a deduction from the general progression observed of the 50 or more per cent category throughout the series of periods A to J.

In period I it is interesting to note that ripe females begin to appear (see Table XI), and this reappearance of the female stage coincides with the attainment of category X (no sex elements developed) in a fair percentage of cases (9·46). It is therefore clear that from 2 to 3 months in the same summer, after spawning as a female, an oyster has completed, or is nearing completion of, its post-gyne-spawning male phase, and may have begun to change, or, indeed, may have completely changed its sex back again to female. In period J, 12 months after the previous female-spawning act, the results obtained are peculiar, but it may first be noted that the number of functioning females has increased on the period I, from 5 out of 227 to 24 out of 180 examined in their respective periods. Now the individuals in period J were mostly examined in the month of July (see Table IX, p. 1025), and since some of these individuals had already changed sex from male back again to female, it is fairly certain that—not only had some individuals changed back to female from male. but that– some had gone still further and changed back again to male. There is every probability that *some* of the individuals in period J with gonad categories V and VI had extruded a batch of larvæ within a few weeks or days prior to the examination, but there is also a strong probability that others of these categories, and particularly those individuals with gonad in category VII, have carried their male phase over the previous winter period into the following summer. At this point of the discussion it must be emphasised that the J period oysters on the whole were found in the first observed female-functioning stage (i.e. the first female-functioning stage, on which observations were made during the course of these experiments; but this female stage is not necessarily the first egg-bearing stage in the life-history of the individuals under observation) later on in the breeding season on the average than those in periods G to I. Since the records of the G to I individuals show that waning of maleness occurs on the average from 2 to 3 months after the onset of this sex-phase it is quite probable that individuals which spawn as females late in the season do not, or may not, complete the post-gyne-spawning male phase in the same summer, and may carry over to the next breeding season the completion of that male phase. The writer has little doubt that this does, in fact, occur.

TABLE IX

RECORDS OF THE INVESTIGATION OF THE GONAD, ETC., OF 444 OYSTERS EXAMINED AT VARIOUS PERIODS (see p. 1022) AFTER EXTRUSION OF THE LARVÆ.

	Gonad.			Condition of			
1	2	3	4	5	6	7	8
Serial No. of oyster.	Ripe sperm-morulæ.	Unripe sperm-morulæ.	Ripe ova left in gonad.	Gonoducts.	Fish.	Period and category of gonad.	Remarks.
84. 1921. MYLOR BANK, WHITESICK, MAY 6/21; EXAMINED JULY 7/21.							
716	∞	f ∞	some	—	—	I6	
85. 1922. EXAMINATION OF OYSTERS, JULY 15–17/22; "SICK," JUNE–EARLY JULY /22; WEST MERSEA, "SICK," 8.6.22.							
717	∞	a few	none	full	f good	H7	
718	∞	none	do.	fairly full	poor	H8	
719	∞	few	do.	full	do.	H7	
720	∞	do.	do.	do.	do.	H7	
721	∞	none	do.	f full	do.	H8	
722	f ∞	f ∞	do.	empty ?	very poor	H6	
723	∞	rare	do.	a little sperm	fair	H7	
724	∞	fair no.	do.	full	fair	H7	
86. WHITSTABLE, "SICK," 23.6.22.							
725	∞	f ∞	none	f full	good	G6	
726	∞	none	do.	full	f good	G8	
727	∞	f ∞	do.	do.	do.	G6	
728	∞	rare	do.	do.	do.	G7	
87. 2 WEST MERSEA, "SICK." 15.6.22.							
729	∞	a few	do.	f full	poor	H7	
730	∞	rare	do.	do.	good	H7	
88. 4 WHITSTABLE "SICK," 16.6.22.							
731	∞	fair no.	none	full	poor	H7	
732	∞	∞	do.	full in parts	do.	H6	
733	∞	a few	do.	full on left side	f good	H7	
734	∞	none	do.	full milky	do.	H8	
89. 2 WHITSTABLE, "SICK," 12.6.22.							
735	f ∞	none	none	little on left	poor and watery	H8	
736	∞	occ.	do.	full	f good	H7	
90. 2 WHITSTABLE, "SICK," 8.6.22.							
737	∞	f ∞	none	full	poor, watery	H6	
738	∞	a few	do.	full	do.	H7	
91. 5 FALMOUTH, "WHITESICK," 26.6.22.							
739	∞	f ∞	none	nearly empty	poor, watery	G6	
740	f ∞	f ∞	do.	do.	fair	G6	
741	f ∞	f ∞	do.	a little	good	G6	
742	∞	fair no.	do.	ca. full	do.	G7	
743	∞	∞	do.	empty ?	f good	G6	
92. HELFORD OYSTERS "SICK," 17–22.6.22, EXAMINED 28.7.22.							
744	∞	rare	none	full	little, watery	H7	
745	∞	rare	do.	do.	do.	H7	

1	2	3	4	5	6	7	8
93. WHITSTABLE "SICK," 20-2.6.22; EXAMINED 28.7.22.							
746	∞	fair no.	∞ patches.	Little Blacksick, ∞ larvæ	poor	H(F)7	See Note **1**, p. 1033, curdled
747	∞	rare	none	full	poor	H7	
748	∞	none	∞ deg.	full	full	H8 Inc. sp,	
749	∞	do.	none	full	N.O.	H8	
750	∞	none	none	full	N.O.	H8	
751	∞	a few	do.	do.	N.O.	H7	
OYSTERS EXAMINED JULY 18/22.							
94. 4 WHITSTABLE WHITESICK, 5.7.22.							
752	none	none	∞ ripe	full	full	ripe ♀	See Note 2
753	∞	f no.	none	nearly full	poor	G7	
754	∞	∞	do.	little	poor, watery	G6	
755	a few	f ∞	do.	empty ?	fair	G5	
95. 3 WHITSTABLE WHITESICK, 11.7.22.							
756	∞	f ∞	none	full	poor, watery	G6	
757	∞	∞	do.	partly full	poor	G6	
758	rare	∞	do.	empty ?	fair	G5	
96. No. 19 WEST MERSEA OYSTER, SPATTED SINCE JUNE, 1921, WHITESICK, 3.7.22.							
759	∞	fair no.	none	N.O.	N.O.	G7	
97. 1923. HELFORD RIVER OYSTER, WHITESICK, 19.6.23; EXAMINED 3.7.23.							
760	some	∞	N.O.	—	—	G6	
98. WHITSTABLE OYSTER, "SICK," 18.7.23, KEPT IN PLYMOUTH TANKS; EXAMINED 3.9.23.							
761	∞	none	none	—	—	H8	
99. WHITSTABLES "SICK," 25.7.23, KEPT IN TANKS; EXAMINED 3.9.23.							
762	∞	none	none	—	—	H8	
763	∞	do.	do.	—	—	H8	
100. YEALM CAGE OYSTER, SICK, 8.7.23; RE-EXAMINED BY BORING AFTER BEING IN SEA, 30.8.23.							
764	few	—	—	little	poor, watery	G9	
101. WEST MERSEA OYSTERS, BLACKSICK IN JUNE AND EARLY JULY; EXAMINED 3.7.24; THE FIRST 13 INDIVIDUALS WERE THE LAST TO BE ISOLATED, i.e. THEY WERE BLACKSICK AT THE END OF JUNE OR ON JULY 1 AND 2.							
765	v ∞	f ∞	none	—		G6	Colour of Digestive gland. chocolate, Note 3
766	∞	∞	do.	larvæ present 200 to 210μ		F6	reddish brown
767	v ∞	v ∞	do.	full ducts		G6	choc.-brown
768	v ∞	f ∞	none	full		G6	good chocolate
769	∞	few	do.	do.		G7	do.
770	∞	f. ∞	do.	empty		G6	greeny-brown
771	∞	do.	do.	full		G6	good chocolate
772	∞	∞	do.	empty		G6	brown
773	∞	∞	do.	do.		G6	yellow-brown
774	∞	f ∞	do.	full		G6	greeny-brown
775	∞	∞	do.	do.		G6	choc.-brown
776	∞	f ∞	do.	½-full		G6	greeny-brown
777	∞	do.	do.	empty		G6	good chocolate

1	2	3	4	5	6	7	8
102. SAME SAMPLE, BLACKSICK IN JUNE; EXAMINED 4.7.24.							
778	∞	f ∞	few	little		G6	light brown
779	∞	∞	none	do.		G6	good chocolate
780	∞	∞	do.	fair		G6	do.
781	∞	∞	do.	empty		G6	do.
782	∞	f ∞	do.	full		G6	do.
783	∞	∞	do.	empty		G6	do.
784	∞	∞	do.	full		G6	do.
785	∞	fair no.	do.	fair amount		G7	do.
786	∞	do.	do.	full		G7	do.
787	f ∞	fair no.	do.	little		G7	light brown
788	∞	∞	do.	empty		G6	good chocolate
789	∞	∞	do.	f full		G6	do.
790	f ∞	fair no.	do.	do.		G7	do.
791	∞	f ∞	do.	full		G6	do.
792	∞	do.	do.	empty		G6	do.
793	∞	∞	do.	full		G6	do.
794	∞	f ∞	do.	empty		G6	do.
795	∞	∞	do.	full		G6	do.
103. YEALM CAGE OYSTER, "SICK," 24.6.24; EXAMINED 16.7.24.							
796	∞	few	rare			G7	
104. 26 WEST MERSEA OYSTERS, BLACKSICK JUNE–JULY, 1924; EXAMINED AT PLYMOUTH 21 AND 25.8.24.							
817	∞	none	none	21 full or nearly full		I8	See Note 3
822	∞	do.	do.	5 little to empty		I8	
105. 100 OYSTERS WHITESICK, WEST MERSEA, JUNE–JULY, 1924; EXAMINED AT PLYMOUTH 28–29.8.24.							
832	∞	none	some degenerating	10 individuals		I8	Digestive gland. mostly very light fawny colour*
835	few	none	do.	3	do.	I9	do
918	∞	none	none	83	do.	I8	do.
920	none	none	some degenerating	2	do.	I10	do.
922	none	none	none	2	do.	I10	do.
106. OYSTERS FOUND WITH LARVÆ, JUNE 28–JULY 7, 1922, AT WEST MERSEA; EXAMINED JULY 14, 1923. (KEPT IN EXPERIMENTAL CAGE).							hell growth in 1923.
923	not observed			Grey embryos			12 Note 4
924	∞	few	none	ducts full		J7	6
925	∞	∞	do.			J6	6
926	fair no.	none	do.			J9	nil
927	do.	rare	do.		poor	J7	8
928	∞	few	do.		good	J7	7–9
107. FOUND WITH LARVÆ OR EMBRYOS, END OF JULY, 1923 (PUT IN EXPERIMENTAL CAGE); EXAMINED OCT. 12, 1923 (2–3 MONTHS AFTER SICKNESS).							
929	none	none	none	gaping		I10	
930	∞	?	none	do.		I8	

* K. and V. 128 D.

1	2	3	4	5	6	7	8
108. SAME SAMPLE, EXAMINED JUNE 8, 1924.							
931	none	none	none	gaping	poor	J10	—
932	∞	∞ nearly ripe	do.	do.	f good	J6	—
109. YEALM CAGE OYSTER, "SICK," JUNE, 1923; PUT IN CAGE IN SEA; EXAMINED 24.6.24.							
933	∞	very few	rare small relict	—		J7	
110. SAME SAMPLE EXAMINED JULY 1 TO JULY 8, 1924.							Shell growth in 1924.
934	∞	none	none		f good	J8	sl. d
935	—	—	—	Whitesick	—	—	7–12, Note 5
936	∞	few	none	Blacksick ?	—	(J7)	10–11
937	none	none	∞ ripe	ripe ♀			5–10
938	∞	f ∞	none		good, fat	J6	nil d
939	∞	∞	do.		good	J6	5–11
940	∞	none	do.		do.	J8	5–6
941	∞	∞	do.		f g	J6	1–6
942	∞	few	do.	ducts full on left	do.	J7	6–12
943	none	∞	few	Whitesick	fair	B4	10–5
944	∞	f ∞	none	little in ducts	f g	J6	3–4 ?
945	none	none	none	empty do.	f	J10	3–9 ?
946	∞	rare	do.	do. do.	f g	J7	?
947	∞	∞	do.	little in do.	f g	J6	
948	∞	∞	none	ducts empty	good	J6	3–13
949	∞	few	∞ ripe degenerating ?	do. do.	very good	J7	3–10
950	∞	none	do.	do. a little	do.	J8	3–12
951	∞	few	∞	empty	do.	J7	5–13

111. INDIVIDUALS FOUND BLACKSICK, JULY 1 TO 9, 1924, AT WEST MERSEA; PUT IN EXPERIMENTAL CAGE; EXAMINED JULY 13–15, 1925.

JULY 13, 5 WEAK INDIVIDUALS EXAMINED.

952	∞	none	none		fair	J8		8		
953	∞	do.	do.		do.	J8		8		
954	∞	do.	do.		good	J8		9		
955	few	f no. v young	few	Whitesick	poor	C4*		15	Note 6	
							L.	Br.	Sh.	
956	∞	few	none	—	fair	J7	68	75	13	
				JULY 14.						
957	∞	f ∞	do.	full	do.	J6	68	78	5	sl. d
958	∞	f ∞	do.	f full	do.	J6	60	61	5	sl. d
959	f ∞	∞	do.	Blacksick	do.	F6	65	67	9	
960	∞	none	none	—	poor	J8	55	65	10	
961	∞	fair no.	do.	f full	do.	J7	67	68	16	
962	∞	few	do.	do.	good	J7	67	67	5	sl. d
963	∞	f ∞	do.	—	do.	J6	70	75	7	
964	∞	f ∞	do.	f full	do.	J6	71	73	12	
965	∞	rare	do.	empty	fair	J7	72	73	11	
966	v ∞	rare	do.	—	do.	J7	79	86	5	
967	v ∞	none	do.	f full	poor	J8	65	70	10	
968	∞	rare	do.	little	fair	J7	66	67	15	
969	∞	f ∞	do.	—	good	J6	73	69	8	thin sl. d
970	∞	f ∞	do.	—	fair	J6	64	62	11	

1	2	3	4	5	6	7	8			
971	∞	f ∞	none	full	do.	J6	68	67	13	
972	∞	∞	do.	full on left	do.	J6	65	62	10	
973	∞	rare	do.	f, do.	poor	J7	72	72	12	
974	none	none	∞ ripe	ripe ♀ full	v g		72	78	15	
975	∞	few	none	f full	f g	J7	67	71	12	
976	none	f ∞	none	Whitesick	f	C4	72	68	11	
977	∞	rare	none	f full	g	J7	79	75	13	
978	∞	none	∞ relict	— curdley	v g	J8	81	82	10	
979	none	∞ to 35μ	few	Whitesick	poor	C3	76	69	15	
				JULY 15.						
980	∞	∞	none	—	poor	J6	80	89	10	
981	few	none	none	—	poor	J9	79	82	20	
982	f ∞	f ∞	do.	—	f	J6	84	70	11	
983	∞	none	do.	—	f g	J8	72	79	11	
984	f ∞	none	do.	—	f g	J8	62	65	11	
985	∞	rare	do.	—	poor	J7	61	60	11	
986	few	none	do.	empty	good	J9	60	61	5	d
987	∞	∞	do.	f full	f	J6	78	82	12	
988	rare	none	do.	empty	f	J9	71	66	11	
989	∞	none	do.	full	f	J8	68	72	10	

112. OYSTERS WHITESICK JUNE 10 TO JULY 9, 1924, PUT IN SEA IN CAGE IN DEEPS, WEST MERSEA, JULY 9, 1924; EXAMINED JULY 3–16, 1925.

				JULY 3, 1925, 5 WEAK INDIVIDUALS.						
990	∞	none	none		poor, watery	J8		7		
991	none	do.	do.		do.	J10		11		
992	few	few	do.		poor	J7		14		
993	∞	do.	do.		fair	J7		9		
994	∞	∞	do.	Blacksick	poor	F6	8	Note 7		
				JULY 14.						
995	occ.	f ∞ to 60μ	few patches	Whitesick	fair	C5	68	71	15	
				JULY 15.						
996	none	∞	do.	Whitesick	poor	C4	60	65	13	
997	∞	none	none		f	J8	60	68	10	
998	none	none	∞ patches relict		good	J10	58	66	10	
999	∞	none	none		f	J8	62	65	10	
1000	∞	do.	do.		f	J8	70	66	15	
1001	f ∞	none	∞ degen.	curdled	—	J8	70	69	15	
1002	∞	f ∞	none		f	J6	57	60	8	
1003	∞	none	none	—	f	J8	65	72	10	
1004	∞	none	do.	full	f	J8	60	63	8	
1005	∞	do.	do.	little	g	J8	55	64	10	
1006	∞	do.	do.	do.	poor	J8	60	63	16	
1007	∞	few	do.	do.	g	J7	67	70	5	
1008	v ∞	none	∞ relict	curdled	v g	J8	59	64	12	
1009	few	none	none	empty	f	J9	63	72	9	
1010	∞	few	do.		f	J7	68	73	14	
1011	∞	none	do.		g	J8	73	74	10	
1012	none	none	∞ relict	curdled gonad	f	J10	67	68	9	
1013	few	none	big patches relict	do.	g	J9	62	65	6	
1014	∞	fair no.	none		g	J7	64	82	18	
1015	∞	few	do.		f	J7	65	69	7	
1016	fair no.	fair no.	do.		g	J7	70	77	8	
1017	few	none	do.		f	J9	94	80	10	
1018	∞	few	do.		v g	J7	50	60	8	d

1	2	3	4	5	6	7	8			
1019	∞	none	none		g	J8	60	60	5	thin
1020	f ∞	few	do.		f	J7	63	63	4	
1021	∞	none	do.		p	J8	60	65	14	
1022	∞	rare	do.		g	J7	62	69	6	
1023	∞	none	do.		g	J8	60	71	12	
1024	f ∞	none	do.		f	J8	68	68	12	
1025	∞	none	do.		f	J8	59	68	6	
1026	f ∞	f ∞	do.		p	J6	54	60	16	sl. d
1027	∞	none	do.		—	J8	65	68	15	
				JULY 16.						
1028	∞	a few	do.		p	J7	65	67	14	
1029	∞	none	do.		p	J8	58	62	7	
1030	f ∞	none	do.		p	J8	66	66	9	
1031	∞	none	do.		f	J8	59	63	8	
1032	∞	f ∞	do.		f	J6	67	68	17	
1033	none	none	fair no. relict in big patch	curdley	f	J10	53	63	4–15	
1034	none	none	none		p	J10	60	65	11	
1035	∞	none	do.		f	J8	61	69	14	
1036	∞	few	do.		f	J7	67	65	9	
1037	∞	occ.	do.		f	J7	53	66	9	

113A. WEST MERSEA, INDIVIDUALS BLACKSICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS, JULY 21, 1925; EXAMINED JULY 3, 1926.

