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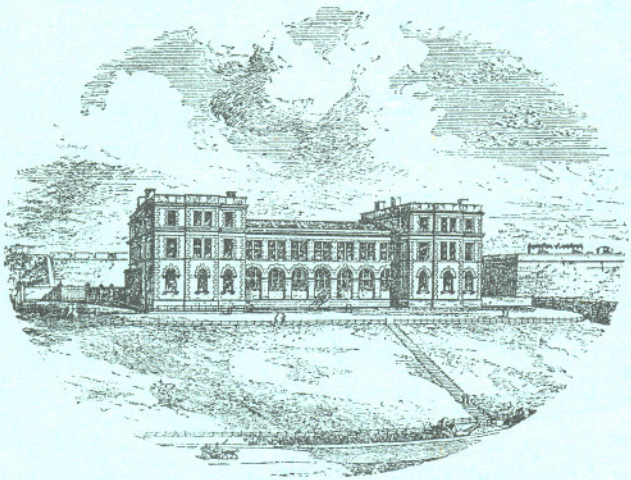

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On Rhythmic Periods in Shell-growth in *O. edulis* with a Note on Fattening.

By

J. H. Orton, D.Sc.,

Chief Naturalist at the Plymouth Laboratory.

With 10 Figures in the Text.

CONTENTS.

Introduction, Method and Material.

During recent years the writer has worked almost continuously—with the exception of the winter period—on the oyster beds in the Fal Estuary, and particularly on those parts of the beds which are administered by the Truro City Council. In this work the functional activities of the oyster, *O. edulis*, including shell-growth, sex-change, sex-conditions, fattening and feeding, have been studied in relation to the general environmental conditions. This paper deals with the observations on shell-growth. Visits have been made to the beds almost weekly during the pre-breeding, breeding, and post-breeding seasons during the last two years (1926, 1927) with the object of obtaining consecutive data for the cycles of changes occurring during this period. It is only in this way that reliable information on the increase in size of shell can be obtained. The method of working has gradually improved, so that in 1927 it was possible to examine, for various purposes, between February and November about 8,000 individuals, mostly in samples of 100 each, from different parts of the beds. In order to ensure proper sampling of the beds seven key situations, representing large sections of the beds likely to differ bionomically, were chosen for sampling, and one sample of 100 individuals from each of these situations was regarded as a single complete sample representing the general conditions in the part of the Fal Estuary being investigated. An examination of complete samples was not, however, considered necessary every week.

On the Relation between Shell-shoots and general Shell-growth.

In this paper the main observations are of increase in shell-area (as shown in Fig. 1, p. 367), but it has been shown **(2)** that it is probable that nacreous layers are laid down simultaneously with—or shortly after—the deposition of the shell-shoots. It has been found that the new shell-shoots harden and thicken within a period of one month to six weeks, and there is good reason to believe that the nacreous layers on the inside of the older part of the shell receive deposits at the same time. In order to obtain some definite expression of the amount of shell laid down in a shell-shoot, the new growth on the left valve of the shell shown on the right in Fig. 6, p. 379, was cut off and weighed. This new growth had occurred in the autumn of 1923, after August 2, and was found on October 22 to weigh 2·92 grams, while the whole clean dry shell, including the new growth, weighed 29·51 grams. Thus the new rim of only the left valve of the shell weighed $\frac{1}{10}$ as much as the whole shell, i.e. both valves. This kind of relationship between weight of new shell within one to two months of the beginning of deposition of new shell, and the weight of

the whole shell may be accepted as normal; moreover, since sections show that the layers of the shell-shoots are continuous with nacreous layers on the inside of the shell (**2**, 1927), there is good reason to suppose that the nacreous layers (of shell) are laid down on the inside of the shell contemporaneously with the deposition of the new shoots which increase the area of the shell, and that therefore general deposition of a nacreous layer or layers occurs at the same time as increase in shell-area. The period during which general shell-growth occurs in *O. edulis* is an important phase in the life-history, and it is hoped that further information may be obtained by examination of seasonal collections of shells and seasonal chemical analyses and studies of the blood in connexion with calcium metabolism.

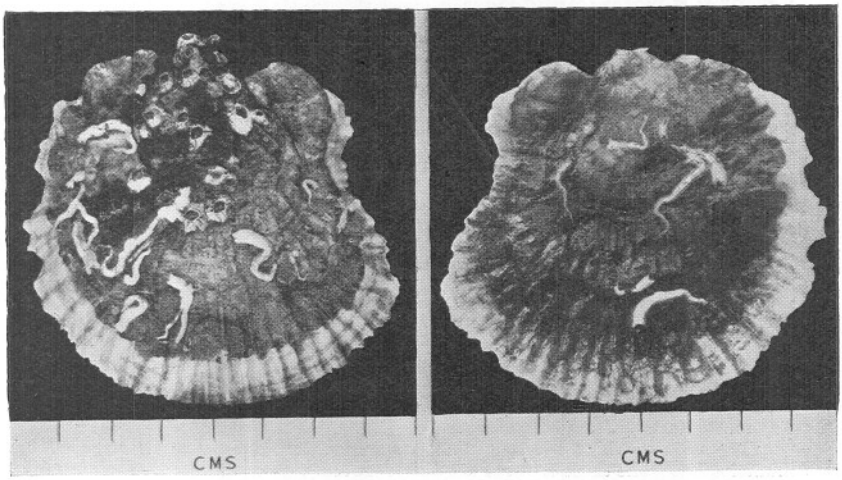

FIG. 1.—Photo[1] of right and left valves of *O. edulis* from Turnaware Bar at extreme low-water mark, November 10, 1927, showing the nature and size of the increase in shell-area effected since October 5, 1927 (from photos by Mr. A. J. Smith). The white rim which shows more effectively in the left-hand view (also the left valve) is entirely new shell-growth.

LOCAL BIONOMICAL OYSTER BEDS IN THE FAL ESTUARY.

The situations of the localities chosen for sampling can be readily seen from Fig. 2, p. 369. In the figure the whole of the beds north of the line WX are administered by the Truro Corporation. The wide upper portion of the Fal Estuary forms a lake, which may be conveniently termed the Truro Lake, with a channel zigzagging across it. The boundary of the Channel is shown by lines which mark the edges of the Banks. Along these edges the depth varies from 1 to 3 fathoms, but at all places the

[1] I am indebted to Mr. A. J. Smith for this photograph, and also for those shown in Figs. 5, 6 and 7.

Channel deepens rapidly, so that the 5-fathom lines at all parts lie close to the edges of the Banks. The steepness of the sides of the Channel is well shown at the lower parts of the Truro Lake, where the 10-fathom line is seen to approach very closely to the line marking the edge of the Bank. The steep sides of the Channel are known as the "Edges," which are a very important part of the beds. Thus the steep side of the Channel off P.B., Parson's Bank, is called the Parson's Edge, and off M.B., Mylor Edge, or off E.B., East Edge, and off Turnaware Bar, Turnaware Bar Edge, and so on. Above Turnaware Bar the Channel is continued as the River, without any extensive banks, but with narrow flats here and there.

The localities chosen for obtaining samples are as follows :—

1. Turnaware Bar ; a considerable portion of the Bar itself is exposed at low-water spring tides.
2. Turnaware Bar Edge ; at various depths to about 6 fathoms.
3. Parson's Bank ; mainly the part above the letters, P.B., nearer the edge of the Bank than the shore.
4. East Bank ; mainly the part below E.B.
5. Mylor Bank ; a strip of the Bank, about 100 fathoms wide about the middle third near the Edge.
6. Mylor Edge ; on the Edge off the above-mentioned strip about the middle third of the N.E. face of the Edge.
7. East Bank, S. Edge ; in a strip about the middle third of the S.W. face of this Edge.

FIG. 2.—Chart of the Fal Estuary and River Fal showing the situation of the local oyster beds[1] (scale : 1 inch=ca. 1,400 yds.). Reduced from Admiralty Chart No. 32, Falmouth Harbour.

The beds north of the line W–X are under the administration of the Truro municipality, while those south of the line W–X and west of the line Z–Y are administered by the Falmouth municipality, excepting private layings, which are situated mostly in the creeks and upper part of the river from Turnaware Bar, and are apparently always at, and above, low-water mark.

The chief oyster beds are as follows :—

	Truro beds.	Depth in fms.		Falmouth beds.	Depth in fms.
M.B.	Mylor Bank	$\frac{1}{4}$ to $1\frac{1}{4}$	N.B.	Falmouth North Bank	$\frac{3}{4}$ to $1\frac{3}{4}$
E.B.	East Bank	$\frac{1}{4}$ to $1\frac{1}{4}$	St.J.B.	St. Just beds	$1\frac{1}{4}$ to $1\frac{3}{4}$
P.B.	Parson's Bank	$\frac{1}{4}$ to $\frac{3}{4}$	V.B.	Vilt Bank or	
	Turnaware Bar	0 to $1\frac{1}{4}$		St. Mawes beds	$\frac{3}{4}$ to 2
R.R.	The River beds	0 to 9	F.F.	Falmouth West Banks[2]	2 to 3
T.R.	Trelissick Reach	0 to 9	K.Q.B.	Kiln Quay beds	$2\frac{1}{4}$ to $2\frac{3}{4}$

Other salient features are H.H., Higher Trelease ; T.H., Trelissick House ; F.H., Porthgwidden House ; G.H., Great Wood House.

The chart is drawn to show the exposure of the beds at low water, ordinary spring tides, as at Turnaware Bar ; the tongue of ground exposed on the East Bank is known locally as Brown Rose Bar. The Channel is marked by lines which denote the edge of the Banks where the depth is mainly 1-2 fathoms, but shelves rapidly in places to 3 fathoms, and fairly rapidly everywhere to 5 fathoms. The inner contour-line in the Channel, which ends opposite the middle of the East Bank, is a 10-fathom line, and gives an indication of the general steepness of the sides of the Channel.

[1] I am indebted to Mr. D. B. Stevenson for the original drawing for this figure, which was originally reproduced in **1**, 1926.

[2] Oysters are not usually found on these Banks.

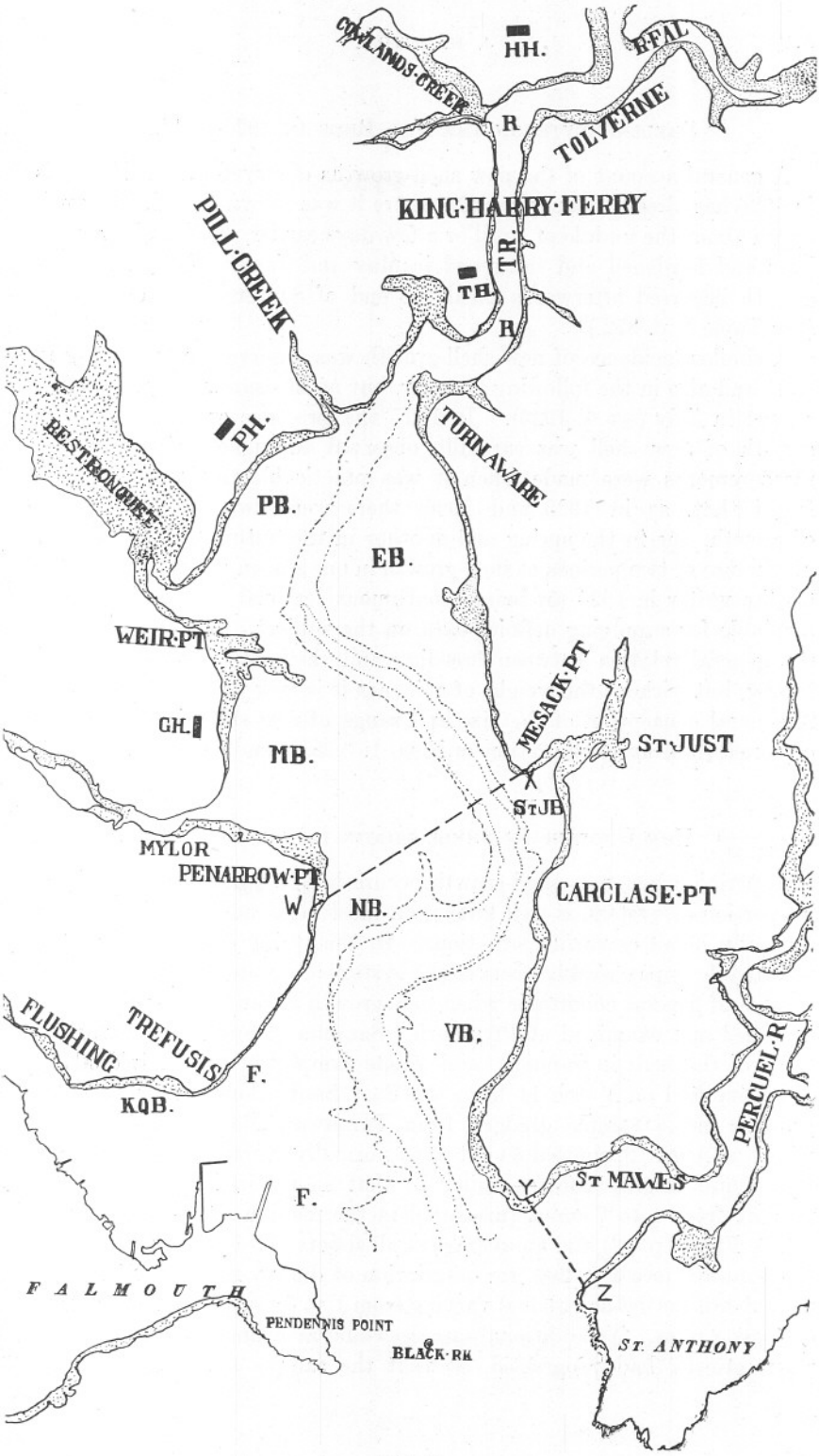
HH.
COWLANDS CREEK
R
TOLVERNE
KING HARRY FERRY
PILL CREEK
TR.
TH.
R
PH.
BESTBONQUET
TURNAWARE
PB.
EB.
WEIR PT
GH.
MB.
MESACK PT
ST JUST
STJB
MYLOR
PENARROW PT
W
NB.
CARCLASE PT
FLUSHING
TREFUSIS
F.
KQB.
VB.
PERCUEL R
F.
ST MAWES
Y
Z
FALMOUTH
PENDENNIS POINT
BLACK RK
ST. ANTHONY

FIG. 2

Shell-growth on the Fal Beds in 1925–1927.