1038	∞	f ∞	none		f g	J6	86	87	10	
1039	∞	∞	none		g	J6	69	63	9	
1040	∞	∞	do.		g	J6	84	82	9	
1041	f ∞	none	∞ ripe	Ripe♀♀	v g		77	71	0	Note 8
1042	f ∞	f ∞	none		f g	J6	64	65	5	
1043	v ∞	f ∞	do.		g	J6	79	85	5	
1044	v ∞	few	do.		v g	J7	68	74	5	
1045	v ∞	fair no.	few relict?			J7	57	65	8	
1046	none	none	∞ ripe	ripe♀	f g		72	75	10	
1047	v ∞	few	none		f	J7	53	54	0	
1048	∞	none	none		f g	J8	80	78	3	

Seventeen individuals, determined as obviously males by the naked eye, were not examined microscopically.

113B. WEST MERSEA OYSTERS FOUND WHITESICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS, WEST MERSEA, JULY 21, 1925, AND EXAMINED JULY 7, 1926, FOR SIGNS OF FEMALENESS.

1049	none	none	∞ ripe	ripe♀	f g		68	67	16	
1050	none	none	few patches	Whitesick	poor	C1	69	72	10	
1051	none	none	∞ ripe	ripe♀	v g		67	67	12	
1052	none	none	∞nearly ripe	ripening♀	f g		74	67	10	
1053	few	∞	one patch	Greysick	f g	E5	71	69	12	
1054	∞	none	none	—	v g	J8	56	57	4	
1055	∞	few	none	—	g	J7	67	65	5	
1056	∞	f ∞	none		v g	J6	73	71	10	
1057	∞	none	fair no. relict?		v g	J8	80	76	14	
1058	fair no.	∞	occ. patches	Whitesick	f	C5	68	68	6	
1059	fair no.	none	∞ ripe	♂♀♀	v g		61	67	14	

Thirty individuals, obviously male to the naked eye, were not examined microscopically.

1	2	3	4	5	6	7	8		

113C. FALMOUTH OYSTERS BLACKSICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS, WEST MERSEA, JULY 21, 1925; EXAMINED JULY 3, 1926.

1060	∞	f ∞	none	♂	v g	J6	66	66	10
1061	f ∞	none	∞ ripe	♂ ♀ ripe	v g		60	64	13

Five other individuals, obviously male to the naked eye, not examined microscopically.

113D. FALMOUTH OYSTERS WHITESICK IN JULY, 1925, PUT IN SEA IN CAGE IN DEEPS, WEST MERSEA, JULY 21, 1925; EXAMINED JULY 3, 1926.

1062	none	none	∞ ripe	ripe ♀	v g		68	69	17

Five other individuals, obviously male to the naked eye, were not examined microscopically.

POST-SPAWNED OYSTERS.

114A. OYSTERS BLACK- OR GREY- "SICK" JULY 29/26 KEPT IN RIVER CAGE, TRELISSICK REACH, FAL ESTUARY; HAULED AND EXAMINED ON SEPT. 29/26.

							L.	Br.	Sh.	
1063	v ∞	none	few relict	GD ram B		I8	72	79	8	
1064	f ∞	none	none	GD ram A		I8	82	78	3	
1065	∞	do.	do.	ff ♂ A		I8	59	63	7	
1066	∞	do.	do.	GD ram B		I8	60	52	8	
1067	none	none	none	do.		I10	61	62	4	
1068	do.	do.	do.	do.		I10	59	67	8	
1069	do.	do.	∞ deg.	do.	gonad spotty	I10	63	62	9	
1070	∞	do.	none	GD st. to ram B		I8	61	63	8	
1071	few	do.	do.	sq. and trs.		I9	66	61	10	
1072	none	none	none	GD ram B to ff ♂ B		I10	60	64	6	
1073	f ∞	do.	do.	ram B		I8	69	72	11	
1074	∞	do.	do.	st. B—ram B		I8	62	59	8	
1075	f ∞	do.	some young ?	st. A		I8	63	65	11	
1076	v ∞	do.	do.	do.		I8	72	79	6	
1077	v ∞	do.	none	ram B—f trs.		I8	59	62	6	
1078	∞	do.	do.	st. B—f trs.		I8	75	71	9-22	
1079	lost			ram B—st. A		—	62	60	9	
1080	none	none	none	ram B—ff ♂ B		I10	65	65	3	
1081	do.	do.	do.	ram B—ff ♂ B		I10	74	74	11-25	
1082	rare	do.	do.	st. A		I9	67	70	13	
1083	do.	do.	do.	st. B—ram B		I9	78	75	14	
1084	fair no.	do.	do.	sq. & trs.—st. B		I9	69	78	6	
1085	few	do.	do.	ram B		I9	61	66	9	
1086	f ∞	do.	do.	ram B—ff ♂ B		I8	75	76	7	
1087	∞	do.	do.	do.		I8	65	66	8	
1088	v ∞	do.	do.	ram B		I8	61	62	12 ?	
1089	none	none	none	Blacksick ram B & trs. ∞ embryos 190 × 170μ		F1-10	62	63	6	See note 9.
1090	do.	do.	do.	ram B		I10	59	59	6	
1091	do.	do.	do.	ram B—ff ♂ B		I10	72	75	8	
1092	do.	do.	do.	do.		I10	57	59	6	
1093	∞	do.	do.	st. A. g.w.d.		I8	60	65	5	sl. d
1094	none	none	none	sq. & trs., blood cells v ∞		I10	55	61	3	
1095	a few	do.	do.	ram B		I9	65	64	2-10	
1096	not observed			poor watery, chambered		—	56	53	nil	
1097	f ∞	none	none	ram B		I8	70	72	nil	
1098	rare	none	none	ram B (sq. & trs.)		I9	57	61	7	

1	2	3	4	5	6	7	8			
1099	v ∞	few	none	ff ♂ B		I7	64	65	3–8	
1100	few	none	do.	ram B (sq. & trs.) blood cells v ∞		I9	68	60	4–11	
1101	∞	do.	do.	sq. & trs. (big green cyst)		I8	68	74	12	
1102	fair no.	do.	do.	ram B—st. B		I9	60	71	6–14	
1103	v ∞	odd ones	do.	st. A		I7	62	65	nil	
1104	v ∞	none	do.	ff ♂—sq. ♂		I8	59	61	6–12	d
1105	v ∞	do.	do.	st. A V.G. fish		I8	54	60	2	d
1106	none	none	do.	do. blood cells v ∞		I10	52	67	7	d
1107	f ∞	do.	do.	do. & sq. & trs. V.G. fish blood cells v ∞		I8	54	65	5	d
1108	few	do.	do.	sq. & trs. to sq. ♂		I9	55	65	8	d
1109	v ∞	do.	do.	ff ♂ B & sq. & trs., blood cells v ∞		I8	60	67	2	d
1110	v ∞	do.	do.	sq. ♂ to sq. & trs.		I8	51	60	nil	d
1111	rare?	do.	do.	sq. & trs. to ram B, big granular cells v ∞		I9	46	55	3	d
1112	∞	none	none	ram B to st. A blood cells ∞		I8	54	61	3	d
1113	none	occ. ?	none	Blacksick sq. ♂ larvæ 180–190μ f ∞		—	52	64	6	d
1114	v ∞	none	none	st. A in parts		I8	59	71	0	d
1115	∞	do.	do.	st. B—ram B		I8	55	58	0	d
1116	∞	fair no.	do.	st. A, B, and sq. & trs., blood cells ∞		I7	55	57	6	d
1117	∞	none	none	sq. & trs., blood cells ∞		I8	54	62	4	d
1118	none	none	none	ram B, new chamber ∞ big granular cells, blood cells ∞		I10	57	63	2	d
1119	v ∞	do.	do.	ff ♂ B		I8	55	63	3	d
1120	v ∞	do.	do.	ff ♂ B—ram B		I8	56	60	3	d
				Two normal and one dump dead.						

114B. OYSTERS FROM RIVER FAL, TRELISSICK REACH CAGE, WHITESICK JULY 29/26; EXAMINED SEPT. 29/26.

1121	∞	fair no.	none	sq. & trs.—ram B	I7	59	66	8	sl. d
1122	∞	∞	none	ram B, V.G. fish	I6	61	68	10	d

115A. OYSTERS FROM THE CAGE MOORED TO POLE'S ROCKS, FAL ESTUARY, BLACKSICK JULY 21, 1926; EXAMINED SEPT. 30, 1926.

1123	few	none	none	ram B	I9	61	58	?
1124	v ∞	do.	do.	st. A	I8	65	61	2
1125	v ∞	do.	do.	do.	I8	60	65	0–2
1126	∞	fair no.	do.	do.	I7	59	62	nil
1127	∞	none	do.	ram B	I8	70	65	0–3
1128	∞	do.	do.	st. B	I8	62	65	0
1129	v ∞	do.	do.	ff ♂ B	I8	69	70	0
1130	rare	do.	do.	ram B	I9	61	65	0
1131	∞ ducts full	f ∞	do.	ff ♂ B—ram B	I6	60	70	0

1	2	3	4	5	6	7	8			
1132	fair no.	none	∞ young	st. A		I9	57	60	0	See note 10
1133	∞	do.	none	ram B		I8	63	61	4	
1134	∞	do.	few relict	ram A		I8	63	63	0	sl. d
1135	few	none	none	? trs.—st. B		I9	60	55	0	
1136	∞	∞	∞ young ?	SLATESICK sq. & trs.—st. B embryos f ∞ 170–180μ		F6	86	80	0	See note 11
1137	none	none	none	st. B		I10	60	57	0	
1138	not observed (preserved)			WHITESICK, sl. sq. & trs. embryos only f ∞ heart shaped not ciliated		C ?	56	60	0	sl. d
1139	fair no.	none	none	sq. & trs. ∞ big granular cells		I9	58	57	0	
1140	v ∞	few	do.	ff ♂ B—sq. & trs.		I7	50	59	0	sl. d
1141	∞	none	do.	st. B—ram B		I8	62	60	0	
1142	v ∞	few	do.	ff ♂ B—sq. & trs.		I7	47	62	0	d
1143	few	none	do.	st. A & sq. & trs.		I9	52	58	0	d
1144	∞	do.	do.	do.		I8	61	66	0	d
1145	fair no.	do.	do.	sq. & trs.		I9	51	59	0	d
1146	do.	do.	fair no. young ?	do.		I9	54	59	3?	d
1147	few	do.	some young ?	sq. ♂ & st. A		I9	59	77	0	d three others dead

115B. OYSTERS FROM CAGE MOORED TO POLE'S ROCKS, FAL ESTUARY, WHITESICK JULY 21, 1926; EXAMINED SEPT. 30, 1926.

1148	∞	none	none	ram B		I8	63	70	3	
1149	v ∞	do.	do.	do.		I8	62	67	0	
1150	v ∞	do.	do.	st. B		I8	57	61	0	
1151	∞	do.	do.	ram B		I8	53	56	6	
1152	none	none	none	st. B		I10	62	59	0–3	
1153	few	do.	do.	ram B		I9	70	68	0	
1154	none	none	∞ young ?	st. B—ram B		I10	67	65	5	
1155	few	none	none	ram B		I9	59	58	4	
1156	none	none	none	do.		I10	66	62	3	
1157	∞	do.	do.	do. V.G. fish		I8	68	73	6	
1158	∞ in ducts	do.	do.	ff ♂ B		I8	75	87	0	
1159	v ∞	do.	some relict	ram A probably incompletely spent		I8	69	73	0	
1160	v ∞	fair no.	none	sq. & trs.		I7	54	73	3	d
1161	v ∞	none	none	do.		I8	47	58	2	d
1162	few	do.	do.	do.		I9	45	48	0	d none dead

NOTES ON TABLE IX.

The abbreviations used are the same as those employed in Tables II, IV and VII, those employed in lots 114 and 115 will be described in Part II of the paper when this is published later.

Note 1. No. 746, found blacksick 36 days after previously being found sick, is best considered as an individual which has retained its larvæ unusually long, although it is possible that an incomplete spawning may have been followed at some later period by a more complete—but as the records show still incomplete—spawning.

Note 2. No. 752 is an example of an oyster which has spawned only very slightly, and retained most of its ova even a fortnight after its incomplete spawning. Such cases do not occur frequently, but it is possible in some circumstances that they may interfere with experimental results, unless care be taken to choose those individuals which extrude masses of spawn and to record the numbers of individuals dealt with.

Note 3. Lot 101 of individuals recently found blacksick, were kept for a few days in an oyster pit —covered or freshened at most high tides—until examined. Lots 104 and 105 were portions of the same sample taken to Plymouth from the West Mersea oyster beds and examined at Plymouth. Lot 104, examined at Plymouth, Aug. 21 to 25, had fawny and pale fawny coloured digestive gland (about 137 Klincksieck et Valette, Codes des Couleurs). Lot 105, examined Aug. 28–29, had rather paler digestive glands (ca. 128 D, K. et V.). Both 104 and 105 lots had probably fed little after leaving Mersea at the end of July, and possibly Stage VII of maleness had been hastened for this reason. The gonads of these lots are, however, similar to lots 114 and 115, when one takes into consideration the fact that the Mersea individuals had spawned earlier in the season than the Falmouth samples. It is an interesting fact that very few of these previously blacksick individuals had unspawned eggs left in the gonad at the time of examination; a circumstance which indicates that unspawned ova may normally be extruded later through the gonadial aperture.

Note 4. No. 923 is an individual which carried larvæ in 1922 and spawned as a female again in 1923.

Note 5. Nos. 935 to 937 and 943 are individuals found with larvæ in 1923 and again found ♀ or ♀-functioning in 1924.

Note 6. Nos. 955, 959, 974, 976, 979 were found blacksick in 1924 and again found ♀ or ♀-functioning in 1925.

Note 7. Nos. 994, 995, 996 were found whitesick in 1924 and again found ♀ or ♀-functioning in 1925.

Note 8. Nos. 1041, 1059 and 1061 were found respectively black- and whitesick in July, 1925, and again hermaphrodite female in 1926. Other sick individuals in 1925 again found ♀ or ♀-functioning in 1926 are 1046, 1049 to 1053, 1058 and 1062.

Note 9. No. 1089 and 1113 were found with shelled larvæ on July 29, 1926, and again after being in the sea until Sept. 29, 1926, were found carrying shelled larvæ. Presumably these two individuals had spawned twice in the same season, especially as their larvæ were normal or not quite full-sized. The gonads of these two individuals are characteristic for the time of the year.

Note 10. No. 1132 is an individual found blacksick, July 21, 1926, and now in male-phase No. IX, but beginning to develop femaleness. If this individual retains its ripe sperm-morulæ during the period of egg-development it will become one of the mixed sexes.

Note 11. Nos. 1136 and 1138 were found with shelled larvæ, July 21, 1926, and again found, respectively, slate- and whitesick on Sept. 30, 1926, and have both, therefore, had two batches of larvæ in the same year. The whitesick individual is especially interesting, as it can only have spawned a few days before being examined.

General Review of the course of the Male Phase following Egg-spawning.

It is now possible to review all the changes observed in the gonad of oysters after such individuals have spawned as females. For convenience the records of the whole of the individuals examined are brought together in one comprehensive table, Table XII, given on p. 1035. From this table it is possible to follow easily the rapid development of maleness in periods A to F and its subsequent slowing down in periods G to I, with the recurrence of femaleness in the period I and the greater development of femaleness—some of which, however, may have passed undetected—in period J. Ripe sperm are produced in such oysters commonly within about $3\frac{1}{2}$ days after the female-spawning, and the whole of the sperm becomes ripe within about 2 months from the time of female-spawning, if so long a summer period remains in the same summer in which the female-spawning act occurs. There is a strong probability that if an oyster spawns late in the breeding season, the developmental period

TABLE XII.

Correlation between progressive Male Phases and Age of Gonad observed after and reckoned from the date Oysters spawned as Females.

Mean age* of gonad at each period.	Progressive periods of age of gonad.	Numbers and percentages (in brackets) of progressive male phases (categories I to X) in each period.										Ripe ♀'s or ♀-functioning individuals.	Total examined in each period.	Mean stage of development of maleness.
		I..	II.	III.	IV.	V.	VI.	VII.	VIII.	IX	X			
2¼ hours	A	5 (20·9)	2 (16·6)	12 (*50*)	5 (20·9)	0	0	0	0	0	0	—	24	2·71
14 hours	B	1 (1·97)	4 (7·85)	25 (*49·1*)	19 (*37·3*)	1 (1·97)	1 (1·97)	0	0	0	0	—	51	3·26
45 hours	C	1 (0·77)	1 (0·77)	26 (20·1)	83 (*63·9*)	14 (10·8)	5 (3·85)	0	0	0	0	—	130	3·95
3½ days	D	0	1 (0·9)	12 (10·9)	39 (*35·2*)	33 (*29·8*)	26 (23·5)	0	0	0	0	—	111	4·65
4½ days	E	1 (0·77)	0	3 (2·31)	25 (19·3)	27 (20·8)	74 (*57·1*)	0	0	0	0	—	130	5·31
8½ days	F	8 (3·12)	0	0	6 (2·34)	31 (12·1)	197 (*76·9*)	11 (4·29)	3 (1·17)	0	0	—	256	5·73
24 days	G	0	0	0	0	2 (4)	36 (*72*)	10 (20)	1 (2)	1 (2)	0	0	50	6·26
45·7 days	H	0	0	0	0	0	3 (10·4)	16 (*55·2*)	10 (34·5)	0	0	0	29	7·25
77·5 days	I	0	0	0	0	0	3 (1·35)	8 (3·61)	164 (*73·9*)	26 (11·7)	21 (9·46)	5	222+5	8·24
About 12 months	J	0	0	0	0	1 (1)	24 (24)	28 (*28*)	34 (*34*)	6 (6)	7 (7)	13	100+13	7·41
Total no. in each category		16	8	78	177	109	369	73	212	33	28	18	1121	
Total per cent	do.	(1·43)	(0·71)	(6·97)	(15·8)	(9·74)	(32·9)	(6·52)	(18·9)	(2·95)	(2·51)	(1·61)		

* Reckoned from the act of egg-spawning

of maleness will be carried over the ensuing winter period and attain completion only in the following breeding season. After the attainment of a well-defined male phase with fairly abundant ripe sperm some individuals pass into a neuter sex condition in the same season in which the female and male phases have been brought to fruition. In a small number of cases a second female condition in one and the same breeding season appears to have occurred (see period J, Tables XI and XII), but such cases will be examined more closely later. The phases which follow the neuter stage up to the attainment of the ripe female condition have been the subject of a special research, which it is hoped will be completed in the near future. There can be no doubt, however, that a significant number of individuals complete the male phase in the same summer as they have spawned as females, and reattain the state of functioning females at the beginning of the following breeding season, as shown by the results obtained in period J, Tables XI and XII.

The duration of the Male Phase following Egg-spawning.

The rate of development of maleness in oysters which are still carrying embryos or larvæ has been shown graphically in Fig. 1, p. 991, to be very rapid. With the additional data given in Table XI, p. 1023, it is possible to construct a graph which will show clearly the information obtained on the duration of the male phase, and at the same time be helpful in discussing various aspects of the phase. The graph given in Fig. 3, p. 1037, is constructed from the data given in Table XII on the mean stage of maleness for each age-period, and the mean age of the gonad—reckoned from the date of egg-spawning—in each period. An obvious defect brought out by the graph is the absence of observations intermediate between the points I and J. It will be possible to fill in observations in the gaps in the future, and in the meantime it may be anticipated that, on most oyster beds, there is a general cessation of gonadial metabolism (that is, in so far as oogonia and spermatogonia are concerned) during a large portion of the winter period. Definite facts are required to substantiate statements of this kind, and an effort is being made to obtain them. Although there are indications of a minimum of gonad activity in the mid-winter period, there is unquestionably in a large number of cases a long preparatory period of storage of reserve products and early development of the gonad in the autumn, and no doubt continued in the early spring. Definite data to support the statement with regard to gonad development in the autumn can be given. It may therefore be expected that the curve in Fig. 3 will remain fairly flat from the point I onwards. Under ideal conditions it would

seem that the curve would maintain its general direction and gradually approach the level of sex-stage X until it finally reaches this figure in a period of about 12 months, as is indicated by the light discontinuous line continuing the curve from I. It has already been noted that the apparent regression of the curve between I and J may be accounted for by

(1) the J experimental individuals retaining undeveloped maleness through the winter, owing to being on the whole later spawners than

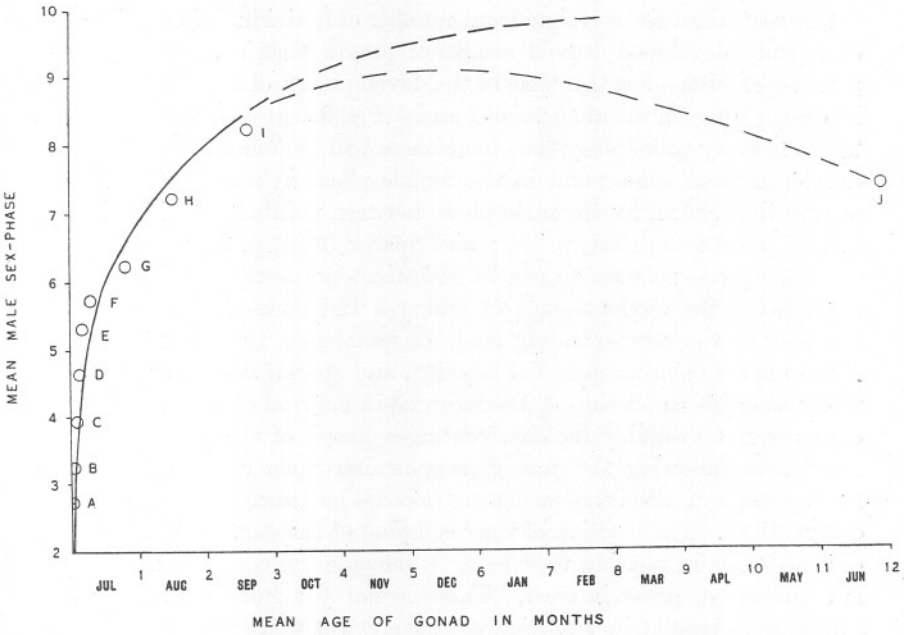

FIG. 3.—Graph showing the rate of development and course of the male sex-phase following egg-spawning in 1,123 individuals of *O. edulis*. (The months of the year apply approximately only, and are inserted to show the general decline of the male-phase towards the approach of winter.)

No observations have yet been made in the period elapsing between I and J; the upper dotted line indicates the continuation of the curve and the probable normal waning of maleness in individuals which spawn early in the preceding breeding season. The lower dotted curve joining I to J gives the mean course of the male sex-phases in a number of individuals which includes some which have already changed back again to the female sex-phase, and probably includes some also which have passed on to a second post-egg-spawning male phase in the period of the observations.

individuals in periods A to H, with a recrudescence of developing maleness occurring in the following summer; and

(2) the occurrence among J of some individuals which have passed the male phase, contemporary with that shown from A to I, and re-attained a spawning female phase which may have occurred early in

the season and escaped notice. In this event a second male phase—younger than anticipated for J individuals—is mixed with the latter, having the effect of reducing the mean male sex-condition of the group. Whether this be the case or not some individuals in this group had passed the male phase, reattained the functioning-female phase, and undoubtedly begun another post gyne-spawning male phase.

The Onset of the Female Phase.

The reattainment by a significant number of individuals in the J period of a fully developed female condition proves that a second curve of gonad-condition—but this time of the development of femaleness—could be drawn between the abscissæ of I and J if sufficient data were available. There is every probability that femaleness will be found to accelerate its development at some point in the female phase in a somewhat similar way to that shown by the male phase between points A and F in Fig. 3, p. 1037 (see Orton, 1924, p. 191 ; and Spärck, 1924, p. 31) ; but whereas the male phase referred to can be investigated exactly at this condition by noticing the obvious signs of embryos and larvæ in individuals, in the case of the corresponding stage of femaleness there is no external sign to betray similar gonadial activity, and special studies are required to discover the exact time of the most rapid internal changes. Although data are not available for constructing a graph of the development of femaleness following the post-gyne-spawning male condition, there is now a clear indication that such a curve could be drawn based on practical observations. The position of the beginning of the curve of development of femaleness in relation to the curve showing the complete male phase is a matter of great interest. There is not yet sufficient information available to predict its situation accurately, but there are strong indications that it would *normally* and generally begin at some point after the gonad has become neutral. There are, however, ample reasons—in the occurrence of various kinds of mixed sexes (see p. 976)—for considering it probable that in other cases the curve of development of femaleness may begin at various points in the male phase, but rarely earlier than when the gonad has attained to category VIII in the scheme outlined above, that is, when all the sperm have become ripe.

Preliminary Remarks on the Physiology of Sex in the Oyster.

The function of sex in the oyster—as in other organisms—is to provide a means for the production of new individuals ; whether the special manifestations of sex in this species are related in any special way to the production of young remains to be shown, and formulates a subject which may be discussed later. The phenomena of sex herein described

however enable at least one fixed point to be determined in the sexual cycle of at least those individuals which produce abundant ripe ova. This fixed point occurs in the sexual cycle or rhythm within a few hours after the individual has spawned as a female, and is signalised by a sudden activity in the gonad in the production of developing sperm. This activity acquires momentum and continues for a period which appears to depend upon external conditions.

In summer—in the warm period—this activity would appear to die down in from one to two months, and is then followed by a quiescent condition of the primordial sex-cells. If the activity of the gonad is maintained until the end of the breeding season, it would appear that that activity may be carried over the winter and continued in the following breeding season. When the male phase being discussed passes during the breeding season there is evidence that it is followed in a significant proportion of individuals by a female phase acquired between the penultimate stages of one breeding season and an early stage in the following one. There is not yet sufficient evidence to show at what period after the male phase the female phase begins, but there is evidence that at some part of this female phase there is an acceleration of egg-development somewhat similar to that found in sperm-development. There exists, therefore, in outline a picture of a male phase as shown in Fig. 3, p. 1037, followed successively by a resting phase, and at some epoch later by a sudden development of eggs (femaleness). There is every reason to believe that an alternation of these male and female phases occurs repeatedly during the lifetime of the individual (probably during each year under normal biological conditions for the species), and it has been shown that although these phases are mostly clear-cut, there is a fair percentage of mixed sexes in nature, a fact which indicates a good deal of overlapping of these phases. The sudden development of both maleness and femaleness suggests the existence of a controlling mechanism, abruptly released, which is most easily visualised as hormonic (as might be effected by a catalytic enzyme), as has already been suggested (Orton, Nature, 1924b, p. 191). It is, however, also possible that the phases may be initiated at the culmination of a series of metabolic processes whereby (1) the completion of storage of reserve materials in the eggs (as at egg-spawning) changes the metabolism and the metabolic rhythm towards the production of substances which when absorbed by the gonocytes are suitable for sperm-production, and the male phase follows; and where (2) the accumulation of reserve products assumes such a concentration in the post-male phase that a slight addition to that concentration causes the beginning of egg-development, that is, the laying down of the reserves in all the gonocytes, which then become eggs, or alternatively only in predestined oocytes.

It is unfortunate that no chemical analyses exist of oysters in different definite sex-phases, The remarkable series of analyses by the Government Chemist given in Russell's paper (1923) were carried out on groups of about 50 oysters of unknown sex, but in view of the demonstration that the percentage of female oysters diminishes and the percentage of males increases during the summer (Orton, 1926, also herein, and unpublished), it can be postulated that the analyses detailed (loc. cit.) would include an increasingly high percentage of males and a decreasing percentage of females from the beginning to the end of the breeding season.

The graphs of percentage of protein and carbohydrate content in samples of oysters examined monthly from January, 1919, to January, 1920, from four well-known oyster beds in the Thames Estuary given by Russell (loc. cit.), show a general inverse variation correlated with the extent of the breeding season. This correlation is especially well marked in the samples from the Whitstable beds, where the breeding season extends normally from about June to September. As the protein percentage composition declines from June to September and the carbohydrate and glycogen content rises from June to September in the Whitstable samples, see Fig. 4, p. 1041, it is clear that with the increasing percentages of males in this period, the metabolism resulting in the storage of carbohydrate (including glycogen) is also increasing, and that resulting in storage of protein decreasing. From the end of the breeding season—about September—in the same series of oysters (Whitstable, loc. cit., Fig. 4 herein). both the carbohydrate—and glycogen—and the protein content increase ; now it is just in this period that we have found a high proportion of males beginning to change into females, and the suggestion is strong that carbohydrate metabolism is predominant in males and protein in females. There is therefore some support for an explanation of sex-changes in the oyster based on rhythmical changes in metabolism, whereby, for example, an excess of *unusable* metabolic products characteristic of one sex induce a reversal of the sex-metabolism and sex-manifestation to that of the other sex.

A rhythmic change in the metabolism of an organism controlling its sex-manifestations must be regarded as a property of that organism in the same way as are the metabolic rhythms producing specific organs in the course of ontogenesis. In both cases the change which occurs must depend upon some physico-chemical factor which may either be formed locally or generally and distributed to various parts of the organism as an activator, after the manner of a hormone, while there may exist in the case of the gonad of the oyster and other organisms an ambi-receptor mechanism, i.e. one tending to produce either maleness or femaleness, in *all* the gonocytes.

A theory of the control of sex by rhythmical changes in metabolism may therefore be conceived with or without the intervention of (circulating) hormones.

A theory of the control of sex in the oyster by vague hormones of unknown origin is less simple than that of a metabolic rhythm just outlined,

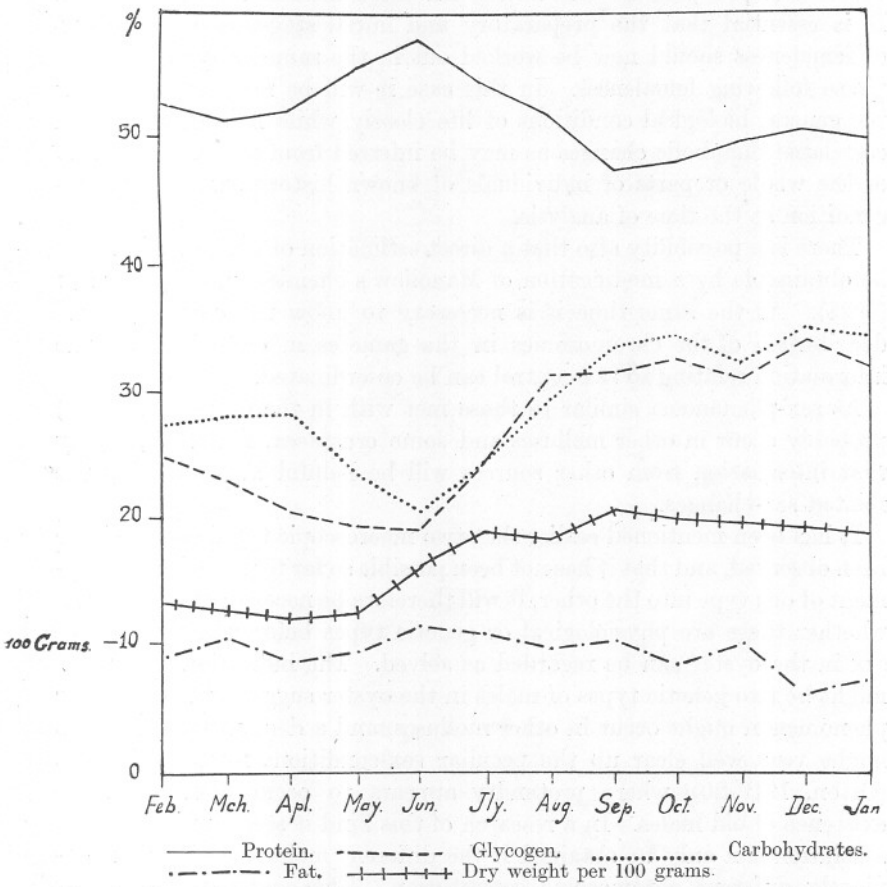

FIG. 4.—Percentage composition in dry weight of oysters* from Whitstable, together with dry weight per 100 oysters, January, 1919–January, 1920. (Reproduced by permission and courtesy of H.M. Stationery Office and Dr. E. S. Russell, from a paper by the latter, 1923.) From analyses by the Government Chemist.

since some stimulus is required in the former theory to activate, or to give greater potentiality to, a male-inducing hormone at one period, and another to activate or give greater potentiality to a female-inducing hormone at another period. A combination of the two views on the

* These analyses were carried out mainly on samples of 50 oysters. (For details see RUSSELL, 1923, p. 16.)

method of sex-control in the oyster is however possible, in that metabolic changes themselves may afford the stimuli for and produce hormonic substances which result in the gonocytes developing alternatively into spermatogonia or oogonia.

A closer insight into the probable controlling factors of sex in the oyster can probably be obtained when more information is available. It is essential that the preparatory and initial stages of development of femaleness should now be worked out in the same way as the male phase following femaleness. In this case it will be necessary to follow the general biological conditions of life closely while investigating such correlated metabolic changes as may be inferred from chemical analyses of the whole or parts of individuals of known history and known sex-condition at the time of analysis.

There is a possibility also that a direct estimation of sex-condition may be obtainable by a modification of Manoilow's chemical reaction for sex (1923). At the same time it is necessary to know the characters and distribution of the chromosomes in the gametes in order that all the information relating to sex-control can be co-ordinated.

As sex-phenomena similar to those met with in the oyster (*O. edulis*) probably occur in other molluscs and some crustacea, it is not unlikely that information from other sources will be helpful in elucidating the related sex-changes.

It has been mentioned earlier that two macroscopic types of male have been observed, and that it has not been possible so far to trace the development of one type into the other, it will therefore be necessary to determine whether these are physiological or genetic types before the problem of sex in the oyster can be regarded as solved. The indication that there might be two genetic types of males in the oyster suggests that a similar phenomenon might occur in other molluscs, and a demonstration of this might very well clear up the peculiar sex-conditions found in Patella (Orton, 1919–20), where protandry appears to occur along with the existence of old males. In a research of this kind it seems probable that a solution can only be obtained if the different male types have an obviously different chromosome constitution. The coexistence of males with hermaphrodite forms is well known in other groups, e.g. some Cirripedia, some Nematoda, and possibly also in some Gephyrea, so that the phenomenon may have a general fundamental significance in the true physiology of sex, namely, in its relation to the biology of the species.

SUMMARY.

The gonads of 1,121 oysters have been examined at various periods from a few hours to twelve months after the individuals had spawned as females; the material for the research was obtained by collection and

experiment. In 702 individuals taken with young in the mantle cavity the gonad shows a progressive development of maleness in its primary sexual characters; within a mean period of $2\frac{1}{4}$ hours after spawning eggs, the gonad was found in 50 per cent of cases with only young sperm-masses developing, followed at later periods by a progressive ripening of the sperm-masses, until in individuals carrying shelled and black-coloured larvæ 77 per cent contained abundant ripe sperm-masses as well as advanced developing sperm-masses.

In 444 individuals examined at various periods after extruding their larvæ, the development of sperm was found to continue for about a month after egg-spawning, and to abate in about the second month. In from 2 to 3 months after egg-spawning sperm-development is completed and the male phase begins to wane, and a small percentage of individuals may become female or actively female-functioning again. In 12 months after the last egg-spawning a significant number of individuals become once more functional females.

The varieties of mixed sexes found in *O. edulis* are defined and their frequencies shown by an analysis of samples—from two widely separated beds—examined at the beginning of the breeding season in 1926. Experiments on the rate of growth of sperm-masses and on determining of age at different stages of development in embryos and larvæ are given.

The rapidity and course of development and waning of maleness can be shown graphically by an asymptotic (hormonic) curve.

The general biological conditions accompanying the development of femaleness—following the male phase observed—have not yet been fully worked out.

The cause of sex-control in the oyster is discussed in a preliminary manner.

It is suggested that sex-change in the cases observed is due to a metabolic rhythm in two phases; there is some evidence—as yet, however, incomplete—that in one phase protein metabolism is predominant, and is accompanied by egg-development; while in the other, carbohydrate—and especially glycogen—metabolism is predominant, and is accompanied by development of sperm.

The theory is advanced that the accumulation of *unusable* products of one kind of metabolism above a certain concentration is the stimulus for the change-over to the other phase of metabolism, with its accompanying sex-change. The rhythm is regarded as a specific property of the species. This theory involves a fresh orientation with regard to our ideas of sex-control, in that sex-control is assumed to reside in the general nature of the metabolism.

It follows from this theory that all gonocytes have the potentiality of becoming oogonia or spermatogonia.

The establishment of a sex-change from femaleness to maleness at or within a few hours after the instant of egg-spawning, furnishes a fixed point in the sexual rhythm of the oyster: it will therefore be possible in the future to utilise this fixed point in efforts to unravel all the phenomena associated with the change of sex, and in investigations designed to determine all the sex-changes which may occur during the life of at least those individuals which pass through a number of female phases.