A general account of the new shell-growths observed on the Fal beds in 1926 has already been given (**3**), where it was shown that shell-growth began about the middle of April or a few days earlier, continued over the beds and hardened and thickened in May and June. No general new growth occurred afterwards until the end of September and October. (See Table I, p. 372.)

A similar incidence of new shell-growth was observed in the spring in 1925 and also in the following October, but no measurements were made except in July (see **4**, 1926). In 1927 the presence or absence of the growth of new shell was carefully observed throughout the year, and measurements were made when it was practicable to do so. It was found that, as in 1925 and 1926, there were two definite periods of growth, one in the spring and another in the autumn. The possible occurrence of two periods of shell-growth in one season was noted vaguely by the writer in 1924 (**5**) before continuous seasonal observations were available for supplying definite data on the subject. At the same time the general relation between breeding and shell-growth was discussed briefly, but without the weight of evidence it is now possible to produce. A general conception of the size and range of new shell-shoots may be obtained from an examination of Figs. 1, 3, 5, 6 and 7 herein.

The Growth of Shell-shoots in the Spring.

A period when new shell-growth occurs in the spring, in a variable proportion of oysters, is well known on most beds, and probably occurs normally in all estuarine situations. In the spring of 1927 the writer was unable to pay weekly visits to the oyster beds to determine the actual dates and general conditions when new growth began, but samples were obtained and examined at Plymouth. Samples of oysters from various parts of the beds in January, and single samples of 100 individuals in February and on March 11 from the East Bank, showed no new shell-growth, but a sample dredged from Turnaware Bar, near low-water mark, on April 12, showed 30 out of 61 normally grown oysters with new thin white fragile shoots—similar to that shown in Fig. 1, p. 367—ranging from 1 to 7 mms. (measured in the median dorso-ventral line), (see **1**, Fig. 2, p. 12) and an average of all shoots of 3·5 mms. ; and 7 out of 44 dumpy (see **4**, p. 200, for description of dumpy individuals) oysters with shoots (as defined above) varying from 1 to 4 mms., with an average of about 2 mms. No additional samples could be examined until May 18, when growth had progressed, so that the sample taken on April 12

provides the earliest material for fixing the date of the beginning of new shell-growth in 1927. It will be seen later that the size and nature of the shoots in the April sample leaves no doubt that growth began early in that month. It is not improbable that growth may have begun a few

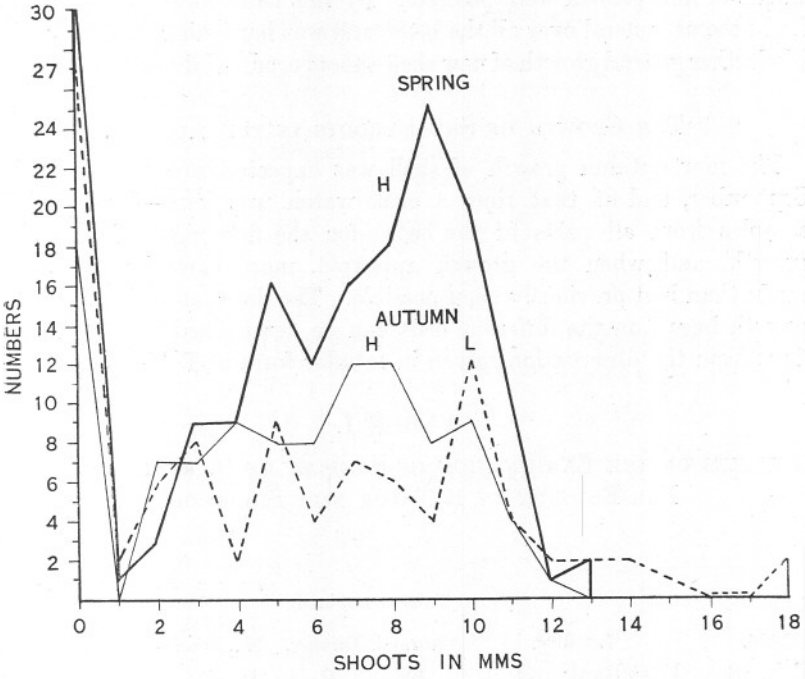

FIG. 3.—Graphs[1] showing the range and frequency of shell-shoots in samples of *O. edulis* from the same situation, namely, low-water springs at Turnaware Bar, Upper Fal Estuary, in the spring, May 18 (H), and autumn, November 10 (H and L), of the same year, 1927.

The spring sample consisted of 71 $2\frac{1}{2}$–$2\frac{5}{8}$ inches oysters and 101 small, i.e. about 2–$2\frac{1}{4}$ inches, broody individuals. The autumn sample consisted of 101 normal individuals, ranging from $2\frac{5}{8}$–3 inches in length.

H. gives the range and frequencies of shoots measured in the dorso-ventral median line, i.e. in increase in height, or a vertical direction in Fig. 1, p. 367.

L. gives the increase in length of the oyster, and is obtained by subtracting the length of the individual before growth occurred from that of the increased size of shell, i.e. in a horizontal direction in Fig. 1, p. 367.

days earlier on the River beds, and somewhat later on the beds below the region of Turnaware Bar.

On May 18 the sample from Turnaware Bar gave 47 with new shell-shoots (66%) out of a total of 71 normal individuals, with shoots ranging from 2 to 11 mms. (average 6 mms.), and 12 out of 54 dumpy individuals with slight indefinite shoots, but also one with a shoot of 4 mms. On the same day from the East Bank 8 out of 25 normals showed good shoots

[1] I am indebted to Mr. J. Bowden for the drawing for this figure, and also for those for Figs. 4, 8, 9, and 10.

and 5 traces of shoots, while of 21 dumps 7 showed traces of growth. (See Table II, p. 373.)

From June 7 full general samples were examined regularly during the month, particularly for sex-condition and spawning, and no measurements of new growth were possible. By this time, however, the growth had become general over all the beds, and was hardening, i.e. thickening. No further general growth of new shell-shoots occurred during the summer.

The Growth of Shell-shoots in the Autumn.

The new autumn growth of shell was expected towards the end of September, and at that time a close watch was kept—by examining samples from all parts of the beds—for the first signs of new shell-growth, and when the growth appeared, more careful records were made than had previously been possible. The dates at which new shell-growth began on the different beds can be determined to within a few days from the observations given in tabular form in Table II, p. 373.

TABLE I.

Results of the Examination of Samples of *O. edulis* from the Fal Estuary in 1926 for new Shell-shoots.

		Totals examined.		Total with new shell-shoots. Normal.			Dumpy.
1926.	Locality.	Normal.	Dumpy.	No.	Range of shoots in mms.	Average of shoots in mms.	No.
Feb. 18	East Bank and Penarrow	60	0	0	–	–	–
April 21	T. Bar ca. L.W. dredged	73	47	53	1– 9	4·2	–
May 20	East Bank, S. Edge	54	0	45	2– 9	5·4	–
,, 26	T. Bar, dredged	50	71	46	2–12	5·7	49[1]
,, 26	T. Bar, dredged ; small normal	80	–	64	2–10	5·4	–
June 1	Penarrow Pt.	41	–	34	2–13	5·4	–
,, 2	T. Bar	26	–	22	2– 9	5·8	–
,, 2	,, small	125	–	108	2–13	5·6	–
June 15 to Sept. 15	All grounds ca. 5,000. Shoots hardened—no new growth.						
Sept. 21	T. Bar, shore, L.W.	106	65	a few	–	–	–
,, 25	Do. dredged	103	22	a few	–	–	–
Oct. 5	Do. dredged	101	18	many	2– 7	–	–
,, 6	Trelissick Reach	82	25	common	2–10	–	–

Oct. 7	Mylor Bank	82	17	few	7	–	–
,, 11	T. Bar dredged	129	22	29	2– 7	4·0	2
,, 11	Parson's Edge	64	10	25	2– 7	–	4
,, 12	East Bank	226	108	44	2– 7	–	7
,, 12	East Edge opp. Pill Creek	84	22	31	2– 9	–	2
,, 12	Mylor Bank	70	31	14	2– 8	–	5
,, 13	King Harry	165	26	74	2–11	–	–
,, 13	Pill Shore	113	35	43	2– 7	–	3
,, 13	Parson's Bank	20	17	4	to 6	–	1
,, 13	T. Bar dredged	145	28	60	2– 7	4 to 5	5
,, 20	E. Bank, S. Edge	86	13	30	2– 7	4·0	0
,, 21	,, B.R. Bar	98	35	57	2–10	5·4	19
,, 26	Parson's Bank	65	20	35	2–11	–	4
,, 26	T. Bar dredged	98	14	55	2–10	–	4
,, 26	Pill shore (off T. Bar)	86	10	60	2–10	4 to 5	4
,, 28	Falmouth, N. Bank	96	12	47	2– 7	4·5	3
,, 28	East Bank	80	26	37	2–10	4 to 5	–
,, 28	Channel near Poles	101	14	16	2– 7	3 to 4	0
,, 29	Mylor Bank	70	33	42	2–10	4·4	8

NOTE TO TABLE I.

[1] The shoots of the 49 dumpy individuals ranged from 2–9 mms. with an average of 4·0 mms. This average is greater than occurred in any other samples of dumps recorded in the table, where the shoots ranged usually from 1–3 mms. with only rare cases of wider shoots.

TABLE II.

RESULTS OF THE EXAMINATION OF SAMPLES OF *O. EDULIS* FROM THE FAL ESTUARY IN 1927 FOR NEW SHELL-SHOOTS.

1927.							
Jan. to Feb.	Various beds	300		0	–	–	–
Mar. 8	T. Bar shore L.W.	50	28	0+1 ?	–	–	0
,, 11	East Bank	80	22	0	–	–	0
April 12	Turnaware Bar	61	44	30	1– 7	3·5	7
May 18	,, large	71	54	47	2–11	4·0	12
,, 18	,, small	101	0	94	2–13	8·1	0
,, 18	East Bank	25	21	8	3–12	6·7	7
May and June	All grounds. ca. 2,000. New growth hardening.						
July to Sept. 28	Do. ca. 5,000. No new growth.						
Sept. 28	Parson's Bank	86	15	0	–	–	0
,, 29	Turnaware Bar Edge	96	5	0	–	–	0

1927.		Locality.	Totals examined. Normal.	Dumpy.	Total with new shell-shoots. Normal No.	Normal Range of shoots in mms.	Normal Average of shoots in mms.	Dumpy. No.
Oct.	3	Mylor Bank	90	9	0	–	–	0
,,	4	East Bank, S. Edge	93	7	0	–	–	0
,,	4	East Bank	88	12	0	–	–	0
,,	5	Parson's Bank	91	9	12[1]	1– 3	–	0
,,	5	Turnaware Bar Edge	96	4	1[2]	3– 4	–	0
,,	6	Mylor Edge	94	6	0	–	–	0
,,	6	River, Tolvern Reach	89	9	?[3]	–	–	0
,,	7	East Bank	89	13	0	–	–	0
,,	11	Parson's Bank	88	14	6	3– 4	–	0
,,	11	Trelissick Reach	89	11	20[4]	2– 4	–	0
,,	12	T. Bar Edge, deep	98	2	18[5]	2– 6	–	0
,,	12	Do., shallow	93	7	23	2– 4	–	0
,,	12	T. Bar, shore	98	2	38[6]	2– 4	–	0
,,	12	Do., young	123	0	98[7]	2– 8	–	0
,,	12	East Bank	87	17	11[9]	1– 7	–	0
,,	14	Mylor Bank	80	21	23[10]	2– 4	–	0
,,	17	Parson's Bank	92	8	51[11]	2–10	4·2	0
,,	18	East Bank	75	25	45[12]	2–10	4·4	3
,,	18	T. Bar Edge, shallow	95	5	54[13]	3– 7	–	0
,,	19	Do., deep	97	3	58[14]	3– 7	–	0
,,	19	Falmouth, North Bank	82	18	30[15]	3– 5	–	0
,,	19	East Bank, West Edge	100	–	24[16]	1– 3	–	–
,,	19	Mylor Edge	60*	–	15[17]	2– 5	–	–
,,	20	Mylor Bank	88	13	63[18]	3– 9	–	1
,,	20	East Bank, S. Edge	92	8	35[19]	3– 6	–	0
,,	24	T. Bar Edge, deep	99	2	53[20]	3– 8	4·5	0
,,	25	Parson's Bank	84	14	59[21]	3–10	6·0	0
,,	31	T. Bar about L.W. dredged	88	13	78[22]	3–10	5·6	8
Nov.	1	Trelissick Reach	94	6	64[23]	3– 9	5·1	0
,,	10	T. Bar, shore L.W.	101	9	81[24]	3–12	6·7	2
,,	22	Mylor Bank	102	5	77[25]	3–12	6·0	3

NOTES TO TABLE II.

[1] Very thin, fragile, white new shoots 1–3 mms. and only a few days old.

[2] A shoot of 3–4 mms.

[3] A large proportion of this sample had thin, brittle, whitish shoots, which were hardened and might have been laid down at least one month. A small oyster from the same place showed on October 3rd a distinct thin brittle new shoot.

[4] Distinct thin, fragile, new white, pink, or brownish shoots of 2–4 mms. ; there were also 5 with doubtful new shoots.

[5] With thin, fragile, whitish new shoots 2–4 mms. mostly and 1 of 6 mms. ; there were 3 with doubtful small shoots.

[6] A sample of large individuals, shoots new 2–4 mms. ; some of the remainder may have had incipient shoots broken off.

[7] A sample of brood oysters, 1–2¼ inches, picked up on the shore at dead low water, showing a very high percentage (80%) with new white shoots which were wider than in the larger individuals picked up at the same time. The high percentage of small individuals with new shoots is undoubtedly significant, although a certain amount of selection is unavoidable, owing to the oysters with new shoots being more easily seen than those without.

[9] A sample of large individuals with a high proportion of dumps. The shoots varied from 1–7 mms. with an average of 3 mms. The percentage of normal with shoots is low, viz. 12·6.

[10] New fragile shoots 2–4 mms.

[11] New shoots, main range in size from 2–10 mms. and average 4·2 mms.

[12] New shoots now range from 2–10 mms. and average 4·4 mms. ; the shoots of the dumps were respectively trace, 3 mms. and 4 mms.

[13] Twenty-one had new shoots 3–7 mms., and 33 slight shoots making an edging of about 2 mms.

[14] Twenty-one had new shoots 3–7 mms. and 37 with slight shoots making an edging of about 2 mms.

[15] Only 6 had good new thin growth of 3–5 mms., and 24 had an edging to about 2 mms. of new shell. The sample was from the outer part of the Bank in the slightly deeper water.

[16] This sample was from the deep part of the Edge, and the new shoots in the sample ranged only from small edgings to 3 mms. The number of dumps was high, but was not recorded.

[17] Only a small sample of about 60* seen in the boats ; the shoots ranged to about 5 mms. and a percentage with shoots, of at least 25, estimated only.

[18] Forty-three had good new shoots mostly concentric from 3–9 mms. wide ; 20 had only slight new growth from a trace to 2 mms. One dump had a good new growth.

[19] Fifteen had well-marked new shoots 3–6 mms. and 20 with a trace to 2 mms.

[20] Twenty-three had distinct new shoots 3–8 mms. with average 4–5 mms. and 30 had only slight shoots.

[21] A large and old sample with a very high percentage (50) of new shoots 3–10 mms. (average 6·0 mms.) and some hardening. Seventeen showed a trace of new growth. Altogether 70% of the normals were growing new shell.

[22] This sample was dredged about L.W. mark and is remarkable in showing a percentage on the whole sample of 86 with new shell-growth, and of nearly 89% of the normals with new growth. Of the 78 normals with new growth, the growth was good, showing 3–10 mm. shoots, with an average of 5·6 mms. in 71.

[23] Of this sample 38 had good new growth shoots 3–9 mms., average 5·1 mms. and 26 only had slight growth, an edging to 2 mms. ; 30 normal and 6 dumpy showed no recognisable new growth. The sample was composed of rather young individuals.

[24] The sample contained a high proportion of young individuals, 3–4 years old, which, owing to rapid growth in the preceding month have attained a legal size, i.e. will hang in a ring of diameter of 2⅝ inches. The new shoots in this sample ranged from 3–12 mms. with an average, however, of only 7·1 mms. The increase in length, however, in this sample varied from 0–18 mms. (see the graph in Fig. 3) with an average among those with good growth of 7·2 mms. practically the same as the increase in height. The average increase in length in all the normal was 5·8 mms. An example of an individual with a good concentric shoot is shown in Fig. 1, p. 367.

From the beginning of October to November 10th the individuals in this sample which grew shell increased from an average length by height of 60·5 by 58·3 to an average of 67·7 by 65·4 mms. Taking the sample as a whole the average length by height on October 1, before growth began, was 61·5 × 60·3 mm. and after growth on November 10th 66·6 × 65·8 mms. Thus the average increase in the whole sample is only 5·1 mms. in length and 5·5 mms. in height.

[25] Amongst the normal individuals in this sample the shoots ranged from 3–12 mms. (average 6·8 mms.) in 65 cases, and about 2 mms. in 12 others. Amongst the 5 dumps, 3 had slight growth from a trace to ca. 2 mms. The growth is now hardening distinctly, and it will soon be difficult to distinguish a new growth from an old one.

The records given in Table II, p. 373, show clearly that the autumn growth of shell-shoots began in the first few days of October on some parts of the beds under examination. New growth first appeared on the Parson's Bank beds and at Turnaware Bar Edge on about October 2 or 3, but was then absent from Mylor Bank, Mylor Edge, the East Bank, and East Bank, South Edge. A week later, however, the growth had become general on all the Banks as well as at Turnaware Bar, and samples taken a fortnight later, October 19, showed that growth was general on the East and Mylor Bank Edges, and on the Falmouth North Bank.

The beds in the River, that is, above Turnaware Bar, had not been examined during the summer, and opportunity for obtaining samples only arrived when the beds were opened on October 1. The conditions on the River beds in September were therefore unknown, but it was anticipated that growth might have begun earlier there than lower down. The sample obtained from Tolvern Reach, an upper reach of the River (see Fig. 2, p. 369), could not be interpreted satisfactorily; it would appear that new growth had not occurred in this sample during the last few weeks, as the shell-shoots present were hard, though very brittle, and might have been laid down at least one month. In order to understand new shell-shoots and to interpret them correctly, it is necessary to follow the new growth week by week and familiarise oneself with the changing appearance of the growth.

In the sample from Trelissick Reach, however, a part of the River adjacent to, and just north of, Turnaware Bar (see Fig. 2, p. 369, R., below T.R.), there was no doubt about the shell-shoots being new and similar to those obtained a day later at Turnaware Bar.

From October 11 the records show that (1) an increasing number of individuals began to grow shell, and (2) that the range in size of the shoots and the average shoot increased on the Banks, but that (3) the shoots appeared later and remained small on the Edges and among the dumpy oysters, and (4) in most situations more than 50% of the individuals with normal shells put on new shell-shoots, (5) there is evidence in the material from the shore at Turnaware Bar on October 12 that smaller and younger individuals begin to grow shell a little earlier than older individuals, and that among similar large individuals a greater proportion had begun to grow shell on the shore than in deeper water. In Fig. 3, p. 371, the range and frequencies of shoots of *O. edulis* from Turnaware Bar at low water in the spring and autumn of 1927 are shown graphically to give definite expression to the nature of shell-growth in random samples of the same population.

The records of the sizes of shell-shoots given in Tables I and II, and especially those for Turnaware Bar, shown graphically in Fig. 3 p. 371, prove that a proportion of individuals grow shell at consecutive periods

of growth. It is of interest, however, that samples never show 100% growing new shell, and that the percentage growing new shell has generally been found higher in the younger than in the older individuals.

The growth of new shell-shoots by oysters on Turnaware Bar Edge may be taken as representative of that occurring generally over the beds

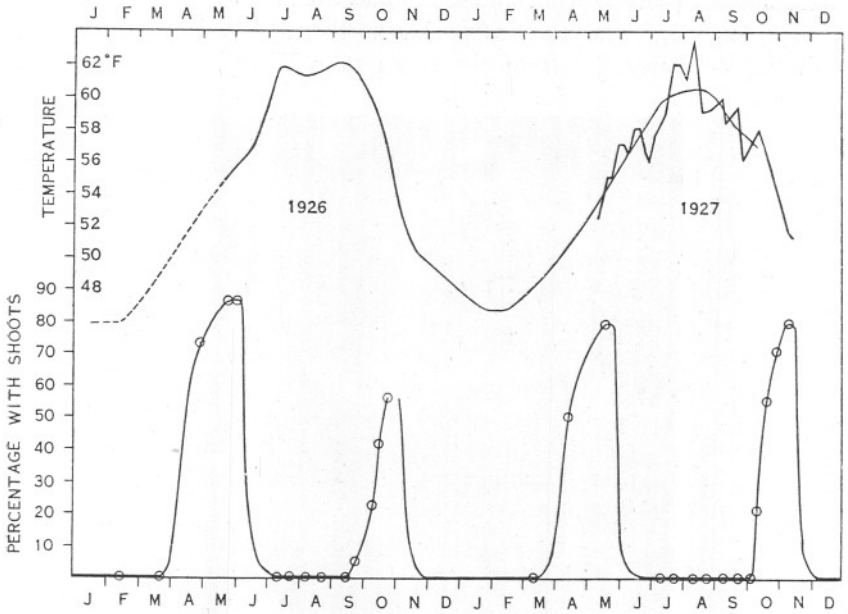

FIG. 4.—Mean percentage of *O. edulis* growing new shell-shoots at Turnaware Bar in 1926 and 1927, with correlated temperature variation at the East Bank station.

The oysters ranged in size mainly from 2¼ to 3 inches, and were of an age estimated at 3 to 5, and rarely 6 years, old, with a mean age of about 4 years. They were dredged about and below low-water mark.

(see Tables I and II). The percentages of normal individuals, showing new shell-shoots on these beds during 1926 and 1927, are plotted in Fig. 4, to show graphically the recurring new growth in the spring and autumn.

ON THE OCCURRENCE OF SPRING AND AUTUMN SHELL-SHOOTS ON OTHER BEDS.

A. *River Blackwater, West Mersea.*

The writer has not had the opportunity of examining regularly throughout the year and in person other beds than those in the Fal Estuary, but frequent visits to other beds have furnished valuable information on the subject of shell-growth. The growth of spring shell-shoots is well known on the West Mersea beds, River Blackwater, but the autumn growth is less well known there. At my request the dredgerman kept a look-out for the

first sign of shell-growth in 1927, and new growth was reported only on May 1. In the spring of 1927 samples of oysters were examined on the beds at West Mersea with the following results. On May 25, 20% of a sample of 101 oysters from the Noss End beds showed recent shell-shoots of mainly 3 to 8 mms., and similar small percentages with only slight shoots were observed (a) in similar samples from my experimental cage in Deeps, May 25, (b) in samples from the northern (Tollesbury) shore of the River Blackwater, (c) from the shore near West Mersea Church on

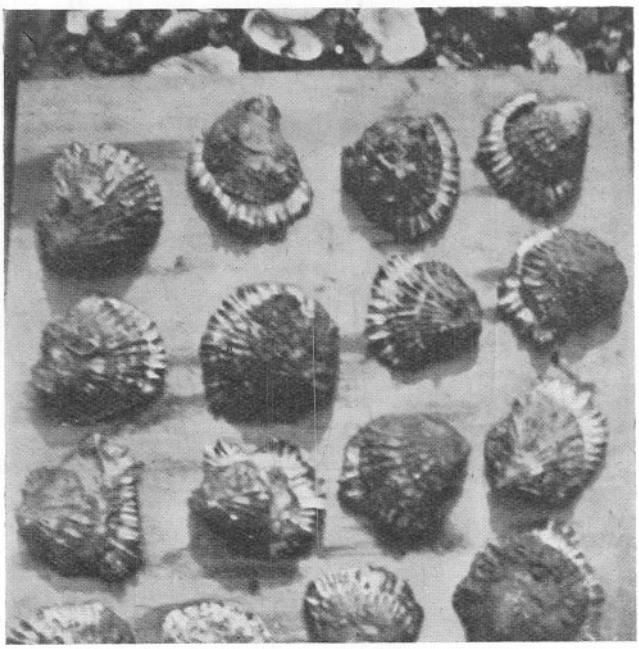

FIG. 5.—Photo of *O. edulis*, showing a large autumn shell-growth at West Mersea, River Blackwater, Oct., 1923. The new growth shows white against the blacker shading of the older part of the shell in most of the individuals. These oysters were proved to be male in July, 1923, and were put into the sea on August 2, 1923. × ca. $\frac{2}{7}$. (Photo enlarged from a snapshot on the beds.)

May 26 and 30, while 87% showed new small shoots from 2 to 8 mms. in a sample of small individuals from Thornfleet Edge picked at low water on May 31. Another sample from the Noss End on May 31 showed only a small proportion with shoots, but these now measured up to 10 mms.

On June 2 a sample from the Mersea shore showed 40% with fair to good new growth 3 to 10 mms., and showed that the spring growth had become general but slight on the beds. After leaving the beds on June 4 I examined samples from West Mersea regularly during the summer at Plymouth, until August 17, but no further new shell-growth was observed.