Observations are given pointing to the possibility of the existence of two types of male in the oyster.

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A Note on the Physiology of Sex and Sex-determination.

By

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CONTENTS.

In a previous paper in this Journal (Vol. XIV, p. 967) a theory of the control of sex in the oyster by rhythmical changes in the general metabolism has been outlined and discussed briefly with the information at present available. As the connexion between metabolism and sex has long been regarded as important, and by some, e.g. Geoffrey Smith (1913), as all-important, this relation may be considered briefly with regard to modern views on the physiology of sex.

The Function of Sex.

The function of sex is to provide a special means for the reproduction of the organism, therefore the relation of the variety of manifestations of sex to the correlated modes of reproduction in species is the true physiology of sex, which is clearly, though paradoxically, a biological problem ; for it is not an unreasonable assumption that there is a general significant relation between sex-manifestations and particular needs in reproduction.

Motion and Sex-manifestation.

In a review of sex-phenomena in the animal kingdom as a whole, it is a fact that sedentary and parasitic and to a less extent sluggish forms are mainly hermaphrodite, whilst active animals are preponderantly bisexual ; thus it would appear that mode of life is significantly related to sex-manifestation, and that bisexuality is favoured or rendered possible by an active life, whilst hermaphroditism meets the needs of reproduction

in sedentary or parasitic forms; or it might be inferred that hermaphroditism has to meet the needs of such animals when one considers the remarkable instances of complemental males not infrequently associated with hermaphroditism (Cirripedes, Copepods, and others): bisexual sedentary animals are mostly aquatic, and effect cross-fertilisation—and apparently thereby avoid hermaphroditism—by extruding their genital products generally freely into the water.

As an example of the generalisations just outlined may be given the case of Crepidula and Calyptræa. The group to which these animals belong has as a group character bisexuality, and consists of moderately active members; but Crepidula and Calyptræa are sedentary forms (having adopted this mode of life in the course of ages) and are hermaphrodite (having apparently been obliged to assume the condition of sexuality as a result of departing from the ancestral mode of life). Similar cases in other groups could be cited. How then do these animals become hermaphrodite? It is not possible to discuss here all the possible answers to this question, but let it be assumed—in conformity with the general phenomena of sex—that hermaphroditism is imposed upon these organisms by the mode of life, and that, as the characteristic of the mode of life is simply environmental immobility with uniformity in habits of the adult, special arrangements become necessary for the purposes of reproduction. In sexual reproduction in general, however, cross-fertilisation appears to be a fundamental requirement, which, in the case of hermaphrodite individuals, may be met by various devices of alternating sex-phases (protandry, protogyny, alternating-hermaphroditism). If then hermaphroditism and cross-fertilisation be imperative in a sedentary species, it is obvious that a great variety of sex-arrangements might be evolved from those of its bisexual ancestors to satisfy these demands, and no general statement is likely to cover them. In the case of species, which have recently acquired hermaphroditism, active complemental males might be expected, or, indeed, active non-feeding males and sedentary females. It would appear that hermaphroditism in sedentary and parasitic species results from the necessity of providing the maximum possibilities for cross-fertilisation, and also for egg-production in all the individuals of the species which attain the state of food-absorption. But as—so to speak—anything can be a male, that is, very little organisation or food-reserve is necessary to produce a male, and as all individuals possess the potentiality to become male or female, it can be readily understood that an early general male phase should occur in the life-history followed by a female phase in the adult food-absorbing stage. In the latter stage there is every reason to believe that the fundamental metabolic processes are necessarily different from those existing in a male phase. It might indeed be argued that the type of metabolism imposed

upon the adult stages in sedentary and parasitic animals is such as to demand femaleness as the main sex-phase, and that this is frequently one main cause of hermaphroditism.

Evidence is accumulating of a general difference in metabolism in males and females in bisexual species of animals, and many cases are now known where a change in metabolism results in a change of sex; the most striking of such cases being the change in the secondary—and the incomplete change in the primary—sexual characters in the spider-crab, Inachus, as a result of infection by Sacculina, shown by Geoffrey Smith (Q.J.M.Sc., **59**, 1913).

Sex-metabolism and Sex-determination.

The literature on sex abounds with a recognition of the importance of particular types of metabolism associated with maleness and femaleness. (Goldschmidt, in Mechanism and Physiology of Sex-determination, 1923, gives the more important ones.) It would appear therefore that differential male and female metabolism occurs generally within a bisexual species, and the ground is prepared for the recognition of a cyclical or rhythmical change of metabolism during the life of the individual in certain hermaphrodites, and special conditions in those hermaphrodites in which eggs and sperm develop simultaneously—if, indeed, any such cases actually occur.

In recent investigations on sex-change in the Oyster (*O. edulis*) and *Crepidula fornicata*, in both of which sex-change occurs—rhythmically and alternating in the former, and once in succession protandrically in the latter—the importance of metabolism in the sex-change has been impressed upon me. In *Crepidula fornicata* the duration of the male phase depends upon the capacity of the individual to function as a male (Orton, *Nature*, Vol. 110, 1922, p. 212), and may vary from about two to seven years. The conclusion to be drawn from this fact is that in this species the successful emission of sperm reacts on the general metabolism for the production of more sperm, and conversely, the failure to utilise sperm results in the cessation of a male metabolism, and the onset of a female type with production of eggs in the gonad. It follows, therefore, that sex, after the attainment of the initial male phase, is controlled in this case by some factor which concerns the whole organism—such as an accumulation of characteristic male reserve products—rather than by the production of a particular sex-hormone, which when it is formed runs a set course. In this case, therefore, the factor governing sex is that which calls forth the sex-hormones, if indeed sex-hormones—of the existence of which in this and other similar animals we have as yet no direct evidence—are produced. The information available on the factors controlling sex in *O. edulis* have been

discussed in the Journ. Mar. Biol. Assoc., Vol. XIV, p. 1039, where it has been suggested that there occurs a metabolic rhythm controlling sex in two phases, in one of which protein metabolism is predominant and results in the production of eggs in the gonad, while in the other carbohydrate metabolism is paramount with the production of sperm in the gonad. Experimental evidence is now available that *O. edulis* does pass successively through the phases female, male, female, male, and indirect evidence that this sequence is repeated, but to an unknown extent (Orton, *Nature*, Vol. 114, p. 191, 1924). It is therefore further suggested that the production of carbohydrate products—especially glycogen—in excess of a certain concentration may be the stimulus, on the one hand, which causes the metabolism to begin in the protein phase with a consequent production of eggs in the gonad, while, on the other hand, the existence in the body of unusable protein—as at the phase immediately following egg-spawning—causes the metabolic rhythm to swing back to carbohydrate production with consequent sperm-formation in the gonad, and that this cycle of changes may be repeated several times. From the results of examining over 1,000 oysters which had previously spawned as females, there is clear evidence that the change from femaleness to maleness takes place normally within about twenty-four hours, usually much earlier but sometimes later, after spawning, and there is evidence that oysters in mass change over from protein to carbohydrate metabolism after spawning as females. In these sex-changes it may be assumed that separate generations of gonocytes take part in each sex-phase, and that the metabolic rhythm is a property of the organism.

These suggestions are made as an alternative to the ordinary sex-hormone theory and have much to recommend them. The idea of a particular type of metabolism being associated with, if not controlling sex, has been accepted, or favourably entertained, by many biologists in the past, and is one which in recent times even Goldschmidt is reluctant to relinquish (1923, *passim*).

The theory of sex-control in the oyster, outlined above, and arrived at independently, is similar to that arrived at by Geoffrey Smith in his work on spider-crabs parasitised by Sacculina (1913). The theories which assume the type of metabolism to be of paramount importance in the control of sex are, however, generally regarded (e.g. Goldschmidt, 1923) as superseded by the sex-chromosome and sex-hormone theory. If, however, it is possible to reconcile the two theories, ancient and modern, and at the same time obtain a better general explanation of sex-phenomena, it is probable that progress is being made.

On the Function of X and Y Chromosomes in the Zygote.

The modern view is that sex is determined in the zygote, and by combinations, or the absence, of the peculiar X and Y chromosomes. A very large proportion of sex-phenomena—though by no means all—are satisfactorily explained on these lines, but it is submitted that a wider explanation of sex-phenomena may be obtained by incorporating the old idea of the importance of metabolism. It is suggested, therefore, that the X and Y chromosomes when present have the function of superimposing on the general metabolism of the species a metabolism of a particular type to which the gonad responds by producing eggs *or* sperm. On this view, therefore, *all gonocytes have the potentiality* (as is recognised by Goldschmidt) *of becoming either oocytes or spermatocytes.* On the sex-chromosome theory the gonad must (strictly) be assumed in certain cases to be either solely egg-producing or solely sperm-producing, and when such an organism produces gonocytes of the opposite kind to that expected—as in Smith's crabs, the Gipsy moth, and many other cases—special strain has to be put on the sex-chromosome theory to bring it into line. It is certainly significant that in those cases in which the sex-chromosome theory—in its present form—breaks down—as in those cases in which occurs either an assumption of hermaphrodite characters, or a change of sex, or a heterosex condition—there is evidence of a change in the metabolism of the individual, as in Inachus parasitised by Sacculina and similar cases, Orchestia and similar cases, middle males in Crustacea, and in the remarkable alternative sex-condition in Bonellia and similar cases ; all of which are easily understood in terms of metabolic control, in the same way as the well-known sex-phenomena in bees, Cladoceras, and rotifers. Finally, the sex-phenomena in the remarkable geographical races in Lymantria and frogs, in the crossing of which the X and Y chromosomes functions are turned topsy-turvy, are explained with less difficulty if the races be visualised as having developed different sex-metabolisms, which in their ontogenesis lose sex-specificity on "hybridisation." The case of Lymantria undoubtedly points to the function of the so-called sex-chromosomes being that of producing an environment for a sex rather than the sex itself. In fact, Lymantria and frogs provide us with what we have so long been looking for, namely, definite and measurable physiological variation within the species.

It is interesting to observe how such difficulties, as are mentioned above, are explained on the assumption that sex is controlled by special chromosomes. Goldschmidt (loc. cit.) confronts these difficulties in a definite manner, and has also perceived the undoubted correlation between differential metabolism and differential sex, as may be inferred from the

following quotations. In the first place, in a review of the basic facts (1923, p. 138) the conclusion is drawn that "Every developing individual of a bisexual organism (species) contains the substances whose action can call forth the one or the other sex." From this broad generalisation alone it is permissible to consider whether sex may be controlled by the general nature of the metabolism—oriented by the peculiar chromosomes—or that these chromosomes themselves directly control sex. Again, in considering cases of successive hermaphroditism—such as that of the oyster (*O. edulis*)—(p. 180), "In regard to the conditions underlying the differentiation of both sorts of germ cells we know at least a very little. Both Ancel* and Buresch† have shown that the same primordial germ cells (in Helix) may become eggs or spermatozoa, according as they enter into relations with so-called nurse-cells or not. What this means physiologically we do not know. An indication is given perhaps by the following. We‡ were able to show that the differentiation of a sperm-cell into a spermatozoon was to a certain extent controlled by osmotic conditions whose regulation was a function of the follicle cells—and these are probably related physiologically to the nurse-cells of the eggs." . . . "The conception of special quantitative conditions or reaction conditions of the sex-enzymes does not suffice as an explanation (*of these cases*). The special physiological condition with its localised mosaic-like or temporal variations, must rest somehow on a peculiarity of genetic constitution which up to date is both mechanically and physiologically unknown. Nor is it explained by the phrase—Factor for Monœcism." From this quotation and from others which could be given, it is clear that Goldschmidt recognises difficulties in the chromosome sex-control theory and is not afraid to demonstrate them. In dealing with intersexuality developed through parasitic castration, he remarks: "Now there can be no doubt that these facts (*the transformation of secondary and primary sexual characters induced*) are of great significance from the point of view of the sex problem, but their analysis has not in our opinion progressed far enough to permit of definite conclusions being drawn from them . . . for if the point of view advanced below turns out to be correct, there would be a good prospect of fitting in the keystone to the physiology of sex-determination." Then after discussing Geoffrey Smith's work on Sacculina and his theory of *metabolic stimuli*, Goldschmidt continues: "Nevertheless we believe there is a nucleus of truth in Smith's idea when freed from the exaggerated criticism of the hormone theory." The present writer here is in full agreement with Goldschmidt, who, following up the same subject, remarks that "The facts previously considered have brought us to the point where the hormones of sex-differentiation com-

* Ancel, P. Arch. Biol., **19**, 1903. † Buresch, J. Arch. Zellf., **7**, 1912.
‡ Goldschmidt, R. Arch. Zellf., **14**, 1917.

mence their activity. In regard to the mode of action of these bodies we have so far formulated no idea. Naturally there is nothing mystic about it, it is a chemical process and more than likely after all an action of the general metabolism. The action of the hormones probably calls forth a specific type of metabolism, and this is the ultimate and direct cause of the morphological differentiation of the sexes. If this were correct it would be the last word in the elucidation of the sex problem, and at the same time one which could be subjected to exact analysis."

The modified theory advanced herein that the X and Y chromosomes control sex-metabolism, and not strictly speaking sex itself—as by the direct production of sex-hormones—may indeed be regarded as one which has been tentatively accepted by Goldschmidt, as the preceding quotation shows. But Goldschmidt, having committed himself deeply to the sex-hormone theory, rejects G. Smith's theory of metabolic stimuli in calling forth sex-characters, although his written words show that he does not reject the underlying fundamental idea. It is obvious from the quotations given above that the views which have developed from the sex-chromosome theory are ripe for a change in the direction first advocated definitely by Geoffrey Smith, and it is probable that just as the latter may have underestimated the importance of hormones, so the sex-chromosome adherents may have erred in the opposite direction. It may not be necessary always to look for either a *sexual formative substance* or a specific sex-hormone; hence there is no need to despair if, for example, sanguinary transplantation experiments do not always give the result that certain sex-theories demand. The stimulus for the production of particular germ cells may vary greatly in kind throughout the animal kingdom, and, moreover, may vary in such a way that the definition of a sex-hormone may become merely a very general statement.

So far the theory of control of sex by special metabolic conditions has been discussed in relation to invertebrates mainly, but there are clear indications that the method of control of sex in animals has undergone evolution in the same way as other physiological processes and morphological characters. Experiments on transplantation of the gonad and/or injection of gonadial secretions show that in birds and mammals, and possibly also Amphibia, the secondary sexual characters are under the control of the gonadial system, while in invertebrates (and probably many cold-blooded vertebrates) the gonad has no such control. Thus in birds and mammals the gonad controls secondary sexual-characters in the same way as the thyroid controls growth, that is to say, the control of sex-function, *once the sex has become fixed*, has passed to a subsidiary centre. In this respect it seems probable that the acquisition of a definite bodily temperature has rendered easy the introduction of a decentralised

control of sex-characters—and, indeed, other bodily functions—and in any case the importance of external physical conditions has become no longer of such great importance on the general effect on metabolism, as in cold-blooded animals, since all the enzymes in the body can function in a constant or almost constant temperature, being subjected only indirectly to the influence of external conditions.

Thus, in the warm-blooded vertebrates, birds and mammals, sex-potentiality—in terms of the theory outlined above—is determined primarily by the metabolic potentialities (which may, however, be delegated in highly developed forms to a single sex-hormone) of the zygote (in its chromosome constitution), but this sex-potentiality is modifiable at an early stage or later by the secretions of the early developing gonad which takes over to a large—but uncertain—extent the directing influence of the general metabolism. On the other hand, in invertebrates the control of both the primary and sexual characters would appear to lie in the general organisation of the organism as determined primarily by the metabolic potentialities of the zygote (from its chromosome constitution), but modifiable by a fundamental change in the metabolism during the life of the individual. With regard to monœcious forms in invertebrates, it follows that if the theory outlined is tenable, rhythmical or cyclical variation in metabolism correlated with sex-phases, as appears to be the case in *O. edulis*, should always occur, and a field for research is indicated. Cyclical change in the production of different sex-forms correlated with metabolic changes is known to occur in some species over a number of generations, so that the concentration of these changes in a single monœcious individual is merely a difference of distribution of life-phases in time, and affords one more instance of the fascinating adaptability of the organism in sex-contrivances.

The theory that sex is controlled by a particular type of metabolism—whether this be produced by bio-physico-chemical events set in motion by X and Y chromosomes, or by the imposition of a particular mode of life on the individual—is in harmony with sex-phenomena in gross in the animal kingdom, in which the active species have generally males and females with different organisations and functions to perform correlated in many (and probably most) cases with a different general metabolism, while sedentary and parasitic forms in their adult anabolic stage are mainly either wholly female or partly female according to the possibilities for fertilisation in particular forms.

The theory of sex-control by a type of metabolism normally unfolded by X or Y chromosomes enables us to consider these latter entities as of essentially the same nature as the autosomes, but with the function of adding to a stable unit, which we may call the *specific neutral soma*, the peculiarities of sex. Non-sexual characters inherited with sex would

therefore be generally expected to have their determinants wholly or in part in the X or Y chromosome.

Since the function of sex is to reproduce the organism, the mode of reproduction employed in particular cases must be of greater importance than the actual process of sex-control, and will determine the nature and incidence of sex-control. Sex-control is, therefore, a matter of secondary importance in a broad consideration of sex-phenomena, and it would appear that these can only be properly understood as a whole, and indeed in particular cases, when considered in relation to phylogeny and bionomics.

The Influence of Plankton on the Phosphate Content of Stored Sea-Water.

By

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With 2 Figures in the Text.

THE possibility of a sample of sea-water, untreated and unfiltered, suffering change in its soluble phosphate concentration during storage is well recognised. Matthews (1917) observes that "if the sample is allowed to stand without previous sterilisation the phosphates decrease and may be entirely removed in a few weeks." Atkins (1923) gives actual figures in illustration of this decrease with reference to insolated sea-water, though he also states "that open sea-water stored in the dark in bottles used for chloride samples, appears to undergo but little change for a couple of weeks in spring." He exposed sea-water to a strong light, and found that the original phosphate concentration, of about 40 mgms. P_2O_5 per cubic metre, decreased to the order of 2 to 3 mgms; the rapidity of the decrease being greatest in the spring months. The elimination of soluble phosphate in this way is ascribed to the uptake of this essential plant food by organisms during the process of their growth and multiplication, and continues until practically no available phosphate remains.