On September 15 in a sample of 100 individuals from the Mersea shore a few shells were found with new thin white shoots, and on October 12 a similar sample from the South Shore of the River Blackwater showed that recent growth had occurred in some individuals, but had hardened, and had therefore been laid down some weeks ago, and a similar result was obtained from a sample dredged in Thornfleet on October 19, except that not all the shoots had hardened and some had certainly been laid down recently. Thus there also occurred on the River Blackwater beds in 1927 a spring and an autumn growth of shell-shoots, but the observations are less decisive than those made at the same time on the Fal Estuary beds. There is, nevertheless, little doubt that at Mersea shell-growth began later in the spring and earlier in the autumn in 1927 than on the beds of the Fal Estuary mentioned above (excluding the River,

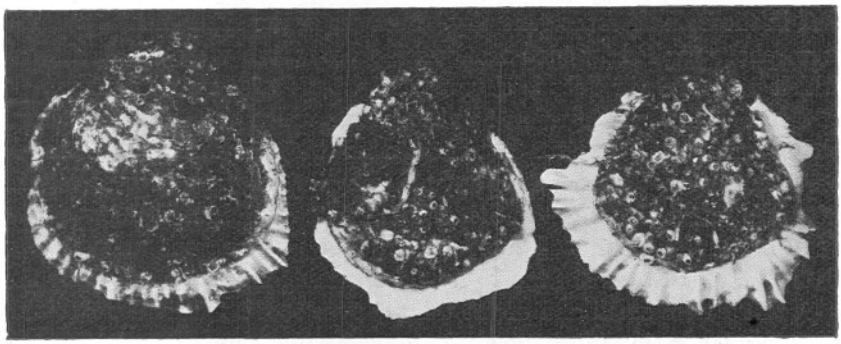

FIG. 6.—Photo of three individuals of *O. edulis*, showing a heavy autumn shell-growth at West Mersea, River Blackwater, October 22, 1923. These individuals were proved to be ripe female individuals in July, 1923, and put into the sea on August 2. × ca. $\frac{2}{3}$. (From a photo by Mr. A. J. Smith.)

where no observations were made until October). In previous years at West Mersea experiments with oysters in cages (**6**, p. 1027) have enabled definite observations to be made at various times on the occurrence of new shell-shoots. In these experiments the oysters have been placed in the cages generally in July or August and re-examined the following June or July, but in 1923 an additional examination was made in October.

During the years 1922 to 1927 a certain amount of new spring growth has always been observed and recorded, but the amount has rarely been greater than was noticed in 1927. But proof that the growth had occurred in the spring is obtained from the fact that when oysters are left some time in contact with rusting iron—the cages were made of galvanised iron wire—their shells become coated with reddish brown material—by absorption of iron in some form—as though the oyster shell itself had rusted. (The tunicin of Ciona and other Ascidians will absorb iron rust in the same way and become stained brown in the region of the body adjacent

to the rusting iron.) When the new shell-growth appears it is white, and does not acquire the appearance of being dyed with rust for some considerable time. The new growth is therefore distinguished easily and with certainty. From the same sets of experiments proof was also obtained of a summer or autumn growth, for the oysters showed in each June or July, besides the spring growth, an increase of hardened new shell from the previous June or July, but the conditions of working during preparation of the experiments were generally such as to prohibit the taking of the measurements which would have supplied definite and accurate information about the growth.

In 1923 experimental material put out in early August was examined in October the same year, and an unusually large new but hardened growth discovered (shoots of 10 to 18 mms.). This kind of new growth, it is important to note, had occurred both in the experimental oysters and in those on the beds generally. Samples of the experimental oysters were photographed by snap-shots on the beds; one view of individuals which were male in July is shown in Fig. 5, p. 378, and another view of 3 individuals, photographed at Plymouth, which were ripe females in July is given, see Fig. 6, p. 379, but 9 other ripe females kept in the same experimental cage did not show any new growth. In these experiments in 1923 the material was put in the sea on August 2 and hauled October 17; of 101 individuals proved male in July, 77 put on good shell-shoots of 10 to 18 mms., and of the 19 living remaining individuals showing no growth 15 were small and of the dumpy type; of 28 individuals found carrying larvæ in July–August 2, only 2—also dumpy individuals—failed to grow new shell, while the remainder showed mainly 10 to 15 mm. shoots; of 4 individuals found to be hermaphrodite in July, 2 showed no growth in October, 1 a shoot of 10 mms. and 1 a narrow shoot up to 5 to 6 mms. on the ventral edge. The new growth in the right-hand individual in Fig. 6, was cut off, and found to weigh about one-tenth the weight of the whole shell. As growth generally over the beds was similar to that shown by this individual, the increase in weight of shell observed (which does not however include any due to internal deposition on the older parts of the valves) may be taken as representative of the general growth at this period.

The autumn growth on the Blackwater beds has often been found similar to, but rarely quite as good as, that found in 1923. In November this year Mr. Louis French, who has been in charge of oyster cultivation on these beds for a great number of years, informed me, in reply to my question, that there are always two growths of shell at West Mersea (R. Blackwater). The first one starting about April–May and then becoming hardened. The next time growth begins is about August–September, or possibly sometimes at the end of July, and this growth is

always looked for as the oysters leave off spawning, but no record had been made of any year when new growth began in August. These observations, which are given in a general way covering the accumulated experience of a large number of years, are exceedingly valuable, and are confirmed by my own observations both on experimental material and growth on the beds. Except, however, for the indecisive observations

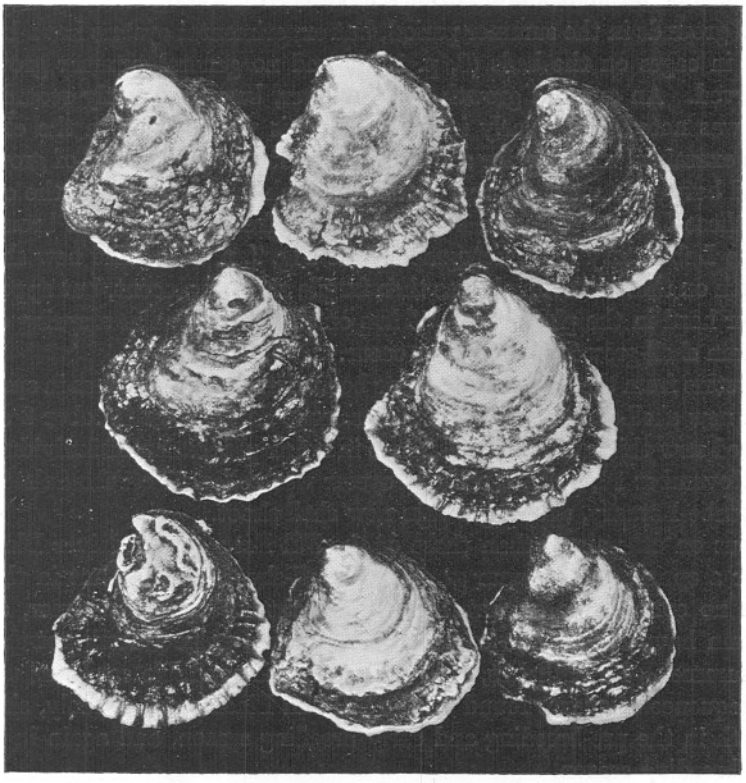

FIG. 7.—Photo of *O. edulis*, showing good autumn shell-growth in the River Yealm from August 30 to October 1, 1923. × ca. $\frac{2}{3}$. (From a photo by Mr. A. J. Smith.)

in May and September, 1927, there is as yet little definite information of the dates—and conditions—at which a general shell-growth has occurred on these beds in any particular year, and additional work is needed to establish the exact time, in relation to the temperature of the sea, the close of the breeding season, and the amount of, and changes in, the available food supply, at which such a general outburst of new shell-growth occurred, as has been described on the Upper Fal Estuary beds. It is, however, clear that, as in 1927, the spring growth begins in

April–May—a little *later* than on the Fal, and the autumn growth in August–September, some weeks *earlier* than on the Upper Fal beds.

B. *River Yealm and other Beds.*

The spring growth of shell is well known on the River Yealm oyster beds, near Plymouth, occurring about April–May and then hardening. No general continuous observations have been made on these relatively small grounds in the summer period, but experimental oysters have been kept in cages on the beds (**6**, p. 1027) and no general summer growth observed. An autumn growth has, however, been frequently recorded, and was noted particularly in 1923. In this year oysters in the cages were examined monthly for spawning individuals, and a burst of growth found between August 30 and October 2, both in individuals in the cage and those dredged from the beds. A sample from the cage was brought to the Laboratory and photographed for Fig. 7, p. 381. The new shell-growth on these individuals was then fragile and translucent, but appears rather hard in the photograph. Thus on the River Yealm a spring and autumn shell-growth is known to occur.

Oysters from the Saltash beds have been seen at various times in spring with new shell-shoots, and in 1926 a sample dredged on October 3 also showed new thin autumn shell-shoots in a fair proportion of individuals. On November 10, 1927, a solitary oyster was collected on the Salstone, Salcombe Estuary, showing a thin new shell-shoot.

Thus on other beds than those of the Fal Estuary and River Blackwater a spring and autumn growth of shell-shoots occurs, but in these cases no consecutive observations throughout the spring, summer, and autumn have been made to prove the absence of new shell-growth in the summer. Nevertheless, such evidence as is available conforms with the sequence of events found on the Fal and Blackwater, namely, shell-growth in the pre-breeding and early breeding season, and again in the post-breeding season.

The Incidence of the Shell-growing Periods in the Fal Estuary.

The foregoing records and observations have now established that in 1926 and 1927 in the Fal Estuary *O. edulis* put out generally over the whole estuary new shell-shoots in the spring about the beginning of April, and also in the autumn about the end of September. The records show slight differences of incidence of new growth on the local beds—and a greater difference between the Upper River beds and those below Turnaware Bar—but the local differences in most of the beds examined

do not amount to more than about one week, although there is an indication in the records for 1926 that new growth began one to two weeks later in the autumn on the Falmouth North Bank than at Turnaware Bar. New growth appears first—in the beds examined—in the Trelissick Reach of the River and is quickly followed by new growth on Turnaware Bar. The oysters at about low-water mark on Turnaware Bar began growth a few days earlier than in the deeper water immediately adjacent to that bar. Growth on Parson's Bank begins slightly earlier than—or as soon as—on Turnaware Bar at about low-water mark, and earlier on both these beds than on the East and Mylor Banks, while oysters on the Edges begin in turn to shoot slightly later than those on the Banks; those in the Channel—judging by the few records which have been obtained—are later than those on the Edges. New growth in the autumn is least in the Channel in range and average of shoots and in percentage shooting, and is successively greater on the Edges and on the Banks. There is a strong indication that in the shallower beds on the River the new growth is as great in the autumn as that on the Banks, and there is no doubt that the extent of the shoots is greater in shallower than in deep water. In general the oysters which have the largest shell-shoots are those which have the flattest, or shallowest, concave, i.e. left, valves, and are the thinnest oysters, but there are exceptions to this generalisation.

Within a period of one to two weeks, therefore, general shell-growth began in early April and about the end of September on the Fal Estuary on the beds defined in 1926 and 1927. It has been seen that new shell-growth probably occurred similarly in 1925.

It is well known that the years 1925 and 1926 were warm years, while 1927 was cooler than the average. There can be no doubt, therefore, that the occurrence of new shell-shoots in *O. edulis* in the Fal Estuary in the spring and in the autumn is a normal sequence in normal or sub-normal years. It may be anticipated, however, that different results may be obtained in highly abnormal seasons.

The Relation of the Shell-growing Periods to the Breeding Period in the Fal Estuary.

In the years 1925, 1926, and 1927 the periods in which shell-shoots occurred were in all three years just before the beginning and at about, or just after, the completion of the spawning period. The observations on breeding will be tabulated later to substantiate this statement. It is clear, therefore, that in *O. edulis* in the Fal Estuary the internal and/or external conditions for shell-growth (to be precise, increase in shell-area) are different from those which are necessary for breeding. Thus there is shown a distinct cycle of metabolic manifestation, which is broadly:—shell-growth—spawning—and shell-growth. Into this cycle will

be interpolated later, phases of gonad proliferation and the laying down of reserve food materials, i.e. fattening in a strict sense ; but to complete the series, data on rate of feeding are required, and these are only available at present from cursory examination of stomach contents.

The Incidence and Relation of the Shell-growing Periods to the Breeding Period on other Estuarine Beds.