Atkins (1925), in a later paper, refers to increases in soluble phosphate observed in stored sea-water. These increases are undoubtedly due to the death of organisms originally present, and, by bacterial or other action, the subsequent dissolution of their bodies, although in some instances such increases on storage have been traced to enrichment of the sample by the glass of the bottle, more especially where soft white glass is used (Atkins, 1926). Numerous published analyses, it is clear, are erroneous owing to this decomposition, the error being more appreciable the longer the interval between collection of the sample and analysis. Atkins (1925, p. 716) cites a case in point. A series of samples from surface down to 775 metres was taken from the deep water N.E. of the Wyville-Thomson ridge on August 8, 1924, and analysed September

3, 1924, nearly four weeks elapsing between the two operations. The following values were obtained :—

Depth, metres	0	10	25	50	75	100	150	200	300	400	500	600	775
P_2O_5, mgm. per m.^{3}	74	76	54	85	54	57	85	68	66	83	91	94	109

The values for the upper layers were all extraordinarily high, surface and 10 metres depth giving 74 and 76 mgms. P_2O_5 per m.^{3} respectively ; and no regular gradient was observed as usually obtains in the summer months from surface to bottom. One of the reasons advanced for the explanation of these puzzling and irregular results was the leakage of phosphate from the white glass sample bottles, and it was later discovered (Atkins, 1926, p. 448) that similar bottles did, in fact, yield phosphate to distilled water. But from the data put forward below it would appear that the real cause resided in greater part in the decomposition of organisms originally present in the samples.

FIG. 1.

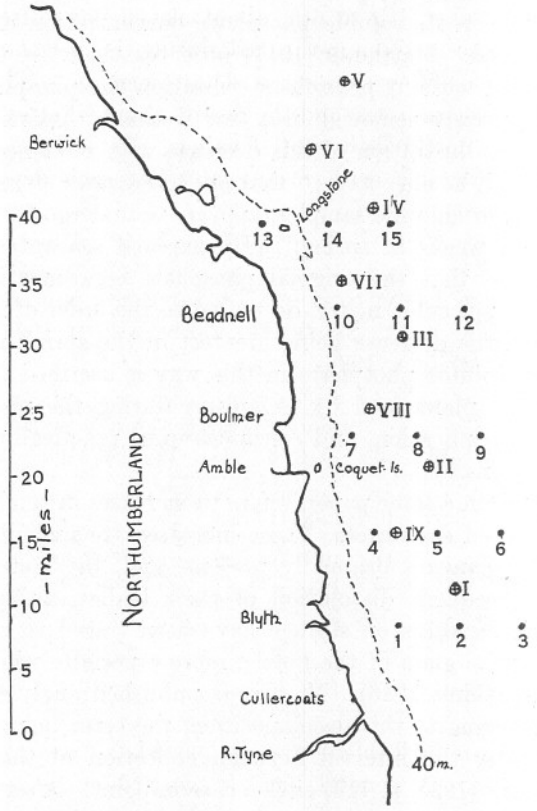

FIG. 1.—Hydrographical Stations off Northumberland Coast, Nos. 1–15. Plankton Stations, Nos. I–IX.

Phosphate Content of North Sea Water off Northumberland Coast.

Employing the cœruleo-molybdic colorimetric method of Denigès (1921) for the estimation of phosphate in sea-water, as elaborated by Atkins (1923, p. 144 ; 1925, p. 719), periodical observations have been performed in the North Sea off the Northumberland coast. The attached chart (Fig. 1) indicates the positions of the fifteen stations worked.

The results of a cruise in July, 1926, were abnormally high and erratic, and pointed to considerable alteration having occurred in the samples during the storage period between collection and analysis, which was unduly prolonged. It was determined to trace this change in the samples of a later cruise.

This following cruise was made on September 23rd to 25th, 1926, when all stations were visited and sampled at each 10 metres depth from surface to bottom. The phosphate content of each sample was first determined on October 4th to 6th, about eleven days after collection, the bottles having been stored in the dark during this period. It is highly desirable that phosphates should be determined as soon as possible after collection of the samples, and the results obtained after eleven days' delay probably do not give the initial values. Table I below gives the results obtained, together with mean values at each depth and each station over the area :—

TABLE I.

Phosphate, mg. per m.^{3}, at Stations 1–15 off the Northumberland Coast. Samples taken September 23rd to 25th, 1926, analysed October 4th to 6th, 1926.

	Inshore Stations.					Middle Stations.					Offshore Stations.					
Depth.	1	4	7	10	13	2	5	8	11	14	3	6	9	12	15	Mean
0 m.	8	11·5	12	14·5	24·5	7	12·5	12	23·5	17	9	9	12	12·5	17	13·5
10 m.	12	11·5	12	21	24	10	12·5	11·5	23	25	8	11·5	12	12·5	13	14·6
20 m.	16	12·5	10	20		11	17	13·5	21	24	8	17	13·5	12	25	16·4
30 m.	16	11·5	11	20		11	19	16	22	24·5	8·5	20	12·5	12·5	26·5	16·5
40 m.	12	17	12	18		23	18	23·5	22	26·5	15	26	35·5	18	28	21·0
50 m.				22		20	28	26·5	25		19	40	37·5	28·5	25	27·1
60 m.							26	24·5	31·5		22	40	35·5	35·5	28	30·3
70 m.											23	43	36·5	37·5	33	34·6
80 m.											24·5					
Mean	12·8	12·8	11·4	19·3	24·2	13·7	19·0	18·2	24·0	23·4	15·3	25·8	24·4	21·1	24·5	

The values shown in Table I are comparable to Atkins' results for September samples. A general increase with depth is recorded, the mean surface content being 13·5 mg. P_2O_5 per m.^{3}, while at 70 m. the mean value is 34·6 mg. P_2O_5. Summarising the conditions over the

area investigated, it is seen that the surface values at the northern stations (10–15) are higher than the surface values at those stations to the south (see chart), while the inshore surface waters are richer in phosphate than the offshore surface waters. The mean phosphate content, in mg. P_2O_5 per m.^{3}, for the inshore, middle, and offshore stations at 0 m., 40 m., and 70 m. depth is given below :—

	Inshore.	*Middle.*	*Offshore.*
0 m.	14·1	14·4	11·9
40 m.	14·7	22·6	24·5
70 m.	—	—	34·6

Results after Storage in the Dark.

The sample bottles used (of green glass, yielding no phosphate to distilled water) were of about 350 c.c. capacity, and, after the first determination of phosphate content, sufficient material remained in each bottle to enable a second determination to be made. Each bottle was therefore restoppered and returned to its box, and the whole stored in the dark. The second analyses were performed on November 12th to 16th, 1926, after forty days of such storage. The temperature obtaining during this period was the varying one of the laboratory.

TABLE II.

Phosphate, mg. per m.^{3}, in September 23rd to 25th Samples, after forty days' storage in the dark. First analysed October 4th to 6th. Re-analysed November 12th to 16th, 1926.

	Inshore Stations.					Middle Stations.					Offshore Stations.					
Depth.	1	4	7	10	13	2	5	8	11	14	3	6	9	12	15	Mean
0 m.	—	35	17	26·5	—	—	23	17	41	28·5	—	16	39·5	28·5	27	27·1
10 m.	—	35·5	16·5	28	31	—	25	22	38·5	33	—	15	34·5	29·5	29·5	28·0
20 m.	—	39	23	24		—	44	24	35·5	33·5	—	17	43	27·5	30	31·0
30 m.	—	—	23	30·5		—	39	23·5	32	30	33·5	20	30	38·5	29·5	29·9
40 m.	—	32·5	17	28·5		—	32·5	37·5	32·5	27·5	35·5	25	46	30	28	31·0
50 m.				32·5		—	39·5	36·5	37		43	24·5	40·5	28·5	34·5	35·1
60 m.							39	35·5	32·5		40	37·5	38·5	37	30	36·2
70 m.											44	40	37·5	39·5	33·5	38·9
80 m.											40·5					—
Mean	—	35·5	19·3	28·3	—	—	34·5	28·0	35·6	30·5	39·4	24·4	38·7	32·4	30·2	

Table II gives the results of the redetermination of phosphate content after storage. A general increase in soluble phosphate is observed, the mean surface value for all stations having increased during storage from 13·5 mg. to 27·1 mg. P_2O_5 per m.^{3} The increase at 70 m., however, is only 4·3 mg. from an original mean value of 34·6 mg. to 38·9 mg. The

differences between the original means at the various depths and the means after storage are given below :—

Depth in metres	0	10	20	30	40	50	60	70
Mean P_2O_5 increase	13·6	13·4	14·6	13·4	10·0	8·0	5·9	4·3

It is seen that the magnitude of the increase is greatest in the upper 30 metres of water, the maximum being at 20 metres.

Comparative Plankton Population in the same Waters, September 14th to 17th, 1926.

That the upper layers of water should increase to roughly 200% of its original phosphate concentration, while the bottom waters showed only a 12% increase, pointed to the decomposition of planktonic organisms as the cause of the phenomenon. It is fortunate that data are available indicating the relative density of plankton over the same area of water on September 14th to 17th, little more than a week prior to the collection

TABLE III.

Plankton Hauls, in c.c., at Stations I–IX, September 14th to 17th, 1926.

Depth.	I	II	III	IV	V	VI	VII	VIII	IX	Mean.
0 m.	12	8	10	26	42	16	20	18	32	20·4
10 m.	14	17	18	16	50	26	25	22	30	24·2
20 m.	10	22	21	18	50	40	28	21	37	27·4
30 m.	10	17	16	18	38	36	32	20	35	24·6
40 m.	14	21	12	15	34	32	28	14	36	22·9
50 m.	17	16	18	16	26	30				20·5
60 m.			20	17	26	20				20·7
Total	77	101	115	126	266	200	133	95	170	

of the water samples (September 23rd to 25th). The positions of the nine plankton stations worked are given in the chart in Fig. 1. Catches were made at each 10 metres depth, and the figures given in Table III refer to 10-min. hauls at each depth, the catch being measured in c.c. on settling.

These values, though not absolute, are certainly comparative, and may be taken as representing roughly the distribution of plankton over the area at the time in question. The mean hauls at each depth are given in the Table, and it will be seen that the maximum appears at 20 metres, the mean haul being 27·4 c.c.

Relation between Mean Phosphate Increase and Mean Plankton Haul.

Considering the mean increase at each depth of soluble phosphate on storage and the mean plankton haul, a close relation is observed. The graph in Fig. 2 gives these values plotted according to depth.

Both curves show a maximum at 20 metres depth, and from this point down to 50 metres they run almost parallel. A discrepancy is observed

Fig. 2.

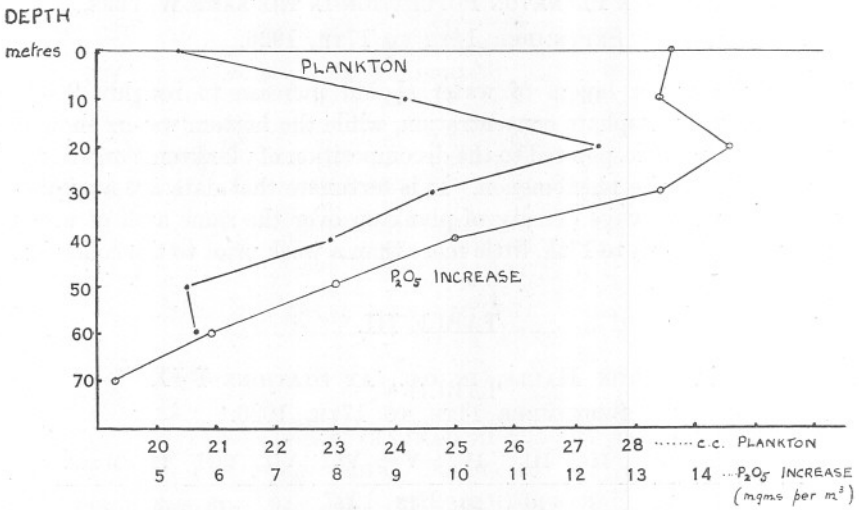

Fig. 2.—Mean plankton haul and mean increase in soluble phosphate on storage.

{ Plankton collected, Sept. 14–17, 1926.
{ Water samples ,, Sept. 23–25, 1926.

in the surface and 10 metres regions, but this is very feasibly explained by the coarseness of the mesh of the plankton nets used (23 strands per cm.). This mesh is not sufficiently fine to include the bulk of the phyto-plankton, which naturally would be most abundant in the upper layers of water, and which would undoubtedly affect the phosphate content of the water samples on storage. In view of this, the plankton values for the surface layers used in the compilation of the graph in Fig. 2 probably do not represent the true bulk of planktonic organisms inhabiting these regions.

Storage of Winter Samples.

A second series of experiments was conducted along exactly similar lines as described above, upon samples collected on January 6th to 8th, 1927. The first analyses were made on January 13th (Table IV), and

the second analyses on March 19th to 21st, after a period of sixty-five days' storage in the dark (Table V). The fifteen stations on the chart in Fig. 1 were not all visited, owing to the inclemency of the weather, and only ten points were sampled.

TABLE IV.

PHOSPHATE CONTENT, MG. P_2O_5 PER M.^{3}, AT STATIONS 1–12. SAMPLES COLLECTED JANUARY 6TH TO 8TH, 1927. ANALYSED JANUARY 13TH, 1927.

	Inshore Stations.			Middle Stations.			Offshore Stations.				
Depth.	1	7	10	2	8	11	3	6	9	12	Mean.
0 m.	18	22	23	15·5	23·5	23	18	20	22	22	20·7
10 m.	18·5	23	25	17·5	24·5	24	17·5	—	27·5	22	22·2
20 m.	18	23	24·5	18	23·5	21·5	16	21·5	25	24·5	21·5
30 m.	19	22·5	25	17	25	22	16	—	23	25	21·6
40 m.	17·5	24·5	25	18	23	21	19	20	22	24·5	21·4
50 m.			25·5	19	27	23	17·5	—	24·5	25	23·1
60 m.						23	18	21·5	24	21	21·5
70 m.							19	—	25·5		22·3
Mean	18·2	23·0	24·7	17·5	24·4	22·5	17·6	20·7	24·2	23·4	

TABLE V.

PHOSPHATE, MG. P_2O_5 PER M.^{3}, IN JANUARY SAMPLES, AFTER SIXTY-FIVE DAYS' STORAGE IN THE DARK. FIRST ANALYSED JANUARY 13. RE-ANALYSED MARCH 19TH TO 21ST, 1927.

	Inshore Stations.			Middle Stations.			Offshore Stations.				
Depth.	1	7	10	2	8	11	3	6	9	12	Mean.
0 m.	43	41	27	38·5	42·5	41	45·5	47·5	42	36	40·4
10 m.	42·5	32·5	36	41·5	33	36	45	—	98	44	45·4
20 m.	45	39	40	59	33·5	39	45	47·5	41	40·5	42·9
30 m.	62·5	50	35·5	45	36	43	42·5	—	38	39·5	43·6
40 m.	40	45	35·5	45	36	44	44	46	39	41	41·5
50 m.			31	52·5	38·5	32	43	—	37	41·5	39·3
60 m.						38	50	46	29	38	40·2
70 m.							45·5	—	31·5		38·5
Mean	46·6	41·5	34·2	46·9	36·6	39·0	45·0	46·7	44·4	40·1	

In the following table the differences between the mean values at each depth in Tables IV and V are given, and show the increases which occurred at various depths as a result of the storage treatment :—

Depth, metres	0	10	20	30	40	50	60	70
Mean P_2O_5, Jan. 13	20·7	22·2	21·5	21·6	21·4	23·1	21·5	22·3
Mean P_2O_5, Mar. 19–21	40·4	45·4	42·9	43·6	41·5	39·3	40·2	38·5
Increase, P_2O_5 mg. per m.^{3}	19·7	23·2	21·4	22·0	20·1	16·2	18·7	15·2

It will be seen on comparison with the September storage values that the increases above are of a higher order than experienced previously, doubtless due to the longer period of storage, namely, sixty-five days as compared to forty days. On the other hand, the temperature during the later series of experiments was generally lower, and one would assume the plankton population to be less dense in January than in September. It is therefore somewhat surprising that the January samples should give such relatively large increments. The greatest increase is found in the samples from 10 m. depth, being 23·2 mg. P_2O_5 per m.^{3}, while the minimum increase is observed in the samples from deeper water, 70 m. indicating an increase of 15·2 mg. on the original phosphate content. The upper 40 m. of water again gives the largest increases, confirming the results of the September samples.

It is interesting to note that those stations which originally indicated the lowest phosphate content (see Table IV), gave the greatest increases in soluble phosphate on storage. Thus Stations 1, 2, and 3 showed initial mean values for each column of water of 18·2, 17·5, and 17·6 mg. P_2O_5 per m.^{3} respectively, and after storage (see Table V) these mean values became 46·6, 46·9, and 45·0 mg. Conversely, those stations indicating the greatest phosphate content originally gave much smaller increases, e.g. Stations 10, 8, 11, 12. This may be interpreted by assuming that where low values for phosphate were found, the plankton was numerous, and where the phosphate was high the plankton was sparse.

No plankton figures are available for the area investigated for the month of January.

SUMMARY.

1. The alteration in soluble phosphate content of untreated sea-water during storage is governed by the conditions of storage—a strong light, favourable to growth, produces a decrease, while darkness, unfavourable to growth, produces an increase.

2. Samples from the surface layers of the sea give greater increases on storage in the dark than samples from deeper water, the extent of the increase being conditioned by the number and quantity of planktonic organisms included in the water sample.

NOTE.

A decrease in soluble phosphate was observed by Atkins (1925, Vol. XIII, No. 3, p. 717) in sea-water samples sent out as blanks on a voyage between Liverpool and Colombo. From this decrease, Atkins formulated a factor for the correction of the phosphate values of sur-

face samples collected during the voyage, though this correction was, "it must be admitted, of doubtful validity."

The light conditions during the storage period of the blanks are not given, though it is assumed that the case of boxes was stored in the dark. Storage in the dark, therefore, does not always produce an increase in phosphate, though such was the case in the 140 odd samples of North Sea water described in this paper.

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Marine Biological Association of the United Kingdom.

Report of the Council, 1926.

The Council and Officers.

The Council met in London on four occasions during the year, the average attendance at the meetings being eleven. The thanks of the Association are due to the Royal Society for the use of their rooms.

In April a Committee of nine members of the Council visited and inspected the Laboratory at Plymouth, and in particular examined the new building, which was then just completed and taken into use.

The Plymouth Laboratory.

The Inspection Committee reported that they regarded the new building as a complete success, that it was excellent in design and construction, and nearly doubled the previous accommodation for research. They further stated that for the special needs of physiological and biochemical research there is now admirable provision, and they were much gratified by the good use which had been made of the limited space and money available. In addition to gas, water, and the town alternating electric current, each room has been supplied with low-pressure air for the aeration of small experimental aquaria and similar purposes.

In accordance with the scheme put forward by the Council when the new building was planned, certain alterations have been made in the old building, the room formerly used for the preservation of specimens for sale having been divided into an office and a laboratory for a naturalist, and a new working compartment having been constructed in the main laboratory. With these and certain other arrangements not yet completed the total cost of the building scheme will amount to £4200, towards which the sum of £3700 has been raised by voluntary subscriptions.

The Council are particularly gratified that this sum includes a grant of £750 from the International Education Board, one of the Rockefeller Foundations, which was made in consideration of the number of foreign workers who make use of the Laboratory. The Worshipful Company of Fishmongers contributed £500; Dr. G. P. Bidder, £500; Mr. E. T. Browne, £500; and the Zoological Society of London, £300. To these, as well as to all other donors, of whom a list has been published in the Journal, the Council desire to express their grateful thanks.

The engines and pumps circulating water through the Aquarium have been in constant service throughout the year, and have not needed any replacement. The treatment of the water with small quantities of lime to keep its alkalinity constant continues to meet with success in maintaining the animals, especially the invertebrates, in healthy condition for a longer period than was previously possible. A number of consignments of animals acclimatized to aquarium conditions have been sent to the Aquarium of the Zoological Society of London.

The stone building rented at Fisher's Nose is used for the storage of nets and various gear, and the buildings at Pier Cellars in Cawsand Bay continue to be of service in connection with Dr. W. R. G. Atkins' investigation of the penetration of light into the sea.

The Boats.

The steam drifter *Salpa* has worked continuously, and the cost of maintenance in thoroughly seaworthy condition during the year has been very small.

The 25-ft. motor-boat *Gammarus* has been engaged in collecting specimens in and about the Sound almost every day. The two 3-h.p. paraffin engines, now in their third season, continue in satisfactory working order, only very minor replacements having been required since they were installed.

The Staff.

Mr. O. D. Hunt, Assistant Naturalist, has been transferred for one year to the Natural History Department of the University of Glasgow, where he is acting as Lecturer under Professor Graham Kerr. His place at Plymouth is being filled by Dr. C. M. Yonge, who was already employed as a temporary Assistant Naturalist. It is hoped that Dr. Yonge's services will be retained until Mr. Hunt's return in October, 1927.

Mr. D. P. Wilson, of the University of Manchester, has been awarded a grant by the Department of Scientific and Industrial Research to enable him to do research at the Laboratory under the supervision of the Director.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :—

C. Amirthalingam, London (General Biology of Oysters).
L. E. Bayliss, London (Study of Catch-muscle in Pecten).
Dr. J. Bělehrádek, Brno, Czechoslovakia (Metabolism of Marine Invertebrates).
N. J. Berrill, London (Viscosity of Eggs).
R. K. Cannan, London (Echinochrome).
Prof. H. Graham Cannon, Sheffield (Feeding habits of Crustacea. Feeding habits of Nebalia).
H. J. Channon, London (Squaline).
Dr. E. Marion Delf, London (Algæ).
W. C. De Morgan, Plymouth (Marine Ciliates).
A. C. Downing, London (Physiology of Muscles).
W. E. Drake, Bristol (Algæ).
Mr. and Mrs. Philip Eggleton, London (Biochemistry of muscular tissue in Raia clavata. Carbohydrate catabolism in the coraco-mandibular muscle of the Ray).
Miss E. W. Emmart, Maryland, U.S.A. (Internal structure of Gammarus chevreuxi).
Miss G. H. Faulkner, London (Filograna).
Prof. D. Fedotov, Leningrad (Antedon).
A. R. Fee, London and Canada (Excretion in Dogfish).
K. Furusawa, London (Physiology of Hæmocyanin and Physiology of Muscles. A study on the visco-elastic property of muscles).
Miss A. H. Fyfe, Edinburgh (Amphitrite).
Miss Sylvia Garstang, London (Development of Molgula and Styela).
Prof. E. S. Goodrich, F.R.S., Oxford (Protodrilus).
C. C. Hentschel, London (Gregarines).
Prof. A. V. Hill, F.R.S., London (Physiology of Muscles).
Prof. K. Hirasaka, Formosa (Feeding habits of Protobranchs).
A. D. Hobson, Edinburgh (Thalassema and Echinoderms. Fertilization and artificial parthenogenesis).
Dr. J. P. Hoet, Louvain (Glycogen in Crustacea).
Dr. E. G. Holmes, Cambridge (Carbohydrate Metabolism in the brains of Elasmobranchs and Crustacea).
Prof. Julian S. Huxley, London (Growth in Crustacea. Physiological gradients in early development).
S. Jones, Cardiff (Fish Nematodes).
Mrs. P. M. T. Kerridge, London (Physiology of Hæmocyanin. Physiology of Muscles).
Miss B. Lascelles, Cambridge (Homarus).
Dr. A. Levin, Petrograd (Viscosity of Muscle).
A. G. Lowndes, Marlborough (Specific chromosome numbers in the genus Cyclops).
Miss S. M. Manton, London (Crustacean Embryology).
Dr. T. G. Mason, Trinidad (Plant Physiology).
Dr. J. Morita, Paris (Histological study on the regeneration of Autolytus Edwarsi).
Miss O. S. Mundy, Plymouth (The method of fertilization in the Oyster).
J. L. Parkinson, London (Physiology of Muscles).

F. T. K. Pentelow, Alresford (Myxosporidia).
F. A. Potts, Cambridge (Teredo. Mollusca).
Dr. Hem Singh Pruthi, Cambridge (The influence of some physical and chemical conditions of water on the bionomics of fishes and insects).
Prof. E. H. Starling, F.R.S., London (Excretion in the Dogfish).
Miss E. M. Stephenson, Portsmouth (General Zoology).
Dr. T. A. Stephenson, London (Anemones).
A. Townsend, Oxford (Bottom Fauna).
Prof. H. B. Ward, Illinois.
Prof. D. M. S. Watson, F.R.S., London (General Zoology).
G. P. Wells, Cambridge (Invertebrate muscle).
Miss M. A. Westbrook, London (Reproduction of the Red Algæ).
D. P. Wilson, Manchester (Polychæte larvæ).
J. Wyman, Harvard (Viscosity of Muscle).

The usual Easter Vacation Course in Marine Zoology was conducted by Dr. J. H. Orton, and was attended by thirty-six students from Oxford, Cambridge, London, Aberdeen, Manchester, Birmingham, and Portsmouth.

An Advanced Course in Comparative Physiology and Experimental Biology, conducted by Mr. C. F. A. Pantin, was held during the Summer Vacation and was attended by eleven students.

Mr. J. M. Branfoot brought a class of five boys from Oundle School, Mr. A. G. Lowndes a class of eleven from Marlborough College, and Mr. Henry Foy a class of three from Gresham's School, Holt, during the Easter Vacation.

During Whitsuntide Mr. W. H. Leigh-Sharpe brought a class of six from Chelsea Polytechnic.

General Work at the Plymouth Laboratory.

During the past summer Dr. Orton has concentrated mainly on a continuation of his work on the spawning of the native oyster. As a study in marine bionomics it was conceived that a careful comparison of the spawning behaviour of the oyster at simultaneous epochs on the East- and West-coast beds would give information that work at one place only could not give. Accordingly, samples, each of not less than 100 individuals, have been examined from the Mersea and the Fal Estuary beds at least once every week without omissions, during the pre-spawning, spawning, and post-spawning periods. In addition special studies were made of the general spawning conditions on the Mersea beds in July, and also of those on the Fal Estuary beds in a series of about twenty visits. The nearness of the Fal beds to Plymouth has made it possible to combine extensive field work with laboratory work.

During the period in which these studies have taken place it is believed

that adequate records have been made of temperature variations, while sufficient observations of salinity have been made on the same beds this summer, or under comparable conditions in former summers, to give the approximate range in salinity variation for the locality. From the data obtained it will be possible to correlate spawning with temperature, and, more roughly, with salinity conditions. It is to be regretted that it was not possible to examine all other environmental conditions, but the experience gained in this work will be of great advantage in similar work in the future when a combined effort might be made to include the investigation of the complete environmental factors. On the Fal the pre-spawning and post-spawning periods were fixed by the examination in each case of several thousand individuals with negative results, but other and probably adequate methods were employed for obtaining the same information from the distant Mersea beds.

The results of this work are now being compiled, but it is of interest to report that significant spawning may be stated to have begun at Mersea on the new-moon tides about the beginning of the second week in June, but at Falmouth on the full-moon tides towards the end of June, correlated in both cases with the attainment of a temperature about 15°–16° C. Spawning continued on both beds until the supply of females was almost exhausted, but practically ceased on the East coast bed after a relatively heavy spawning in the middle of August, and on the West coast beds after a similarly heavy spawning on the full-moon tides at the end of September, six weeks later.

During 1926 there was a good growth of shell in the spring on both sets of grounds, with little growth during the summer on the Fal beds, but again a good growth of shell in October on the Fal grounds. These observations are important in connexion with the relation of external conditions to growth, and indicate that there are two main periods of shell growth in the oyster in a normal summer, namely, in the spring and in the autumn, a view supported by some practical oyster-farmers. Attempts have also been made in this work to obtain statistical information on the seasonal variation in sex-condition of an oyster-population in order to compare different populations.

In addition to the work mentioned above a preliminary study has been made with some success of methods of expressing a criterion of fatness in oysters. It was hoped to obtain additional data during the summer, but the pressure of other work was too great.

Experiments on sex-change from female to female again, through an intermediate male phase, were carried out with some success during 1926 on the Fal beds, and a similar experiment started on the Mersea beds. On both beds, experiments were begun to test the 1926 spatfall, more than 12,000 marked shells being put out on the Fal grounds. At Mersea

other experiments were continued on the rate of growth of experimental oysters reared through their second and third summers, and on the age of spawning of Crepidula spat, reared in the sea in presumed isolation.

The report on the Survey of the Fal Estuary Oyster Beds (1924) with notes on the Biology of the Oyster was published by subscription in September in time for the proposed reconsideration of the regulations pertaining to these beds for the year 1926–27.

Some progress has been made in publishing work which was nearing completion at the time investigations were begun on the unusual oyster mortality in 1920, and it is hoped to complete the remaining work for publication in the near future.

Preliminary work has also been carried out by Dr. Orton, when possible, in investigating a biological group of Lamellibranchs, which may reasonably be suspected of undergoing sex-change.

Mr. Ford's work on herring and the herring fisheries, which was referred to in last year's Report, has extended over another year. A further continuance until March, 1927, will enable him to report on his observations of the Plymouth winter fishery during three consecutive seasons. The estimations of age from scales has shown that in the seasons 1924–25 and 1925–26, fishes of one particular year-class so greatly predominated in the commercial landings that it is confidently expected that fishes of that same year-class will still remain in evidence in the catches of 1926–27, although probably less markedly than in the two preceding seasons. The fishes of the year-class referred to showed five summer-growth zones on the scale during the winter of 1925–26, and six summer zones during the following winter; they will, therefore, exhibit seven summer zones in the winter of 1926–27. The age-estimations to be made during the next few months should give some indication of those younger year-classes likely to form the important proportion of the stock in the immediate future.

The steady accumulation of data on the numbers of vertebræ in herrings landed at Milford Haven, Padstow, Mevagissey, Plymouth, Brixham, and Brighton, gives promise of yielding significant information concerning the herring populations in these different areas. The results suggest two main indications. In the first place, there is a marked general tendency for the average number of vertebræ to rise from lower values at the eastern end of the English Channel off Brighton, to higher values at the western end on the trawling grounds of the "Smalls." But, secondly, relatively high values as well as relatively low values have been experienced on almost every sampling area within the range of investigation. It will probably be realised, therefore, that a cautious comparison of the various types of population presented and a possible linking up of those appearing similar may result in a fuller knowledge of the origin of the shoals

frequenting the several grounds. In this respect, the information on growth in length derived from the study of the scales will be of material assistance in deciding the linking up of populations.

Dr. Lebour has now finished her investigations on the Plymouth Euphausiidæ, the final paper, No. III, on *Thysanoessa inermis* being published in the Association's Journal in March, 1926. She has written a general account of larval Euphausiids based on local and foreign material, also published in the Journal, August, 1926, and a further paper published in the Zoological Society's Proceedings (September, 1926), on the larval Euphausiids from plankton collected by Mr. F. S. Russell in the neighbourhood of Alexandria, Egypt. This material, together with Atlantic specimens collected by Mr. C. F. Hickling and those from the Channel, give a good idea of larval Euphausiids in general, and a scheme for identification of the genera from the larval forms has been given which will, it is hoped, be useful to all plankton workers.

Dr. Lebour has since March given her attention chiefly to crab larvæ, in order to identify the various species in the plankton, which are so numerous and so little known. For this purpose she has aimed at rearing from the eggs, and has thus far reared successfully from egg to megolopa the following crabs: *Inachus Dorsettensis*, *Macropodia longirostris*, and *Maia squinado*. Several others were reared through zoeal stages, eighteen species in all being hatched from the egg. Many megolopæ and young crabs were reared from planktonic zoeæ.

For these rearing experiments it was found, after many trials, that a large number of newly hatched planktonic larvæ made the best food, the crabs growing well on oyster larvæ from the mother oyster. When this was not available larvæ from artificial fertilizations of Teredo and of Pomatoceros were used, both of these serving the purpose well. Sometimes the older zoeæ and megalopæ ate other crab larvæ, but the young crabs and megalopæ were usually fed on bits of fresh mussel.

Hydrographic stations between Plymouth and Ushant have been worked by Mr. H. W. Harvey in the *Salpa*, the data collected being sent to the International Council for publication and to the French Fishery Department. We now have a record of the sea temperature and salinity, and their distribution with depth, for every month since April, 1921, for twenty miles to seaward of Plymouth, of the hydrogen ion concentration for the years 1922 and 1923, of phosphate in solution since March, 1922, and of nitrate in solution since April, 1925. The marked inflow into this Plymouth area of definitely oceanic water of high salinity which occurred in November, 1921, has not been repeated, but owing to interchange of the water masses and fluctuation from year to year in the meteorological conditions, particularly those most affecting evaporation, quite well-marked fluctuations have taken place in the temperature of the

sea. It is expected that a knowledge of these fluctuations will have a direct bearing on the quantitative herring investigations being carried out by Mr. E. Ford, since herrings born in the known physical conditions of 1922 are now beginning to form a portion of the shoals which visit this area every winter. During the next two or three years it will be possible to gain an idea of the relative survival of larval herrings during seasons when the physical conditions have been observed. It is also to be hoped that the quantitative investigations by Mr. F. S. Russell on the animal plankton produced in the area during the summer months will eventually link up with the chemical and physical data now being obtained.

The investigation concerning the distribution of nitrate in sea-water is being continued by Mr. H. W. Harvey, who has also been engaged upon a compilation embodying the advances made since about 1912 in our knowledge of the variable chemical and physical conditions of the sea which have a direct influence upon the life of marine organisms. Much of the work carried out during this period has not been previously correlated nor reviewed from the point of view of the biologist. Since the literature dealing with the subject is very scattered, particularly that concerned with the chemistry of sea-water, it is hoped that such a compilation will be of use to zoologists and physiologists engaged upon research in marine biology.

Mr. F. S. Russell has continued his researches on the vertical distribution of macroplankton, including the pelagic stages of young fishes. From April to August he again worked a number of stations with the ring-trawl, fishing at six depths at each station; in all cases the Admiralty depth recorder was in use. These collections were made in the same locality and roughly on the same dates as those in 1925, and should prove a valuable supplement to that year's work.

Mr. Russell has worked out the vertical distribution of all the plankton organisms contained in the 1925 collections, and finds that, as with the young fish, the various species differ in their types of distribution in the daytime. The results will be shortly published. It was noticed that there was a difference in the distribution of the two sexes in *Calanus finmarchicus*, and accordingly in this year's collections special attention is being paid to the behaviour of males and females.

On June 3rd to 4th Mr. Russell carried out a further series of observations on the diurnal movements of the plankton organisms, and was fortunate in obtaining very large catches, the analysis of which should prove of great interest.

Mr. O. D. Hunt has continued his study of the smaller organisms associated with the bottom-deposits, samples having been taken regularly from stations between Whitsand Bay and the Eddystone. The apparatus used to collect these samples has been specially designed for the purpose

and has been described and figured in a short paper published in the Association's Journal in August, 1926. In order to calibrate this apparatus and determine the contour of the samples obtained under various conditions of working, a number of experiments have been conducted in the Laboratory and also at sea, in which samples have been taken with the apparatus from artificially constructed bottoms. These experiments have successfully demonstrated the efficiency of the apparatus. They will be described in a subsequent paper dealing with the quantitative results from the stations under investigation. The number of these stations has been reduced to three of the seven originally chosen, owing to the length of time required for the examination of the samples in the Laboratory. The technique of examination is believed to be satisfactory, but a preliminary attempt to obtain proof of the statistical efficiency of the counts has shown that more data must be accumulated before this can be definitely established.

The station most fully worked out up to the present is Station 7, near the Eddystone, with a bottom of shell-gravel. This bottom has been found to support a rich micro-fauna, consisting chiefly of foraminifera, crustacea, and nematodes. The aberrant, obscurely known nematoid forms Chætosoma, Desmoscolex, and Rhabdogaster occur here in profusion. Seasonal fluctuation in the population as a whole is not very marked, but it is interesting to note that a low winter population of crustacea and nematodes is followed by a rise in April and May, subsequent to the appearance in the bottom-detritus, of a large increment in the diatom-content due to falling planktonic diatoms.

A general account of the anatomy, histology, and function of the organs of feeding and digestion in the oyster, and a detailed examination of the structure and function of the digestive diverticula (so-called liver or hepatopancreas) of the Lamellibranchs, the latter in the *Transactions of the Royal Society of Edinburgh*, have been completed and published by Dr. C. M. Yonge. The unique and characteristic nature of the gut and digestive processes in typical Lamellibranchs appeared to be correlated with the finely divided, and largely vegetable, nature of the food. In order to confirm this it was decided to undertake an investigation of the Septibranchiate Lamellibranchs from the same standpoint. These animals are unique among Lamellibranchs in that they have no gills, and little ciliation, and have been reported to be carnivorous. They are essentially deep-water animals, and in order to study them four weeks were spent at the Biological Station at Trondhjem, Norway, and one week at the Kristineberg Zoological Station, Sweden. The thanks of the Council are due to the respective Directors of these two stations, Dr. O. Nordgaard and Dr. M. Aurivillius, for their kindness and hospitality, and for the help afforded to Dr. Yonge. Living specimens of *Poromya granulata*,

Cuspidaria rostrata, *C. cuspidata*, and *C. obesa*, were obtained and the function of the muscular septum, the process of feeding and the nature of the food were examined, and feeding experiments with a variety of substances were carried out. The septum is used to draw in water and food, the latter being pushed into the large mouth by the *muscular* action of the palps. Cilia are rare in the mantle cavity, and concerned with the removal of fine particles. The food consists largely of small crustacea which are broken up in the stomach, which is here a crushing organ lined with cuticle and not a ciliated sorting organ as in the other Lamellibranchs. The crushed particles of food are taken in and digested intracellularly by the cells of the digestive diverticula, which open into the stomach by unusually wide ducts. The remainder of the gut is ciliated, but mucus glands are rare and phagocytes are never found in the lumen and seldom in the gut wall. It is hoped to finish this research shortly, and by so doing complete extensive researches on the feeding and digestive processes in the Lamellibranchs, and also show that, as previously suspected, the many peculiar features, both structural and functional, of the digestive system of the typical Lamellibranchs are correlated with their highly developed ciliary feeding mechanisms.