Accurate information of the beginning of the shell-growing period in the spring and autumn on other grounds, such as was obtained on the Fal Estuary, is not available, but sufficient is known in some cases to fix these periods approximately. On the River Blackwater it has been shown that growth begins in the spring in April–May and in the autumn about the end of August or early September, but possibly sometimes earlier. Breeding on the Blackwater beds begins earlier than on the Truro Lake, Fal Estuary (see 1927, p. 926, and similar data for 1927 will be given later) and normally finishes earlier. In 1926 spawning continued on the Fal until September 23 (10 to 13% were found blacksick on October 4 and 5), but finished, except for occasional spawners, late in August on the Blackwater beds. Although spawning will undoubtedly vary in these two localities according to the relative warmth of the season, sufficient is now known to permit the statement that normally the breeding season will close earlier on the Blackwater beds than on those on the Fal. In abnormal seasons these conditions may be reversed, and, in fact, effective breeding finished earlier on the Fal in 1927 than on the Blackwater beds. On the Blackwater, therefore, the period of spring shell-growth begins about a month earlier than—and continues to—the beginning of the breeding season ; while the autumn period of shell-growth begins at about the end or soon after the completion of the breeding season at about the end of August or in September. A similar relation of the shell-growing periods to the breeding season holds on the River Yealm, where breeding generally continues into September, as on the Fal, and such observations on growth as have been made show that the autumn shell-growing period occurs also in September or later. Similar relations of the shell-growing periods to the breeding period are strongly indicated to occur on the Saltash beds.

There is therefore evidence that on beds on the east and west coasts of England in estuarine situations, two shell-growing periods occur in *O. edulis* in every normal season, one preceding and one following the breeding period.

On the Fal Estuary these shell-growing periods are normally distinct from the breeding period ; but on the Blackwater beds there is a probability that the spring period may slightly overlap the beginning of the breeding period. There can be little doubt, therefore, that these

relations of the shell-growing and breeding periods will be found to be general in all *estuarine* situations.

On the Correlation of External and Internal Conditions with Shell-growth in *O. edulis*.

The extended and close observations herein recorded on the general incidence of shell-growth in the Fal Estuary—especially in the autumn period—afford data for examining the internal and external (environmental) conditions correlated with a general outburst of shell-growth. All the facts collected during a period of three years, 1925–27, clearly show that there is a general physiological rhythm resulting—at least—in shell-growing periods before and after the warm breeding period under such conditions as normally obtain in English estuarine situations. Such a rhythm may, however, be produced under normal biological conditions by either purely internal conditions, or purely external conditions, or a combination of both. By normal biological conditions may be understood, a normal food-supply, a—chemically and physically—normal sea-water medium and a normal situation on the oyster bed.

It may be assumed, until the contrary is proved, that with regard to conditions for shell-growth *O. edulis* will react similarly wherever it occurs, hence there should be a common explanation of shell-growth for all localities, and therefore the cause of shell-growth on the Fal should be the same as elsewhere. If shell-growth is determined by external conditions then variation in these should result in variation of the phenomena exhibited, and if the conditions in any season should be such as to interpose in the normal breeding period other conditions resembling those occurring in the shell-growing period, an opportunity would be provided for testing whether the rhythm is an internal physiological one, i.e. a time relation, or on the other hand purely an automatic response to external conditions, such as to variations in temperature, light, salinity, pH, or a combination of two or more of these with a variation in food-supply. The deviation from the normal observed in the Fal in August–September, 1927, may perhaps be regarded as too little to test this thesis adequately. It has been shown that a *general* rhythm of pre-breeding shell-growth, breeding, and post-breeding shell-growth does occur on all the beds examined, but, on the other hand, that there is variation in the incidence of the shell-growing period. This variation is clearly marked as between the Fal and the Blackwater beds as follows :—

	Spring shell-growing period.	Normal breeding period.	Autumn shell-growing period.
Fal	Early April	End of June–end of Sept.	End of Sept.–Oct.
Blackwater	April–May	Beginning of June–end of August, Sept.	End of Aug.–Sept.

There is thus a complete difference between the behaviour of oysters on the River Blackwater and those on the Fal; for on the Blackwater the spring shell-growth begins later, and breeding and the autumn shell-growth begin earlier than on the Fal. If the external conditions on the Blackwater beds are wholly different from those on the Fal, it is reasonable to assume that the behaviour of *O. edulis* is determined by the conditions, especially if it can be shown from season to season that the reactions of this mollusc vary with conditions when these deviate from the normal.

(a) *Temperature variation.*

One fundamental difference between the external conditions on the Fal and those on the Blackwater lies in the fact that on the latter beds the range of sea-temperature annually is much greater than on the Fal (Truro Lake), and that the rate of change of temperature throughout the year is also much greater. Whereas on the Fal the temperature ranges from about 46° F. to about 66° F. (on the Truro Lake) on the Blackwater beds temperatures range from about 34° F. to 70° F. or more in similar seasons. The primary causes of these temperature differences are that on and outside the Blackwater beds the water oscillates everywhere over numerous shallow flats and creeks, and so varies in temperature almost directly with local air-temperature and sunshine, while on the Fal the deep channel (8–15 fathoms) in the centre of the beds receives water direct from the English Channel, which for a variety of reasons changes in temperature only slowly. On the Truro Lake the water from the channel spreads over the shallow banks and is affected by air and sunshine only relatively slowly except during neap tides, when oscillation is reduced and insolation or the reverse is accumulative.*

These fundamental differences of temperature variation on the two beds, carrying with them a train of correlated differences, may reasonably be suspected of producing the difference in behaviour of the respective oyster populations, but whether some particular temperature relation, or some other factor dependent upon temperature causes growth of shell remains to be found.

On the Fal it has been shown that shell-growth begins in early April, while on the Blackwater beds, according to the information available,

* The mean daily hours of sunshine over the Falmouth and Blackwater beds are approximately the same throughout the year (see Table III, p. 387). During the period 1881–1915 (7) Falmouth experienced a mean of 4·82 hours of sunshine daily. In the same period Clacton and Southend experienced daily mean of 4·77 and 4·54 hours of sunshine, and the Blackwater, which lies slightly more inland between these two stations, has a similar incidence of sunshine (See 7, Section III), but possibly a slightly higher daily mean than either of these stations. In 1926 and 1927, the daily hours (mean) of sunshine were respectively at Falmouth 4·67 and 4·37, Clacton 4·43 and 4·34, Southend 4·25 and 4·31; the monthly variation of the daily means in these years is shown in Table III, p. 387.

the corresponding time is April–May, and was apparently about early May in 1927. On the Blackwater beds the temperature* ranged between 47°–50° F. in the first fortnight of April, 1927 (see Fig. 8, p. 389), rose to 53°–54° on the 20th to 23rd, but fell again on the 26th to 50° and remained at about this figure until May 1st or 2nd, when it rose to 51°–52°. From May 3rd to the 7th the temperature rose to 59°–60° for 3 days, and then fluctuated between 57° and 54° until May 18th, but remained steady about 58° until the 21st, and then fluctuated between 57° and 59° until May 30.

TABLE III.

MEAN DAILY HOURS OF SUNSHINE BY MONTHS AND YEARS FOR THE YEARS 1926, 1927, AND THE PERIOD 1881–1915. (FROM M.O. PUBLICATION 236, SECTION I, 1919, AND M.O. MONTHLY WEATHER REPORTS.)

	Falmouth.			Clacton.			Southend.		
	1881–1915	1926	1927	1881–1915	1926	1927	1881–1915	1926	1927
Jan.	**1·87**	1·87	*2·17*	**1·87**	1·65	*1·77*	**2·00**	1·49	*1·92*
Feb	**2·98**	1·70	*2·86*	**2·94**	1·98	*2·13*	**2·62**	2·09	*1·91*
Mar.	**4·45**	3·55	*4·38*	**4·23**	4·50	*4·55*	**3·58**	4·25	*4·40*
April.	**6·13**	6·64	*5·91*	**6·03**	4·05	*6·61*	**5·57**	4·18	*6·30*
May.	**7·45**	6·74	*7·00*	**7·52**	6·39	*8·04*	**7·13**	5·90	*8·71*
June.	**7·37**	9·33	*7·03*	**7·33**	6·93	*5·89*	**7·13**	6·50	*6·39*
July.	**7·26**	6·87	*5·16*	**7·00**	6·78	*5·12*	**7·10**	6·82	*5·04*
Aug.	**6·81**	6·08	*6·56*	**6·87**	7·29	*6·46*	**6·68**	7·40	*6·43*
Sept.	**5·43**	4·13	*3·93*	**5·87**	5·47	*4·52*	**5·23**	5·01	*4·13*
Oct.	**3·74**	4·19	*3·83*	**3·61**	3·93	*3·83*	**3·61**	3·55	*3·43*
Nov.	**2·53**	2·90	*2·42*	**2·33**	1·48	*2·05*	**2·20**	1·44	*1·89*
Dec.	**1·77**	1·91	*1·25*	**1·52**	2·41	*1·12*	**1·48**	2·12	*1·23*
Year.	**4·82**	4·66	*4·37*	**4·77**	4·4	*4·34*	**4·54**	4·23	*4·31*

* Daily temperature readings—excepting on Sundays—were taken for the writer at about the time of high and low water by Mr. L. Pearce, the motor engineer in charge of M.V. *Dan*. Mr. Pearce has taken summer temperatures for many years, and recently winter temperatures also. Readings were taken to the nearest degree (Fahrenheit,) especially in mid-Channel in Thornfleet, and in other localities over at least 2 fathoms of water, at a depth of not less than 1 foot with a certificated (N.P.L) sea-surface pattern thermometer (Meteorological Office types). Observations (as yet unpublished) by the writer in Thornfleet, and similar localities, with a modified Nansen-Pettersen water-bottle in winter and summer periods, have shown that *in these (and similar) situations* there occur only slight differences of temperature (of the order of 0·5° F.) between surface and bottom—except in times of flooding after heavy rain—and that surface readings, therefore, give a close approximation to the actual temperature over the beds. Surface readings are liable to be slightly high in warm and slightly low in cold periods. The readings were also made on the low, rather than on the high, side to the nearest degree. The period of the 24 hours during which Mr. Pearce took temperatures extends from 6.0 a.m. to about 3 p.m. The high-water spring tides occur about midnight and noon (G.M.T.), and the low-water spring tides, therefore, about 6 a.m. and 6 p.m. (G.M.T.). Thus no observations were made on the midnight high waters nor the midnight neap

Thus shell-growth on the Blackwater began (about May 1st or soon afterwards) when the sea-temperature was maintained for some time above at least 50°, and became general at a temperature below at most 60°.

On the Fal in 1927 temperature* remained steady over the beds at 49°–50° from March 18th to 30th (see Fig. 8, p. 389). During April, unfortunately, no temperature readings could be obtained on the beds. On May 11 temperatures over the beds ranged from 52°–54°, and on May 18 from 54°–56·5°, with slightly higher temperatures on and near the shore; for instance, 10 fathoms from the shore on the East Bank was a belt of water 59°–60°, but at 200 yards the temperature dropped to a steady level of 55·5°–55·4° to a 1000 yards offshore. Thus on a warm day at low water, and in shallow water inshore, the water will warm up a few degrees higher for a short time than the general body of water.

On May 30, June 1 and 6, temperatures on the Banks were uniformly 57°, but in the Channel on the surface was 56° on May 30th and June 6, but 57° on June 1.

The temperature experienced by oysters between tide-marks on Turnaware Bar will vary between that of the air at low water and that of the water at high water. The temperature of the water at extreme low water and on the Edge at Turnaware Bar varies between that of the River water and the Channel water at high tide, for Turnaware Bar provides an important point in the Estuary where mixing of the River and Estuarine water occurs. In order to obtain temperatures of the River water a station was established at the lower R. in Fig. 2, p. 369, above Turnaware Bar. On May 11 surface temperatures at R. were

low waters, nor on the late spring tide low waters, nor neap high waters in the afternoon. In the summer time the effect of these omissions is to miss part of the diurnal variation, which, in enclosed estuaries, shows maximal and minimal values rarely at any other time than at high and low water. In warm periods afternoon low-water readings—round about 6 p.m.—would give maximal readings for the day, and midnight high-water readings minimal ones, so that the actual range of temperature will be greater than is shown by the readings, and the actual mean may be expected to be rather higher than the observed mean. Thus the error of the observations in expressing the actual mean conditions may be low by as much as 0·5° to 1·0° F. in the summer, with probably a slightly smaller error in the winter.

* Sea-temperatures on the Fal were taken by the writer personally on all the dates mentioned in Table V, p. 396, i.e. once nearly every week during June to October, 1927, but only once in March and May respectively. During this period additional sea-surface temperatures have been taken at various irregular times by Mr. E. Searle, the bailiff of the Truro oyster beds. The readings plotted in Fig. 8, p. 389, are thus mainly from observations by Mr. Searle, who, like Mr. Pearce on the Blackwater beds, reads to the nearest degree Fahrenheit, and who also reads to the lowest whole degree. The Fal surface readings were taken after allowing the thermometer to fall about 1 metre below the surface; but, except for my own readings when the tenths were always estimated, would tend to be low, and of the order of 0·5 to 1·0° F. low. Surface readings in the Channels in the Fal Estuary are rarely the same as bottom readings (at depths of from 8–16 fathoms), but little difference occurs between surface and bottom at the stations established on the Banks (½–2 fathoms), except possibly after heavy rains and in hot calm weather. Low-water spring tides occur on the Fal about noon and midnight, so that the actual maximal, but not minimal, temperatures have been observed, thus the mean of the actual observations as recorded is probably close to the actual mean.

53° and 54° at about H. and L.W. ; on May 18, 56·5°–56·8° on the surface to 1 fathom (but 53·6° on the bottom in 10 fathoms) ; on May 25, 56° (surface) ; on May 30, 57° (surface) ; June 1 and 6, 58° (surface) ; on June 8, 58° (surface) and 1 yard, 56° at 2 fathoms, 55·2° at 4 fathoms, and 54·3° on the bottom in 10½ fathoms at about H.W.