Short observations have also been made by Dr. Yonge on sex change and the formation of calcareous siphonal tubes in *Teredo norvegica*. During a period of leave in February the ciliary feeding mechanisms of the Thecosomatous Pteropods were studied at the Russian Zoological Station, Villefranche-sur-mer, and a paper on this subject has been communicated to the Linnean Society.

The experiments on the inheritance of eye-colour in *Gammarus chevreuxi*, which Mrs. E. W. Sexton is carrying on, with the assistance of Miss A. R. Clark, have made considerable progress during the year, and a preliminary account has been published in *Nature* of a number of new mutations which have appeared. Of special interest are (1) a new red-eyed strain, which when mated with the original red-eyed animals gives all black eyes in the first generation, and blacks and reds in the second, and (2) a white-eyed mutant of the same strain which, when mated with the new red, gives a different result in the reciprocal crosses. Thus a new red male mated with a white female gives all white-eyed young, but the reciprocal cross white-eyed male by red-eyed female gives either all red-eyed young, or gives both reds and whites, according to the constitution of the red female.

Department of General Physiology.

The new laboratories were opened for work early in March, and a considerable amount of the time of the staff was devoted to the details of

their equipment. They are now well supplied with ordinary chemical apparatus and reagents. The equipment as regards physical apparatus is less complete, but as much of this is chosen by individual workers to suit their own needs it would be inadvisable to purchase more than articles of general utility. The visitors who occupied the new laboratories have been shown in the general list of workers, together with their subjects of research.

Dr. Atkins has continued his work on the phosphate content of sea-water through a fourth year. It appears that during this period there has been an approximately closed cycle of events at Station E1, ten miles S.W. of the Eddystone; but there is evidence that E3, off Ushant, some ninety miles south of the E1 area, has been influenced by the ingress of richer Atlantic water. Samples of water from the Para-Liverpool route have also been examined. The study of the seasonal changes in silicate were also continued. In conjunction with Miss E. G. Wilson an examination of methods of analysis of mixtures of phosphate, silicate, arsenate, and arsenite was completed. Arsenic was probably lumped with phosphate in certain of the earlier work on sea-water; accordingly the marked exhaustion of phosphate was masked, for the arsenic was left, as arsenite. Arsenate, if any is present, seems to be used up like phosphate.

Further tests have shown the value of mixing tar or anti-fouling paint with the copper soaps used in net preservation. Cotton and hemp nets thus treated have remained now for over a year without deterioration in strength; during the period they were soaking in salt water, changed every other day. The soap alone is far surpassed by the mixture.

Mr. Pantin has extended his study of the action of ions on amœboid movement. Previous work had shown that calcium was absolutely necessary for amœboid movement. It is now found that in order that calcium may perform its normal functions there must be a balance between it and some other cation (e.g. any alkali metal). This deduction has been made from a critical survey of the effect of non-electrolytes which is still in progress.

Certain non-electrolytes have a very striking effect on amœbæ, but the work has not proceeded far enough for full discussion.

The iso-electric point of the proteins of the amœba has been determined (pH 4·7); since acid inhibition occurs at pH 6·0, the sol $\rightleftarrows$ gel changes in the protoplasm cannot be due to *simple* effects of the Donnan equilibrium with respect to hydrogen ions because these effects are only seen near the iso-electric point.

Amœboid movement has been found to continue for a time in anærobic conditions. Movement ultimately ceases under these conditions, but, for a time, can be recovered on readmitting O_2. The parallel with muscle

and cilia is obvious, though it should be noted that for amœba (and probably for cilia also) there can be no question of the accumulation of lactic acid in the cell.

Mr. Pantin visited the Laboratory at Woods Hole, U.S.A., during the summer, and whilst working there continued with Professor R. Chambers microdissection experiments. Through the kindness of Professor Leo Loeb, he was able to acquire the technique perfected by him for the study of certain invertebrate leucocytes.

Published Memoirs.

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

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ATKINS, W. R. G. *A quantitative consideration of some factors concerned in plant growth in water. Part I. Some Physical Factors.* Journ. du Conseil, Vol. I, 1926, pp. 99–126.

ATKINS, W. R. G. *A quantitative consideration of some factors concerned in plant growth in water. Part II. Some Chemical Factors.* Journ. du Conseil, Vol. I, 1926, pp. 197–226.

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BĚLEHRÁDEK, J. *Influence of Temperature on Biological Processes.* "Nature," Vol. CXVIII, p. 117.

CLARK, R. S. *Rays and Skates. A Revision of the European Species.* Fisheries, Scot. Sci. Invest., 1926, I.

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KING, S. D. *Cytological Observations on Haplosporidium (Minchinia) chitonis.* Quart. Journ. Micr. Sci., Vol. LXX, 1926, pp. 147–158.

LEBOUR, M. V. *The Young of Stylocheiron Suhmii G. O. Sars and Stylocheiron abbreviatum G. O. Sars (Crustacea), from Mediterranean Plankton collected by Mr. F. S. Russell, in the neighbourhood of Alexandria, Egypt.* Proc. Zool. Soc., 1926, pp. 203–211.

LEBOUR, M. V. *On some Larval Euphausiids from the Mediterranean in the neighbourhood of Alexandria, Egypt, collected by Mr. F. S. Russell.* Proc. Zool. Soc., 1926, pp. 765–776.

ORTON, J. H. *Mullet as an Enemy of the Oyster.* "Nature," Vol. CXVII, 1926, pp. 121–122.

ORTON, J. H. *Is the American Slipper Limpet (Crepidula fornicata) an Oyster Pest?* "Nature," Vol. CXVII, 1926, p. 304.

ORTON, J. H. *Can Portuguese Oysters be produced on English Oyster Beds by Artificial Fertilisation in the Sea?* "Nature," Vol. CXVII, 1926, p. 857.

ORTON, J. H. *A Breeding Ground of the Nursehound (Scyliorhinus stellaris) in the Fal Estuary.* "Nature," Vol. CXVIII, 1926, p. 732.

ORTON, J. H. *Report on a Survey of the Fal Estuary Oyster Beds (November, 1924), with Notes on the Biology of the Oyster (O. edulis).* Falmouth, 1926.

PALMER, R. *The Chromosome Complex of Gammarus chevreuxi Sexton. I. Spermatogenesis.* Quart. Journ. Micr. Sci., Vol. LXX, 1926, pp. 541–551.

PANTIN, C. F. A. *On the Physiology of Amœboid Movement III. The Action of Calcium.* Brit. Journ. Exp. Biol., Vol. III, 1926, pp. 275–296.

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SEXTON, E. W., AND CLARK, A. R. *New Mutations in Gammarus chevreuxi Sexton.* "Nature," Vol. CXVII, 1926, pp. 194–195.

STEDMAN, ELLEN, AND STEDMAN, EDGAR. *Hæmocyanin. Part II. The Influence of Hydrogen Ion Concentration on the Dissociation Curve of the Oxyhæmocyanin from the Blood of the Common Lobster (Homarus vulgaris). Part III. The Influence of Hydrogen Ion Concentration on the Dissociation Curve of the Oxyhæmocyanin from the Blood of the Edible Crab (Cancer pagurus).* Biochem. Journ., Vol. XX, 1926, pp. 939–956.

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YONGE, C. M. *The Disappearance of the Crystalline Style.* "Nature," Vol. CXVII, 1926, pp. 691–692.

YONGE, C. M. *Protandry in Teredo norvegica.* Quart. Journ. Micr. Sci., Vol. LXX, 1926, pp. 391–394.

YONGE, C. M. *The Digestive Diverticula in the Lamellibranchs.* Trans. Roy. Soc., Edin., Vol. LIV, 1926, pp. 703–718.

YONGE, C. M. *Ciliary Feeding Mechanisms in the Thecosomatous Pteropods.* Journ. Linn. Soc. Zool., Vol. XXXVI, 1926, pp. 417–429.

The Library.

The thanks of the Association are again due to numerous Foreign Government Departments, and to Universities and other Institutions at home and abroad, for copies of books and current numbers of periodicals presented to the Library. Thanks are due also to those authors who have sent reprints of their papers to the Library.

Finance.

The thanks of the Association are due for the grants for the maintenance of the Laboratory which have been so generously made by the Fishmongers' Company (£600), the British Association (£35), the Royal Society, Gore Fund (£30), the Ray Lankester Trustees (£20), and the Universities of Oxford, Cambridge, London and Bristol.

The thanks of the Association are also due to additional donors to the Building Extension Fund and to the Worshipful Company of Clothworkers for their generous gift of £100.

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The Worshipful Company of Clothworkers	100	0	0
Arthur W. W. Brown, Esq. (Second donation)	25	0	0
"Discovery" Committee (Second donation)	21	0	0
Mrs. E. T. Browne (Second donation)	15	0	0
Ambrose Harding, Esq. (Second donation)	10	10	0
His Grace the Duke of Bedford, K.G. (Second donation)	10	0	0
The Right Hon. Viscount Elveden, C.B., C.M.G.	10	0	0
Mrs. F. J. Weldon (Second donation)	10	0	0
Miss M. V. Lebour, D.SC. (Second donation)	5	15	0
Lady Bayliss	5	5	0
I. N. Budgett, Esq.	5	5	0
Mr. and Mrs. W. Russell	5	5	0
C. F. Hickling, Esq.	4	4	0
W. C. de Morgan, Esq. (Second donation)	3	3	0
Sir Arthur Shipley, G.B.E, D.SC., F.R.S.	3	3	0
Sir Herbert Thompson, Bart. (Second donation)	3	3	0
Borough of Falmouth	2	2	0
Prof. Kyosuke Hirasaka	2	2	0
J. J. Lister, Esq., F.R.S. (the late) (Second donation)	2	2	0
Mrs. F. S. Russell, M.B.E.	2	2	0
F. S. Russell, Esq., D.S.C., D.F.C.	2	2	0
Coates and Co. (Second donation)	1	1	0
E. A. Robins, Esq.	1	1	0
Prof. Julian S. Huxley (Second donation)	1	0	0
Ronald Winckworth, Esq., F.R.G.S.	1	0	0
F. T. K. Pentelow, Esq.	0	10	6
Total	£251	15	6

	£	s.	d.
Year 1924–25	1,823	12	6
Year 1925–26	1,787	5	0
Year 1926–27	251	15	6
Total	£3,862	13	0

THE MARINE BIOLOGICAL ASSOCIATION

Dr. *Statement of Receipts and Payments for the*

GENERAL

	£ s. d.	£ s. d.
To Balance from 31st March, 1926 :—		
Cash in hand	87 15 8	
Cash at Bank	624 3 1	711 18 9
,, Grants :—		
Ministry of Agriculture and Fisheries Grant from Development Fund	10,533 1 3	
Fishmongers' Company	450 0 0	
British Association	35 0 0	
Royal Society Gore Fund	30 0 0	11,048 1 3
,, Subscriptions		177 8 0
,, Composition Fee		15 15 0
,, Donations		2 12 0
,, Sale of Specimens (*less* Purchases)		816 0 8
,, ,, Fish (*less* Expenses)		96 13 8
,, ,, Nets, Gear, and Hydrographical Apparatus		617 11 10
,, Table Rent (including Cambridge University, £52 10s. ; Trustees of the Ray Lankester Fund, £20 ; Birmingham University, £10 10s. ; London University, £50 ; Bristol University, £25 ; Oxford University, £52 10s.; Leeds University, £21)		364 19 0
,, Tank Room Receipts		371 8 0
,, Interest on Investments :—		
4% War Stock	3 2 8	
4% New Zealand Stock (including Repayment of Income Tax)	20 2 5	
Deposit Account	23 14 4	46 19 5
,, Royalties on Films		4 18 7
,, Oyster Nutrition Research Grant, Refund of Amount Transferred in Previous Year		1 10 3
,, Transfer from Publication of Dr. M. V. Lebour's Book		49 5 2
		£14,325 1 7

The Association's Bankers hold on its behalf :—
£410 14s. 8d. 4% New Zealand Stock, 1943–63.
£78 9s. 4d. 4% War Loan, 1929–42.
£51 War Savings Certificates.

BUILDING

	£ s. d.
To Balance at Bank 31st March, 1926	1,338 16 8
,, Donations	251 15 6
,, Interest on Building Fund Deposit	12 14 1
	£1,603 6 3

NOTE.—Further liabilities on the Building Fund to the amount of £300 have been incurred.

OYSTER NUTRITION

	£ s. d.
To Grant from Development Fund	293 0 0
	£293 0 0

PUBLICATION OF DR.

	£ s. d.
To Balance at Bank 31st March, 1926	38 10 7
,, Sale of Book	20 0 7
	£58 11 2

OF THE UNITED KINGDOM.

Year 1st April, 1926, to 31st March, 1927. Cr.

FUND.

	£ s. d.	£ s. d.
By Salaries:—		
Director	1,062 10 0	
Physiologist	910 0 0	
Naturalists	3,211 15 4	
Hydrographer	538 6 8	5,722 12 0
,, Laboratory Wages (including National Insurance)		1,747 12 6
,, Annual Upkeep of Library		492 15 0
,, Scientific Publications:—		
Journal, Vol. XIV, No. 1 (part), No. 2, and No. 3 (part)	653 14 5	
Less Sales	77 10 10	576 3 7
,, Annual Upkeep of Laboratories and Tank Rooms:—		
Buildings and Machinery	576 17 1	
Electricity, Gas, Coal, and Water	304 5 5	
Chemicals and Apparatus	599 10 3	
Rates, Taxes, and Insurance	98 9 1	
Travelling	115 6 10	
,, "Challenger" Society Meetings	22 18 6	
Stationery, Postages, Telephone, Carriage, and Sundries	368 0 2	2,085 7 4
,, Annual Maintenance and Hire of Boats:—		
Wages (including Diet Allowance, National Insurance, and Casual Labour)	1,548 4 7	
Coal and Water	800 6 2	
Maintenance and Repairs, with Nets, Gear, and Apparatus	857 11 4	
Boat Hire and Collecting Expeditions	17 1 3	
Insurance	331 12 5	3,554 15 9
,, Interest on Bank Loans		1 15 7
,, Balance:—		
Cash in hand	75 1 2	
Cash at Bank	68 18 8	143 19 10
		£14,325 1 7

FUND.

	£ s. d.
By Expenditure on Buildings and Equipment	1,465 17 9
,, Balance, Cash at Bank	137 8 6
	£1,603 6 3

RESEARCH GRANT.

	£ s. d.
By Salary and Expenses	291 9 9
,, General Fund, Refund of Amount Transferred in Previous Year	1 10 3
	£293 0 0

M. V. LEBOUR'S BOOK.

	£ s. d.
By Advertising	9 6 0
,, Balance Transferred to General Fund	49 5 2
	£58 11 2

Examined and found correct,

(Signed) N. E. Waterhouse.
Edward T. Browne.
J. O. Borley.
W. T. Calman.

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
26*th April*, 1927.

Marine Biological Association of the United Kingdom.

LIST

OF

Governors, Founders, and Members.

1st May, 1927.

* Member of Council. † Vice-President. ‡ President.

Ann. signifies that the Member is liable to an Annual Subscription of One Guinea.

C. signifies that he has paid a Composition Fee of Fifteen Guineas in lieu of Annual Subscription.

I.—Governors.

The British Association for the Advancement of Science, *Burlington House, W.* 1 ..... £805
The University of Oxford £605
The University of Cambridge £605
The Worshipful Company of Clothworkers, 41, *Mincing Lane, E.C.* 3 £600
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4 £19,155
The Zoological Society of London, *Regent's Park, N. W.* 8 ..... £500
The Royal Society, *Burlington House, Piccadilly, W.* 1 ..... £805
Bayly, Robert (the late) £1000
Bayly, John (the late) £600
Thomasson, J. P. (the late) £970
*G. P. Bidder, Esq., Sc D., *Cavendish Corner, Cambridge* £3008
*E. T. Browne, Esq., B.A., *Anglefield, Berkhamsted* £1035

II.—Founders.

1884 The Corporation of the City of London £210
1884 The Worshipful Company of Mercers, *Mercers' Hall, Cheapside, E.C.* 2 £341 5*s.*
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, E.C.*..... £100
1884 The Royal Microscopical Society, 20, *Hanover Square, W.* 1 ..... £152 10*s.*
1884 Bulteel, Thos. (the late) £100
1884 Burdett-Coutts, W. L. A. Bartlett (the late) £100
1884 Crisp, Sir Frank, Bart. (the late)..... ..... £100
1884 Daubeny, Captain Giles A. (the late)..... £100
1884 Eddy, J. Ray (the late) £100
1884 Gassiott, John P. (the late) £100
‡1884 Lankester, Sir E. Ray, K.C.B., F.R.S., 44 *Oakley Street, Chelsea, S.W.* 3 £101
1884 The Rt. Hon. Lord Masham (the late) £100
1884 Moseley, Prof. H. N., F.R.S. (the late) £100
1884 The Rt. Hon. Lord Avebury, F.R.S. (the late) £100
1884 Poulton, Prof. Edward B., M.A., F.R.S., *Wykeham House, Oxford* £105
1884 Romanes, G. J., LL.D., F.R.S. (the late)..... £100
1884 Worthington, James (the late) £100
1885 Derby, the late Earl of £100
1887 Weldon, Prof. W. F. R., F.R.S. (the late) £100
1888 Bury, Henry, M.A., *The Gate House*, 17 *Alumdale Road, Bournemouth West* £100
1888 The Worshipful Company of Drapers, *Drapers' Hall, E.C.*..... £315
1889 The Worshipful Company of Grocers, *Poultry, E.C.* 2 ..... £120
1889 Thompson, Sir Henry, Bart. (the late) £110
1889 Revelstoke, The late Lord..... £100
*1890 Riches, T. H., B.A., *Kitwells, Shenley, Herts* £430
1902 Gurney, Robert, *Ingham Old Hall, Stalham, Norfolk* ..... £107 1*s.*
1904 Shaw, J., K.C., *Kentchurch Court, Hereford* £113
1909 Harding, Colonel W. (the late)..... £115 15*s.*
1910 Murray, Sir John, K.C.B., F.R.S. (the late) £100
1912 Swithinbank, H., F.R.S.E., F.R.G.S., *Denham Court, Denham, Bucks.* £100
1913 Shearer, Dr. Cresswell, F.R.S., 4, *Fitzwilliam Road, Cambridge* £100
1913 Heron-Allen, E., F.R.S., F.L.S., F.R.M.S., F.G.S., *Large Acres, Selsey Bill, Sussex* £125 15*s*
1920 McClean, Capt. W.N., 1, *Onslow Gardens, S.W.* 7 ..... £100
1920 Buckland of Bwlch, The Right Hon. Lord, *Merthyr Tydfil, Glam.* ... £105
1920 Llewellyn, D. R. £105
1921 Harmer, F. W. (the late)..... ..... £100
1923 Worth, R. H., 42 *George Street, Plymouth*.....£115 15*s.*
1924 The MacFisheries, Ltd., 125 *Lower Thames Street, E.C.* 3 ..... £100
1924 Murray, Lady, 7 *Egerton Gardens, London, S.W.* 3 ..... £100
1925 The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1 ..... £100
1927 Bidder, Miss Anna, *Cavendish Corner, Cambridge*..... £100

III.—Members.

1900 Aders, Dr. W. M., *Zanzibar, East Africa* .....£5 and Ann.
1923 Alexander, Prof. W. B., *The University, Perth, Australia* £10
*1895 Allen, E. J., D.Sc., F.R.S., *The Laboratory, Plymouth* ...£20 10s. and Ann.
1889 Alward, G. L., *Enfield Villa, Humberstone Avenue, New Waltham, Grimsby, Lincs* ..... Ann.
1925 Amemiya, Dr. Ikusaku, *University of Tokyo (Agriculture and Fisheries Department), Tokyo, Japan* ..... Ann.
1927 Amirthalingam, C., *The Laboratory, Plymouth* ..... Ann.
1910 Ashworth, Prof. J. H., D.Sc., F.R.S., *The University, Edinburgh* ..... Ann.
1921 Askwith, The Rt. Hon. Lord, K.C.B., D.C.L., 5 *Cadogan Gardens, London, S.W.* 3 ..... £5 and Ann.
†1911 Astor, The Right Hon. the Viscount, 4, *St. James's Square, London, S.W.* 1 .....£10 and *C.*
1910 Atkinson, G. T., *Fisheries Office, Esplanade, Lowestoft, Suffolk*..... Ann.

1920 Baker, J. R., *New College, Oxford, and The Dell, Malvern Wells*...£1 and *C.*
1923 Barnard, K. H., *South African Museum, Cape Town, South Africa* £10
1923 Barnard, T. T., *King's College, Cambridge* £11
1919 Bawcomb, J. ..... Ann.
1884 Bayly, Miss Anna, *Seven Trees, Plymouth* £60
1921 Bazeley. W. J., *The Cliff, Penzance, Cornwall* ..... Ann.
1885 Beck, Conrad, 68, *Cornhill, E.C.* 3 ..... *C.*
†1907 Bedford, His Grace the Duke of, K.G., *Endsleigh, Tavistock* ...£20 and *C.*
1919 Behrens, Lt.-Col. T. T., *United Service Club, Pall Mall, London, S.W.* 1 ..... Ann.
1926 Bělehrádek, J., M.D., *Docent of General Biology, Masaryk University (Medical Faculty), Brno, Czechoslovakia* ..... Ann.
1925 Berrill, N. J., *Southlands, Knowle, Bristol* ..... Ann.
1903 Bidder, Colonel H. F., *Ravensbury Manor, Mitcham, Surrey* ..... Ann.
1910 Bidder, Mrs. M. G., *Cavendish Corner, Cambridge* ..... Ann.
1925 Birkbeck College, *Bream's Buildings, Fetter Lane, London, E.C.* 4 ..... Ann.
1924 Blake, A. H., c/o *Messrs. Burton Row and Viner, Ltd.*, 11, *Queen Victoria Street, London, E.C.* 4 ..... £5 5s.
1910 Bloomer, H. H., 75–77, *Colmore Row, Birmingham* ..... Ann.
1921 Blundell, H. Moss, *Ministry of Agriculture and Fisheries*, 43, *Parliament Street, London, S.W.* 1. ..... Ann.
1922 Blundell, Mrs. H. Moss, *Callipers Hall, Chipperfield, King's Langley, Herts* ..... Ann.
†1910 Borley, J. O., O.B.E., M.A., *Fisheries Laboratory, Lowestoft* £1 1s. and Ann.
1918 Borradaile, L. A., Sc.D., *Selwyn College, Cambridge* .....£1 1s. and Ann.
1923 Boulenger, E. G., *Zoological Society, Regent's Park, London, N.W.* 8 ... Ann.

*1884 Bourne, Prof. Gilbert C., M.A., D.Sc., F.R.S., *Tubney House, Abingdon, Berks*.....£8 3s. and Ann.

1898 Bowles, Col. Sir Henry, Bart., *Forty Hall, Enfield, Middlesex*..... Ann.

1924 Bowman, Dr. A., *Marine Laboratory, Wood Street, Torry, Aberdeen* ... Ann.

1910 Bradford, Sir J. Rose, K.C.M.G., M.D., D.Sc., F.R.S., 8, *Manchester Square, London, W.* 1 ..... Ann.

*1920 Brand, W. T., 58, *Eaton Place, London, S.W.* 1 ..... £40 10s.

1926 Branfoot, J. M., *Oundle School, Oundle, Peterborough, Northants*..... Ann.

1902 Brighton Public Library (Henry D. Roberts, Chief Librarian) ..... Ann.

1924 Brightwell, L. R., *Wakeford Lodge, High Street, Hampton Hill, Middlesex* Ann.

1918 Brindley, H. H., *St. John's College, Cambridge* .....£2 2s. and Ann.

1886 Brooksbank, Mrs. Mary, *Barcombe Place, near Lewes, Sussex* ..... *C.*

1884 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants* ..... £45 and *C.*

1924 Brown, W. Hargreaves, c/o *Messrs. Brown, Shipley and Co., Founder's Court, Lothbury, E.C.* 2 ..... £10 10s.

1892 Browne, Mrs. E. T., *Anglefield, Berkhamsted, Herts*.....£50 and Ann.

1923 Browne, Prof. F. Balfour, *Department of Entomology, Imperial College, South Kensington, London, S.W.* 7 ..... £5

1925 Bull, Herbert O., *The Laboratory, Plymouth* ..... Ann.

1920 Burne, R. H., M.A., *Royal College of Surgeons, Lincoln's Inn Fields, London*, W.C. 2.....£10 5s. and Ann.

1925 Bush, S. Frank, *Oriel College, Oxford* ..... Ann.

1926 Butler, R. R., *Chemistry Department, Municipal Technical School, Plymouth* ..... Ann.

1897 Byrne, L. W., B.A., 7, *New Square, Lincoln's Inn, London, W.C.* 2 .....£2 2s. and Ann.

*1908 Calman, Dr. W. T., F.R.S., *British Museum (Natural History), Cromwell Road, S.W.* 7 ..... Ann.

1920 Cannon, Prof. H. Graham, D.Sc., *The University, Sheffield* ..... Ann.

1927 Carruthers, J. N., *Fisheries Laboratory, Lowestoft, Suffolk*..... Ann.

1923 Carter, G. S., *Bartlow Rectory, Cambridge* ..... Ann.

*1923 Chapman, His Honour Judge, *Lindum House, Lincoln* ..... £21 and C.

1911 Chilton, Prof. C., *Canterbury College, Christchurch, New Zealand*..... Ann.

*1926 Church, Dr. A. H., F.R.S., *Botanical Gardens, Oxford* .... Ann.

1910 Clark, G. S. R. Kitson, *Meanwoodside, Leeds* ..... Ann.

1911 Clark, Dr. J., *Rosehill, London Road, Kilmarnock, Ayrshire* ..... Ann.

1924 Clark, R. S., D.Sc.. *Marine Laboratory, Wood Street, Torry, Aberdeen*... Ann.

1887 Clarke, Rt. Hon. Sir E., K.C., 2, *Essex Court, Temple, E.C.* 4 ..... £25

1886 Coates and Co., *Southside Street, Plymouth* ..... £3 3s. and *C.*

1925 Cockshott, Lt.-Col. A. M., R.A.S.C., "*Colaba*," *Ryeworth Road, Charlton Kings, Cheltenham Spa, Glos*..... ..... *C.*

1885 Collier Bros., *Plymouth* ..... *C.*

1923 Coonan, J. F., *Balmoral House, Mumbles, Glamorgan* ..... Ann.

1920 Cooper, J. Omer, 6, *Queensland Road, Boscombe Park, Bournemouth*..... Ann.
1925 Cox, P., *Stone House, Godalming, Surrey* ..... £10 10*s*.
1909 Crawshay, L. R., M.A., c/o *The Colonial Secretary, Nassau, Bahamas*... Ann.

*1922 Dale, H. H., C.B.E., M.D., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3 ..... Ann.
1919 Damant, Captain G. C. C., R.N., *Thursford, Cambridge Road, East Cowes, Isle of Wight* .....£5 and *C.*
1920 Darbishire, Prof. Otto V., *Botanical Department, The University, Bristol*..... Ann.
1920 Davidson, Dr. W. Cameron, *Avonleigh, Acadia Road, Torquay* ..... Ann.
1925 Davis, F. M., *Fisheries Laboratory, Lowestoft, Suffolk*..... Ann.
1916 Delphy J., *Faculté des Sciences de l'Université de Paris*, 12, *Rue Cuvier, Paris* ..... Ann.
1906 De Morgan, W. C., c/o *National Provincial Bank, Plymouth* £13 13*s*. and Ann.
1919 Despott, G., *Natural History Museum, Malta*..... Ann.
1915 Dick, G. W., J.P., c/o P.O. Box 28, *The Point, Durban, Natal, South Africa* ..... *C.*
1915 Director of Agriculture and Fisheries, *Travancore, Quilon, S. India*... Ann.
1925 "Discovery" Committee, *Colonial Office, London, S.W.* 1 ..... £73 10*s*.
1885 Dixey, F. A., M.A. Oxon, F.R.S., *Wadham College, Oxford*...£26 5*s*. and Ann.
1910 Dobell, C. C., M.A., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3 ..... Ann.
1924 Dobson, H. V., J.P., *Bath and County Club, Bath* ..... Ann.
1890 Driesch, Hans, Ph.D..... *C.*
*1924 Drummond, Prof. J. C., *University College, Gower Street, W.C.* 1 ..... Ann.
1910 Duncan, F. Martin, 19 *Staverton Road, Brondesbury Park, London, N.W.* 2 ..... Ann.
1920 Dunkerly, Prof. J. S., D.Sc., Ph.D., *The University, Manchester* £2 2*s*. and Ann.
1921 Dunn, Howard, *Mevagissey, Cornwall* .....£2 and Ann.

1927 Eggleton, P., *Physiological Laboratory, University College, Gower Street, W.C.* 1 ..... Ann.
1899 Elveden, The Right Hon. Viscount, C.B., C.M.G., 11, *St. James's Square, London, S.W.* 1.....£45 15*s*.
1885 Ewart, Prof. J. Cossar, M.D., F.R.S., *University, Edinburgh*..... £26
*†1918 Evans, George, 1, *Wood Street, London, E.C.* 2 ..... £98 and Ann.
1923 Evans, W. Edgar, B.Sc., 38, *Morningside Park, Edinburgh* .....£9 5*s*. and *C.*

*1922 Farran, G. P., *Department of Fisheries*, 2 *Kildare Place, Dublin* £2 2*s*. and Ann.
1920 Farrer, The Hon. Noel, M.A., *The Red Cottage, Holmbury St. Mary, Dorking, Surrey* .....£10 10*s*.

1884 Fison, Sir Frederick W., Bart., *Boarzell, Hurst Green, Sussex* ..... *C.*

1885 Fowler, G. Herbert, B.A., Ph.D., *The Old House, Aspley Guise, Bedfordshire* .....£15 10*s.* and Ann.

1920 Fox, Dr. E. L., 9, *Osborne Place, Plymouth* ..... Ann.

1912 Fox, Prof. H. M., *Zoological Department, The University, Edmund Street, Birmingham* ..... Ann.

1925 Fox, Thomas, *Old Way House, Wellington, Somerset* ..... Ann.

1924 Fraser, Miss E. A., D.Sc., *Dept. of Zoology, University College, Gower Street, W.C.* 1 ..... Ann.

1884 Fry, George, F.L.S., *Carlin Brae, Berwick-on-Tweed* £21

*1906 Gardiner, Prof. J. Stanley, M.A., F.R.S., *Bredon House, Selwyn Gardens, Cambridge* .....£30 and Ann.

1920 Gardner, Samuel, *Oakhurst, Harrow-on-the-Hill, Middlesex*...£5 5*s.* and Ann.

*1907 Garstang, Prof. W., D.Sc., 35, *Weetwood Lane, Leeds* ..... Ann.

1924 Gayner, John S., *Hall Cottage, New Earswick, York* ..... Ann.

1925 Gibbons, S. G., 61 *Grosvenor Avenue, East Sheen, London, S.W.* 14 ... Ann.

*1910 Goodrich, Prof. E. S., F.R.S., 6, *Park Town, Oxford* ..... £7 and Ann.

1926 Graham, A. P., "*Inglenook*," 43 *Oakfield Road, Newport, Mon.* ..... Ann.

1912 Gray, J., *King's College, Cambridge* .....£10 5*s.* and Ann.

1920 Greenwood, J. F., *Gledhow, Oxenhope, Keighley, Yorks* £20

1924 Groome, J. R. *Ramridge Cottage, Weyhill, Andover, Hants* ..... Ann.

1900 Gurney, Sir Eustace, *Walsingham Abbey, Norfolk* ..... Ann.

1926 Hacker, Dr. H. P., *Zoological Department, University College, Gower Street, W.C.* 1 ..... Ann.

1920 Hall, Wilfred, 9, *Prior's Terrace, Tynemouth, Newcastle-on-Tyne* ..... Ann.

1924 Harding, Ambrose, *Manor House, Histon, Cambridge* ..... £35 10*s.*

1923 Hardy, A. C., *R.R.S.* "*Discovery*," *c/o Foreign Fleet Division, G.P.O., London, E.C.* 1.....£1 1*s.* and Ann.

*1885 Harmer, Sir Sidney F., K.B.E., D.Sc., F.R.S., *The Old Manor House, Melbourn, near Royston, Herts* ..... £34 11*s.*

1921 Harmer, T. B..... £25

1925 Harmsworth, Cecil B., 28 *Montague Square, London, W.* 1 ... £10 and Ann.

1924 Harvey, H. W., *The Laboratory, Plymouth* ..... £5 5*s.*

1884 Heape, Walter, F.R.S., *Manor Lodge, Bishop's Down, Tunbridge Wells, Kent* ..... *C.*

1924 Heath, C. W., *c/o Messrs. Brown, Shipley & Co., Founder's Court, Lothbury, E.C.* 2 ..... £5 5*s.*

1910 Hefford, A. E., B.Sc., *Marine Department, Wellington, New Zealand* ... Ann.

1926 Hemmeter, John C., Phil.D., M.D., LL.D., 739 *University Parkway, Baltimore, Md., U.S.A.* ..... Ann.

1925 Hentschel, C. C., *King's College, Strand, W.C.* 2 ..... Ann.

1926 Hickling, C. F., *Fisheries Laboratory, Lowestoft, Suffolk* .....£4 4*s.* and Ann.
*1884 Hickson, Prof. Sydney J., M.A., D.Sc., F.R.S., 26 *Barton Road, Cambridge* ..... Ann.
*1926 Hill, Prof. A. V., F.R.S., *Physiological Laboratory, University College, Gower Street, London, W.C.* 1 ..... Ann.
1907 Hill, Prof. J. P., F.R.S., *The Zoological Laboratory, University College, London, W.C.* 1 ..... Ann.
1919 Hillier, W. T., M.R.C.S., 23, *Francis Road, Edgbaston, Birmingham* ... Ann.
1921 Hindle, Prof. E., *London School of Hygiene and Tropical Medicine, 23 Endsleigh Gardens, Euston Road, N.W.* 1..... *C.*
1926 Hirasaka, Prof. K., *Zoology Department, Imperial University, Formosa*.....£2 2*s.* and Ann.
1926 Hobson, A. D., *Zoological Department, The University, Edinburgh*..... Ann.
1925 Hogben, Prof. Lancelot T., D.Sc., *Zoological Department, University of Cape Town, Cape Town, South Africa*..... Ann.
1927 Horne, F. R., *Gresham's School, Holt, Norfolk* ..... Ann.
1920 Howell, Capt. G. C. L., *c/o H. S. King & Co.*, 9, *Pall Mall, London, S.W.* 1 ..... Ann.
1918 Hoyte, P., *Mona House, Coxside, Plymouth*..... Ann.
1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*..... £5 and *C.*
1912 Huxley, Prof. J. S., *King's College, Strand, London, W.C.* 2 .....£4 and Ann.

1921 Jenkins, Mrs. W., *Westhide, Hereford* £50
1927 Jennings, D. A., *New College, Oxford* ..... Ann.
1924 Jesus College, *Oxford* £50
1923 Judge, J. J., 2, *Apsley Road, Plymouth* ..... 10*s.* 6*d.* and Ann.

1920 Keeble, Sir Frederick, C.B.E., Sc.D., F.R.S., *Botanic Gardens, Oxford* Ann.

1897 Lanchester, W. F., B.A. ..... *C.*
1925 Lebour, Miss M. V., D.Sc., *The Laboratory, Plymouth* ..... *C.*
1920 Lewin, Mrs., *Parkhurst, Abinger Common, Dorking, Surrey* £50
1924 Lindley, Miss J., 74 *Shooters Hill Road, Blackheath, S.E.* 3 ..... £25
1926 Lindsay, The Hon. Lionel, *Hambrook House, Chichester, Sussex* ..... Ann.
1926 Lowndes, A. G., *Marlborough College, Marlborough, Wilts* ..... Ann.
1924 Lumby, J. R., *Fisheries Laboratory, Lowestoft, Suffolk* ..... Ann.

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OBJECTS

OF THE

Marine Biological Association

OF THE UNITED KINGDOM.

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, and from that time until 1926 a sum of over £6,500 has been spent on additional buildings. Throughout this period 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 maintenance of a research steamer and other collecting boats, and the salaries 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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