Thus although no temperature readings were taken on the Fal beds in April, it can confidently be stated that temperatures over the beds

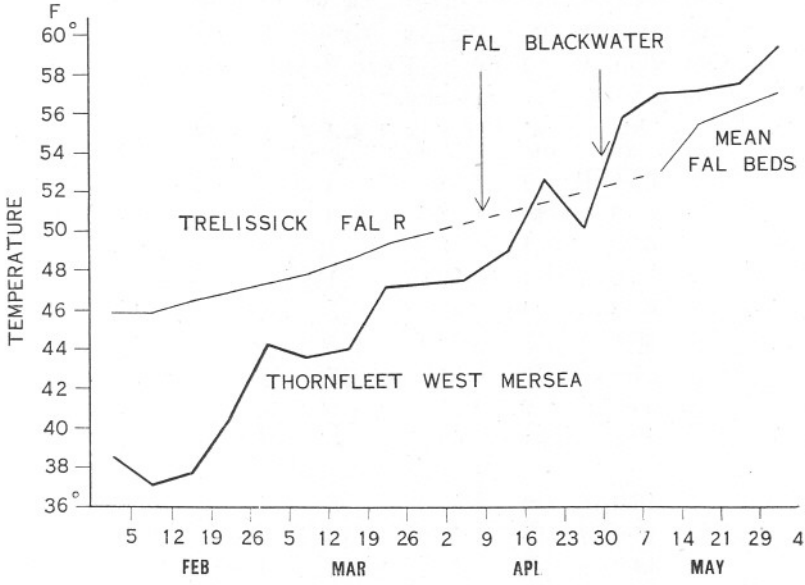

FIG. 8.—Comparison of the surface sea-temperature—from weekly means—on the Thornfleet beds, River Blackwater ; and the upper part of the Fal Estuary, from observations at Trelissick Reach in February and March, and the main Banks on the beds in May. The dotted part of the Fal graph covers a period when no observations were made.

On both sets of beds surface-temperatures have been shown to vary only slightly from bottom readings on the beds concerned, except at Trelissick Reach.

The arrows indicate the approximate times when shell-growth began on the two sets of beds.

generally did not rise above the level of 57° during April–May, the period of general shell-growth, although close inshore and for short periods at low water higher temperatures did occur in May, and would always occur in such situations in warm weather. During April when growth was observed on Turnaware Bar about L.W. mark, it is probable that the temperature of the water over the beds *generally* did not rise above about 51° F., for the maximum temperature obtained at the Plymouth Meteorological Station (in 1 fathom over 3 fathoms of water off the Promenade Pier), which gives records closely similar to a mean of the Falmouth beds, was 50·4° F. It is probable, however, that slightly higher

temperatures occurred for short periods, not infrequently, over Turnaware Bar (where growth was recorded in April), but the increased temperature would not be likely to be more than a few degrees Fahrenheit. Means of the temperature observations on the Truro beds are shown below in Table IV.

TABLE IV.

MEAN SEA-TEMPERATURES (FAHRENHEIT) AT A DEPTH OF ABOUT 3 FEET TAKEN DURING 1926 AND 1927 AT UPPER (RIVER), LOWER (ST. JUST–POLES CHANNEL), AND MIDDLE (EAST BANK) STATIONS ON THE TRURO OYSTER BEDS.

Date, 1926.	River Stn.	No.[1] of Obsns.	East Bank Stn.	No.[1] of Obsns.	Channel Stn.	No.[1] of Obsns.	Observer.
May 20	55·0° F.	1	53·6° F.	2	53·8° F.	2	J.H.O.
June 2–30	57·8	10	56·4	12	56·8	9	,,[2]
July 21	64·2	1	63·9	1	–	–	,,
,, 28	59·8	1	59·2	1	–	–	,,
Aug. 4–12	63·2	4	61·2	5	62·1	4	,,[2]
Sept. 8–29	62·1	3	62·1	5	61·8	4	,,
Oct. 1–22	57·6	15	57·8	17	56·9	11	,,[3]
Nov. 1–25	50·7	9	51·0	9	51·9	8	E.S.
Dec. 4–30	49·1	5	49·2	8	49·5	8	J.H.O., E.S.
1927.							
Jan. 11–31	46·0	3	47·0	5	48·0	5	E.S.
Feb. 1–25	46·3	14	47·0	19	47·1	17	,,
March 8	48·2	1	48·0	1	48·0	1	J.H.O.
March 1–30	48·7	15	48·6	13	48·3	15	E.S.
May 11–30	55·8	6	55·0	8	54·8	7	J.H.O., E.S.
June 1–29	58·2	17	57·0	16	56·9	17	,,
July 4–27	60·9	14	60·0	13	60·1	11	,,
Aug. 1–27	61·0	4	60·7	9	60·5	7	,,
Sept. 5–29	58·6	6	58·4	6	58·0	7	,,
Oct. 5–19	56·7	4	57·1	4	57·0	4	,,
Nov. 10	51·5	1	51·5	1	52·0	1	J.H.O.

[1] The average of all readings about one low water or one high water, is recorded as one observation. [2] One observation at each station by E. S.
[3] Two observations at each station by S.E.

From the observations on temperature in relation to the period of spring shell-growth on both the Fal and Blackwater beds, it is clear that shell-growth began on both beds in 1927 soon after the temperature rose above the level of 50° F. No temperature observations are available for the Fal in April 1926, and no precise growth observations are available for the Blackwater in the spring of 1926. The temperature observations

in 1927, however, show that when shell-growth began on the Fal the temperature of the sea on these beds was higher at that time than on the Blackwater (see Fig. 8, p. 389), and there is no doubt that a temperature of about 50° will generally be attained on the Fal at least a few weeks earlier than on the Blackwater, but in May a few weeks afterwards the conditions will be reversed, and the Blackwater beds will show higher temperatures than those on the Upper Fal Estuary (excluding the upper reaches of the River Fal). These general facts can be made clear from a

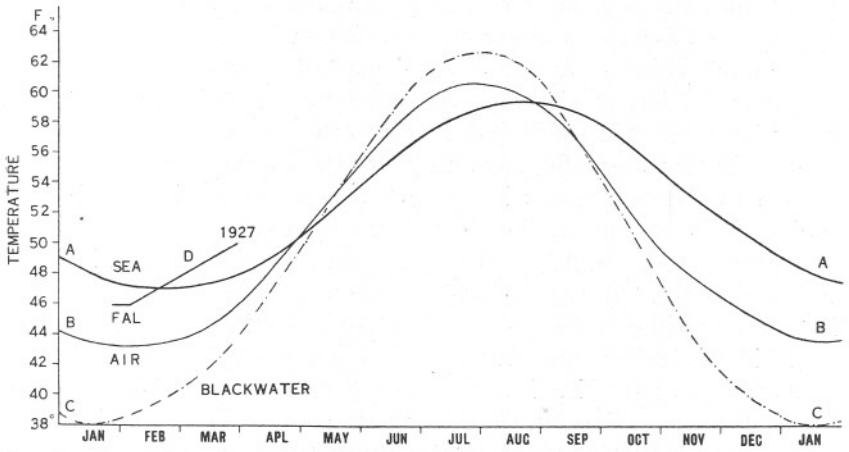

FIG. 9.—Comparison of mean air (from monthly means for a period of thirty-five years) over the Fal Estuary (B) and the River Blackwater (C) and mean surface sea-temperature (A) one mile off the entrance to Fal Estuary for a period of thirty-six years (1872–85, 1894–1915), with observations of sea-temperature (D) in the spring of 1927 over the Upper Fal Estuary oyster beds.

consideration of Fig. 9, above, which shows mean monthly air-temperatures at Falmouth and over the Blackwater beds (for 35 years from *Book of Normals*) (**7**), and monthly means of surface sea-temperature about 1 mile off Falmouth Harbour for the periods 1872–1885, 1894–1915 (**8**). It is known (**4**, p. 213) that on shallow beds such as those on the Blackwater and off Whitstable that mean sea-temperature in winter follows very closely the mean air-temperature with scarcely any lag; but on the Fal, owing to the existence of the deep Channel through the beds and the direct flow of tidal water from the English Channel into the Fal Estuary, the water remains constantly warmer (in short period means) than the air throughout the winter. The difference between mean sea- and mean air-temperature, shown in Fig. 9, above, is, however, slightly greater than will exist on the Upper Fal beds because of the cooling effect of the admixture of River water. The observations in 1927, however, show that the water over the Upper Fal beds is, in winter, only slightly cooler than that just outside the harbour. Since the water outside this harbour

rarely falls below about 48°, only a short spell of continuous warm weather is necessary to raise the temperature to 50°. Now Mill (**9**) and Dickson (**10**) have shown that inshore temperatures in the British Isles are the same as those offshore in about April and September, while Helland-Hansen and Nansen (**11**) have shown that mean air rises *above* offshore temperatures in the *whole* of the region of the East Atlantic about April and falls below again at about September (see also Orton, **12** and **13**). These large-scale observations give reality to the facts that at some time about April and September mean air, mean offshore, and mean inshore temperatures are about the same, and that in inshore situations after September and before April mean sea-temperature will be the nearer to mean air the less the influence exerted by offshore tidal waters, e.g. Blackwater and Whitstable, but nearer to the offshore sea-temperature where offshore water influences an estuary by tidal mixing from a deep channel as Plymouth Sound, Fal Estuary (not River), and Firth of Forth.

Since it is established that inshore sea-temperature will rise above mean air normally in April, it is clear from a consideration of Figs. 8, p. 389, and 9, p. 391, that the winter inshore temperature on the Upper Fal Estuary will only need to be raised about 3–4° F. to attain the level of 50° F. in April, whilst on the Blackwater the required increase of temperature is 10–12° F. Further, in spite of the fact that the temperature rises more rapidly on the Blackwater than on the Upper Fal, the observations in 1927 show that a temperature of about 50° is attained on the Upper Fal beds a few weeks earlier than on the Blackwater, and although the evidence available does not amount to proof, there can be little doubt that what happened in the spring of 1927 is usual and about the normal sequence of events. In a warm winter on the Fal, it is fairly certain that a temperature of 50° F. would be attained earlier than April, especially in the River, and in that case, if shell-growth is dependent upon the attainment of a sea-temperature of about 50°, shell-growth should occur as early as March in such a season on these beds.

In a review of the preceding discussion the following broad facts may be restated : (1) shell-growth begins on the Fal Estuary oyster beds at least some weeks earlier than on the Blackwater oyster beds, and correlated with shell-growth on both sets of beds is the attainment of a temperature slightly above, but not less than, 50° F. on the Fal beds, and a similar or slightly higher temperature on the Blackwater beds, and further that there is every probability that these are normal phenomena.

It is therefore justifiable to assume that the attainment of a temperature slightly greater than 50° in the spring is an all-important factor in inducing shell-growth. It is not necessary to conclude for the present that the attainment of a temperature of about 50° is in itself sufficient to produce the normal kind of growth which occurs on the oyster beds,

as there may be other important factors dependent upon temperature which are necessary before growth can occur. Nevertheless, such evidence as is available indicates, as will be shown later, that providing an oyster be healthy and has even quite small reserves of food material, it will grow shell under the foregoing conditions. I have, indeed, shown (**13**, and several times since) that oysters kept in sterile water in a warm room in March will grow thin papery shoots of shell before growth has begun on the beds, but it still remains to be proved that this kind of shell-growth is the same as that which occurs normally on the beds in spring. A similar kind of thin papery shell-growth may occur in summer in oysters moved from one environment to another entirely different, as from the beds to oyster pits or laboratory tanks. In the latter case it would seem not improbable that the change in salinity alone serves as a stimulus to shell-deposition, but such shell-material as is laid down in tanks is abnormal and apparently pathological, as it is generally accompanied by a puckering of the mantle folds and the formation of blisters or partial chambers. Similar slight shell-shoots have been observed in oysters moved from one part of the beds to another in summer, and although this kind of growth can be regarded as abnormal, it nevertheless indicates that some kind of change (including starving) in the environmental conditions may stimulate individuals to deposit calcareous material, and suggests that a marked change of some kind in the general conditions may be the stimulus causing the normal general outbursts of growth previously described. Experiments on this problem will need to be interpreted very carefully and ultra-critically.

In the autumn of 1926 shell-growth on the Fal began when the temperature over the beds generally fell to about 60° F. On September 29 the temperature was practically homothermal at 59·8°; on October 1, 60°–60·3°; October 2, 59·7°; on October 6 and 7, warm days, 60·7°–61·7°; October 11, 59·3°–58·8°; October 12, 59·2°–59°; October 19, 54°–56°. In 1927 on the Fal shell-growth did not begin until after the temperature over the beds had fallen below about 57° F. On September 29 the water was practically homothermal at about 56·0°; on October 5 temperatures on the beds varied close on 57°, on October 6, 56°–58°; October 12, 56·2°–57·0°; October 19, about 56·2°. During this period in 1927 the oysters were feeding actively and mainly on *Prorocentrum micans* on all parts of the beds. In the same period in 1926 no records were made of feeding conditions, but there is not the slightest doubt that feeding occurred actively also during that autumn period.

The onset of shell-growth in 1926 occurred when the breeding season was completed, but in 1927 the conditions with regard to breeding were peculiar and abnormal (see **22**). In that year effective breeding ceased—as will be shown later owing to the low temperature conditions—about

the middle of August, but ripe females in the high proportion of 10–18% persisted even in early October, when general growth began, and 36% of these ripe females taken during October 11–19 grew new shell-shoots (see Table VI, p. 401).

These facts, while indicating that shell-growth begins at the end of the breeding season, also point to either a time rhythm coinciding with the normal end of the breeding season, or to some environmental conditions which supervene at about this period of the season. With regard to temperature in 1926 the burst of shell-growth occurred on the Fal when temperature was on the downward gradient and in the region 59°–61°–59° ; but in 1927 temperatures over the beds in September ranged from 58°–60° and as low as 56° at the end of the month, *during which period no new shell-growth appeared on the beds in the Upper Fal,* though it is possible that some had occurred on the beds in the upper reaches of the River. Thus the factor of the reduction in temperature to the definite level of 58°–60° F. is discovered to be insufficient alone to account for the production of the autumn shell-growth. There must therefore be some other factor or factors usually associated with the fall in temperature in the autumn which cause shell-growth, if indeed the rhythm observed be not a time factor.

On the Blackwater beds the temperature fell rapidly in September, 1927, fluctuated between 58° and 60° F. in the week ending September 24, fell to 56°–53° in the following three weeks, and afterwards decreased still further ; growth was first observed on these beds from a sample dredged on September 15. In the period September 12–17, daily H. and L.W. temperatures fluctuated from 59°–61°–59° with a mean of 59·8°. The incidence of growth over the whole of these beds was not, however, determined, but the beginning of shell-growth on these beds in the autumn of 1927 resembled that occurring on the Fal beds in 1926, and is consistent with the fact that significant breeding had finished on the beds at that time.

The additional factors which may be considered of prime importance in controlling shell-growth are food, salinity, light, and alkalinity, but there is not sufficient evidence available to discuss them fully.

(b) *Salinity variation.*

The delay in the onset of shell-growth on the Upper Fal Estuary beds until early in October, 1927, after a period of low temperatures in September, points to some other important factor or factors correlated with low temperature in producing shell-growth. Samples of water were obtained from the Fal Estuary whenever possible for salinity determination, and it is possible to discuss briefly the salinity variations on these beds during 1927. The salinity samples—and deep-water temperatures—were taken with a hand-worked Nansen-Petterson water-bottle made by Prof.

Knudsen and the salinity determined at the Government Laboratory by the assistants of the Government Chemist, to whom the writer is indebted for these results. Some of the results are shown in Table V, p. 396. The maximal salinities on the Upper Fal Estuary beds are obtained from the bottom water in St. Just Channel (see Fig. 2, p. 369). The minimal salinities are given by the column of water passing from the lower part of the River into the Channel at and about Turnaware Bar. The salinities over the Banks and the intervening Channel are intermediate between these maximum and minimum values, for the water flowing down Pill and Restronguet Creeks is normally negligible and only important after heavy continuous rains (see Fig. 2).

Table V on page 396 gives an indication of the variation in salinity over these grounds throughout the year, but the records, although taken nearly every week, are probably too few to be conclusive.* In the summer period, i.e. from the end of June, through July, August, and early September, the salinity as judged by the water entering the Truro Lake at St. Just Channel and the water on the bottom of the River was relatively high. At the latter station the water during this period was only less than 34·4 per mille on September 14th, but in the St. Just Channel was mainly 35·0 per mille, and as high as 35·2 on several occasions. In March the single series of observations made shows that the salinities at both these stations were low. The salinity on the East Bank was remarkably uniform at all states of the tide throughout the period of the observation except at L.W. on October 12. Low salinities at the bottom of the River station began to show on September 14 and persisted until October 5, and lower general salinities are also shown by the samples from St. Just Channel during the period September 14–October 19 except on October 5. New growth became general between October 5 and 12, some three to four weeks after the beginning of the indicated period of low salinity. No observations on salinity were made in 1927 on the Blackwater beds at the time shell-growth occurred, so that the relation of variation in salinity to growth on these beds in that year cannot be discussed.

The salinity on the Blackwater beds has, however, been examined at various times during the period June 1921, to October, 1924, and in 171 observations the means of maximal and minimal salinities were found to be respectively 34·0 and 34·53‰, with a range of 32·34–35·36, and a tendency for the lower salinities to occur during the winter.

These observations on salinity do, therefore, indicate that shell-growth,

* To obtain sufficient data on salinity variation in estuarine situations it is necessary in practice to be able to read salinities as one reads temperature. It will not be possible to do this until a device is found for reading salinities direct from the water-bottle. Such a device giving an accuracy of one part in 2,000 would probably serve. Ordinary hydrometer readings in a small boat in wet or rough weather are impracticable.

TABLE V.

SALINITY OBSERVATIONS (‰) AND BOTTOM TEMPERATURE ON THE RIVER FAL AND FAL ESTUARY, 1927.

(From Salinity Determinations by the Government Chemist, Government Laboratory, London.)

Station.[1] Locus of sample. 1927		St. Just Channel. (Depth, 15 fathoms) 0 to 2 f. from bottom.		St. Just Channel. (Depth, 15 fathoms) 1 f.[2].	East Bank. Depth, ½ to 1 f. bottom.		River. Depth, 8 to 8½ f. Bottom.		River. Depth, 8 to 8½ f. 1 f.[2]	State of tide approx.	Approximate lunar period.
Mar.	8	34·87	(*47·8°* f.)	33·87	—	—	33·69	(*47·8°* f.)	29·54	ca. L.W.	Mar. 10, 1st Qr.
,,	8	33·97[3]	(*48·0*)	33·11	—	—	—	—	—	ca. ½-tide	—
May	18	34·92	(*52·6*)	34·57	34·44	(*54·3°* f.)	34·75	(*53·5*)	32·94	ca. ½-tide	May 16, F.M.
June	8	35·03	(*54·1*)	—	—	—	35·01	(*54·3*)	33·22	L.W.	June 7, 1st Qr.
,,	15	34·82	(*57·2*)	34·68	34·71	(*57·8*)	34·17	(*58·8*)	33·87 (s.)	ca. L.W.	,, 15, F.M.
,,	22	35·15	(*54·4*)	34·65 (s.)	34·72	(*56·8*)	34·98	(*55·4*)	32·87 (s.)	ca. H.W.	,, 22, 4th Qr.
,,	29	35·04[3]	(*54·5*)	34·72 (3 f.)	34·78	(*55·6*)	34·13[5]	(*56·7*)	33·85	ca. L.W.	,, 29, N.M.
,,	29	35·04[3]	(*54·5*)	—	34·67	(*55·8*)	—	—	—	ca. ½-tide.	—
July	13	35·04[3]	(*58·0*)	34·9 (6 f.)	34·78	(*58·4*)	34·56	(*58·5*)	34·17 (s.)	ca. L.W.	July 14, F.M.
,,	20	35·04[3]	(*60·6*)	—	34·76	(*61·2*)	34·51	(*61·7*)	34·07 (s.)	ca. ½-tide	,, 21, 4th Qr.
,,	27	—	—	—	—	—	34·44	(*62·4*)	34·02 (s.)	ca. L.W.	,, 28, N.M.
Aug.	3	35·28[3]	(*58·4*)	35·12 (2 f.)	34·94	(*59·7*)	34·80	(*59·7*)	34·57 (3 f.)	ca. ½-tide	Aug. 5, 1st Qr.
,,	3	—	—	—	34·91	(*59·8*)	—	—	—	ca. ½-tide	—
,,	10	35·23[4]	(*62·6*)	—	—	—	—	—	—	ca. L.W.	Aug. 13, F.M.
,,	17	35·24	(*57·0*)	—	35·08	(*57·9*)	34·88	(*58·9*)	—	H.W. to ½-tide	,, 19, 4th Qr.
Sept.	14	35·00	(*57·9*)	34·77	34·31	(*58·5*)	33·63	(*58·6*)	33·44 (3 f.)	L.W. to ½-tide	Sept. 11, F.M.
,,	14	—	—	—	34·32	(*58·5*)	33·77	(*58·6*)	33·36 (4 f.)	after H.W.	—
,,	21	34·99[3]	(*58·2*)	—	34·06	(*59·4*)	33·78	(*59·3*)	33·76 (4 f.)	½-tide to H.W.	Sept. 18, 4th Qr.
,,	28	34·90	(*56·4*)	34·66 (2 f.)	—	—	—	—	—	H.W. p.m.	,, 25, N.M.
,,	29	34·68	(*56·3*)	33·85 (2 f.)	34·22	(*56·3*)	32·79	(*56·1*)	31·66 (4 f.)	ca. L.W. p.m.	—
Oct.	5	34·99	(*56·6*)	34·54 (2 f.)	34·43	(*57·0*)	34·88	(*56·7*)	34·21 (2 f.)	ca. H.W.	Oct. 4, 1st Qr.
,,	12	34·58	(*57·0*)	33·87 (2 f.)	33·65	(*57·2*)	32·32	(*56·6*)	30·86	ca. L.W.	,, 10, F.M.
,,	19	34·81	(*56·6*)	34·27 (2 f.)	34·05	(*56·3*)	34·64	(*56·6*)	34·05 (2 f.)	after H.W.	,, 17, 4th Qr.

The depths given for the stations are depths at low water ordinary springs. F.M.=full moon; N.M.=new moon.
Temperatures are given in degrees Fahrenheit in italics in brackets.

NOTES TO TABLE III.

[1] The Positions of the stations as follows are shown in Fig. 2, p. 369:—St. Just Ch.: Mid-channel on the boundary line W–X off Mesack Pt. East Bank Station: about the B in EB. River Station: slightly above the R nearest to Turnaware Bar.

[2] Unless otherwise stated when f.=fathoms, and s.=surface, i.e. bottle filled about 1 foot from surface.

[3] Samples taken above the St. Just Channel Station owing to bad weather about midway between the station and the bend of the Channel at the extreme west of the East Bank, in a depth of about 12 fathoms.

[4] Sample taken in the middle of the Channel opposite Pill Creek.

[5] At 4 fathoms; the bottom sample having been lost.

at least on the Upper Fal Estuary beds, was correlated with relatively low salinities as well as relatively low temperatures. There is, moreover, a general belief that shell-growth is due to, or favoured by, low salinities, but no critical evidence has yet been offered in explanation. The results given above will be referred to again later.

(c) *Food, Light and Alkalinity of the Sea-water.*

Three remaining factors, namely, food, light and hydrogen-ion concentration, remain to be discussed. Food may be necessary to maintain the organism in a state of physiological activity during a period of shell-growth, and although little is known of the actual quantity of food available on the Fal and Blackwater beds themselves, some indication of the probable concentration of food in the sea-water can be obtained from studies made in each case on neighbouring grounds. In 1916 Lebour (**14**) showed that off Plymouth Sound diatoms were as abundant in the spring at the end of March and in April as at any other time of the year, and conditions off the Fal are in all probability very similar to those off Plymouth.

In 1923–24 Savage (**15**) found in the water in Butley Creek fairly large numbers of diatoms in April, and small quantities of organisms in the stomachs of oysters from the Main Channel, Orford, in March and May, 1923, and April 30, 1924, but nearly empty stomachs at the same time in oysters from Butley Creek. Fortunately Savage gives temperature and density records for Butley Creek. If Savage's temperature records be plotted against the feeding activity, i.e., total volume of food ingested, and the total volume of organisms ingested per oyster per month, and also the total volume of organisms caught in the nets per month, all at Butley Creek, there is *a strong indication* that active feeding does not begin until a temperature about 50° is attained in the sea-water—in spite of the presence of abundance of food—and also that feeding diminishes almost to zero soon after the temperature of the sea falls below about 50° F.

It is therefore not at all improbable that the beginning of feeding and the beginning of shell-growth in the spring are both dependent upon a temperature of about 50° F.* Additional *ad hoc* investigation would probably soon furnish critical data on the problem, and observations

* Since writing the account given above I found in Weymouth's paper on the Life-history and Growth of the Pismo Clam (Fish Bulletin, No. 7, State of California Fish and Game Commission, 1923), a reference to work by Belding (A Report upon the Scallop Fishery of Massachusetts, Boston, 1910) who has shown that growth in *Pecten irradians* " is confined to a period in which the temperature rose above 45° or 49° F." I have not yet seen Belding's original paper, but the graph given by Weymouth, p. 33, indicates a temperature level of about 50° F. as the lower limit for shell-growth in this species.

in the field, such as those made by Savage and Nelson (**16**), are more likely to yield satisfactory evidence than experiments conducted only in a laboratory.

It has already been mentioned that during September and in early October in 1927, definite observations were made that the oysters were feeding actively, and mainly on the Peridinian, *Prorocentrum micans*. During September, 1927, the oysters on the Blackwater were also feeding actively, but on several species of diatoms which were not specially noted.

An autumn maximum of diatom growth is well known, and is shown by Lebour (**14**, 1917) off Plymouth Sound, a locality near to and probably showing similar seasonal variations to the Fal Estuary. Savage (**15**) obtained similar indications of maximal growths of diatoms in Butley Creek and the Main Channel of the Orford River in the Thames Estuary in August to October, and the Orford River is sufficiently near the Blackwater to serve as a guide to the probable conditions on the Blackwater. There is therefore a strong probability that at about the period of the autumn shell-growth on both the Upper Fal and the Blackwater beds there may occur a heavy crop of diatoms or peridinians, Thus on the Upper Fal beds, both in the spring and the autumn in 1927, the factors correlated with shell-growth are relatively low temperatures, i.e. between 50°–60° F., relatively low salinities (more certain in the autumn than the spring), and probably abundant food. On the Blackwater beds at the same time the only certain correlations are relatively low temperatures, and a good supply of—or abundant—food.

An indication that light might be an important factor was obtained in the warm room experiments mentioned above, where one bell-jar situated in a dark position, but otherwise like three other jars being used at the same time, contained oysters which showed no growth, whereas growth occurred in some individuals in each of the other jars. With regard to the conditions of light on the beds in the spring and autumn, nothing can be stated except that there is a probability that somewhat similar intensities may occur at about the periods of spring and autumn shell-growth on the Fal. It is however unlikely that the intensity of light on the Fal beds in early April is as great as on the Blackwater beds in early May.

No observations on the pH of sea-waters were made during the course of these investigations and relatively little of a definite character is known of the range of variation of the factor in estuarine waters (see **13**a). In the English Channel Atkins (**29**) has shown that pH varies only slightly throughout the year, but tends to be high in correlation with sunshine—and probably photosynthetic activity ; and further, that a greater range of pH occurs in inshore situations, as at L1 in Plymouth Sound, than in the more open waters. In the latter

situation, and probably other estuaries, the lowest pH values occur in the winter period when also low salinities prevail.

It would appear, therefore, that shell-growth in *O. edulis* begins in the spring when the water is relatively less alkaline, and that growth ceases when a higher degree of alkalinity may be expected to occur (see **18**). In the autumn, however, shell-growth begins when pH may be expected to be relatively high as compared with that existing at the onset of growth in the spring. In the absence of information regarding the actual process of deposition of calcium carbonate in the oyster, as well as definite correlated seasonal field observations on pH, it is not possible to estimate fully the importance of pH as a factor in shell-growth ; it is however not impossible that a relatively high alkalinity may be inimical to and a limiting factor of shell-growth in *O. edulis*.

(d) *Tides.*

The relation of the beginning of the shell-growing periods to the spring or neap tides may be important. In 1926, on the Fal, good shell-growth was first obtained on April 21 (see Table I, p. 372) during the neaps succeeding the big new moon tides, April 11–16, but the grounds had not previously been systematically examined, and growth may be estimated to have begun either during these latter spring tides or on the preceding neaps. In 1927 on the same beds good shell-growth was first obtained on April 12, towards the end of the neap tides, without previous systematic examination, and growth might have begun on the preceding big spring tides, April 1–6, but more likely—from the size of the new shoots on April 12 (see Table II, p. 373)—at the end of these spring tides. In the autumn period in 1926, on the Fal, the first signs of slight new growth were observed during the full moon spring tides, September 21–25 (see Table I), but growth probably only became general during the following neaps, September 27 to October 6. In 1927, on the Fal (see Table II), growth was definitely found to begin during the first few days in October in the middle period of the set of slack tides, September 30 to October 7, on Turnaware Bar and Parson's Bank, but later during the following spring tides, October 9–14, over the beds generally. Nothing is known of the relation of general shell-growth to the tides on the Blackwater beds. Thus, from the information at present available on this subject, it would appear that shell-growth may begin and become general either during neap or the spring tides.

(e) *General condition of the Oyster Individual.*

In discussing the occurrence of new shell-growth in the spring and autumn, the general condition of those oyster individuals which do

actually exhibit new shell-growth must be a factor of primary importance. It will be important to know, for instance, whether growth only occurs in those individuals which have finished spawning and have accumulated reserve materials, or whether shell-growth occurs only in particular sex-conditions or in spent individuals, or, indeed, whether or not growth occurs in all these categories, and further, whether shell-growth occurs in the individuals in consecutive periods of growth. Since spawning occurs in the summer, certainly mainly outside and between the two periods of shell-growth, the problems stated above offer in a sense a method of investigating whether there exists an internal physiological rhythm correlated with shell-growth. During 1926 and 1927 the general physiological condition in oysters was studied, particularly with regard to sex, and from the experience gained thirty categories of individuals can now be recognised either at sight or with slight confirmatory microscopical examination of individuals. In this way it has been possible to follow through more than one season the series of physiological conditions passed through by various populations of oysters in that period. The categories of individuals recognised will be described fully later, but the general nature of those categories which showed a high percentage of shell-growth, and detailed in Table VI, may be noted briefly, so far as their relation to shell-growth is concerned. This table contains analyses of the physiological state of oysters from the Fal Estuary at the time growth began in the autumn of 1927, and it is a matter of great regret that similar comprehensive analyses are not available for the Blackwater beds. Categories 1–13 and 15–18 inclusive in Table IV are normal summer physiological stages in sexual condition, and consist of spawning or ripening or nearly ripe female-functioning individuals and ripe or ripening males respectively. Owing to the occurrence of cold-weather conditions in and near the Fal Estuary in 1927, category 4, ripe female-functioning individuals, and Nos. 15–16 (some Nos. 17–18), ripe, or nearly ripe, male individuals, failed to spawn during the summer and persisted in high proportion during October and November. The remainder of the categories are spents (Nos. 23, 24, 26, 19, 20), recovering spents (Nos. 23a, 26b, 29, 30), or individuals which have begun again to develop, male or female, gonadial products after spawning (Nos. 27, 14, 14a, 17, 18). Category 22 of females which have failed to spawn a large proportion of their eggs is present in unusually high proportion, and category 21, of individuals which have passed into the male phase after spawning as females, is also present in high proportion for the time of the year. For the purposes of the present paper it is sufficient to note (1) that shell-growth occurred in a high proportion in all categories except Nos. 29 and 30, in which relatively few individuals occur; (2) that the percentage of individuals showing growth is highest in categories

TABLE VI.

ANALYSIS OF SAMPLES OF *O. EDULIS* FROM THE UPPER FAL ESTUARY BEDS IN OCTOBER–NOVEMBER, 1927, SHOWING PROPORTION OF DIFFERENT CATEGORIES OF INDIVIDUALS WITH NEW SHELL-GROWTHS.

Category. No. of.	Description of.	Samples, October 11–19, 1927. Total individuals.	No. with new shell-growth.	% with new shell-growth.	Samples, October 20 to November 22, 1927. Total individuals.	No. with new shell-growth.	% with new shell-growth.
1	Whitesick	2	1	–	0	0	–
3	Blacksick	2	0	–	3	1	–
4	Fully ripe ♀[1], ducts full	114	41	36	67	46	69
6	,, ,, ,, not full	4	2	–	2	1	–
8	Almost ripe ♀	5	0	–	1	0	–
9–12	Developing ♀ type	0	0	–	0	0	–
13	,, ♂ (♀) type	2	1	–	0	0	–
14	Gonad becoming ramose	61	34	56	57	49	86
14a	Gonad distinctly ramose	1	0	–	6	6	–
15	Ripe ♂ gonad v.w. developed	6	0	–	2	2	–
16	,, ,, mod. developed	31	11	35	11	9	(82)
17	As 15, nearly ripe	18	3	16·6	6	5	(83)
18	As 16, nearly ripe	26	12	46	28	25	89
19	As 15, nearly spent	2	0	–	2	1	–
20	As 16, trace of maleness	125	43	34	69	51	74
21	Ripe ♂, post ♀-spawning	67	35	52	21	12	57
22	Incompletely spent ♀	145	48	33	85	42	49
23	A spent type	18	4	22	1	0	–
23a	Slightly recovering spent	77	23	30	59	45	76
24	Spent ♀ type	61	20	33	51	40	78
25	Pathological	6	0	–	3	0	–
26	Resting spent	62	18	29	52	37	71
26a	Recovering spent (a)	0	0	–	8	8	(100)
26b	,, ,, (b)	108	30	28	79	48	61
27	Gonad in 1st stage of dev.	89	50	56	102	71	69
28	Type 22 with ripe sperm	6	2	–	2	2	–
29	Very fat (a) gonad quiescent	16	1	–	5	2	–
30	,, (b) ,, ,,	9	0	–	22	6	27
	Totals and Averages	**1063**	**379**	**35·6**	**744**	**509**	**68·5**

[1] The symbol ♀ is here used in the sense of female-functioning.

14 and 18 in the later period, October 20 to November 22, and in Nos. 14, 18, 21, and 27 in the earlier period, October 10–19; (3) that growth occurs in a high proportion of ripe female-functioning forms, Nos. 4 and 6, and of ripe males, Nos. 16 and 21.

A broad review of the results given in Table VI shows clearly that particular physiological condition is relatively unimportant as regards shell-growth. Nearly all types show a high proportion of growth, though undoubtedly types 27, 14, 18, and 21 are in such a physiological state that growth occurs rapidly, and apparently at once when external conditions become suitable. Growth in oysters from the Blackwater beds in the autumn of 1927 was also first observed in categories 27 and 14.

It is seen, therefore, that although shell-growth begins earliest in individuals in certain physiological states, yet individuals in nearly all the diverse conditions which occur in the autumn do, in fact, grow shell-shoots in high proportion. Thus it would appear that variation in physiological state in the autumn—apart from environmental conditions—is a factor of minor importance so far as shell-growth is concerned. It must be borne in mind, however, that the summer categories, Nos. 1–3, 5, 7–13, are rarely present in the autumn. In the spring very few analyses for physiological state in samples showing shell-growth have been made, but it is known that on the Fal the categories would be similar to those existing in late autumn, but on the Blackwater beds the conditions are somewhat different. During the spring the categories shown in Table VI, p. 401, all develop in such a way that at the beginning of the breeding season 90% of the individuals will fall into categories 1–13 and 15–18 inclusive. On the Fal this period of gonad growth is slow, but on the Blackwater is rapid. Thus on the Fal the spring shell-growth is well established before gonad-growth is well advanced; on the Blackwater shell-growth and gonad-growth occur rapidly and simultaneously. For example, on May 31, 1927, among a sample of 107 individuals from Thornfleet (Blackwater beds), 87 showed new shell-growth and 102 fell in the summer categories noted above. In these cases of advanced gonad-growth the shell-growth had begun in earlier phases (of gonad-growth, mainly Nos. 27, 14, 14a, which appear rapidly in the spring) than were shown at the time of examination; but as the shell-growth was new, it must have occurred simultaneously with some late phases in the development of the gonad. Moreover, the occurrence of shell-growth in the ripe categories, Nos. 4, 6, and 16, as shown in Table VI, shows that deposition of shell is not inconsistent with a *fully* developed gonad. There is not, however, clear proof from the Blackwater oysters—and little indication from the Fal samples—that the later stages of development of the female gonad are accompanied by shell-growth, although proof exists that such growth occurs in equivalent stages in the male phase. Indeed, the absence of

shell-growth during the summer period when the female gonad stages 1–13 are abundant, and the occurrence of growth in the autumn—when these same stages are absent—and in the spring—when these stages are absent or beginning to appear—indicate that the physiological state during the ripening of the female gonad is antagonistic to that coexistent with shell-growth. The weight of evidence for the occurrence of such an antagonism is so great that it is not seriously shaken by the occurrence of well-developed female gonads with recent shell-growth in such a situation as the Blackwater, where the period of spring shell-growth is known to be a short one and rapidly followed by the breeding period.

The observations on physiological state during the spring and autumn periods of shell-growth show, therefore, that new shell may be laid down in almost any state, but new shell is deposited least in two categories : one in which individuals are laying down (glycogen ?) reserves, and the other consisting of individuals in the later stages of ripening a female-functioning gonad. The latter category is, however, only produced in the breeding season, at the end of the spring shell-growing period, and rarely in the beginning of autumn shell-growing period. These observations in turn indicate strongly that the cause of shell-growth must be sought for not in any particular one of the internal physiological states noted, but in the effect of external conditions on that general physiological state which occurs outside the breeding period.. Hence two main physiological states may so far be recognised, namely, the breeding, and the non-breeding or shell-growing, physiological states.

(f) *The accumulation of reserve Food-products.*

The relation of the seasonal phase during which an accumulation of reserve food-products occurs to the period in which shell-growth takes place is worthy of special attention. The condition of fatness, which in *O. edulis* is that state in which food-material is stored up for future use in the form largely of glycogen and other carbohydrates, is usually attained in the autumn and maintained through the winter. Although the degree of fattening can be recognised by the naked eye by the degree of development of the whitish to yellowish creamy homogeneous and somewhat translucent glycogenous vesicular tissue, it is difficult to obtain real comparative values to express fatness without chemical analyses of similar categories of individuals of about the same age, but it will be shown that useful information can be obtained from relative weight of equivalent individuals. Chemical analyses of oysters throughout the season of 1919 (Russell and Government Chemist (**17**), 1923) have shown that glycogen and carbohydrate, and to a less extent protein, increased during the autumn in the percentage dry weight of oysters

from the Thames Estuary, and especially from Whitstable. Fattening does not occur in any locality equally well every autumn, and may be generally poor in some localities; but oysters off Whitstable fatten probably as regularly as anywhere, so that the analyses made in 1919 are of considerable value, and can be used, with some reserve, in general discussions. Similar analyses made in conjunction with a comprehensive investigation of breeding and shell-growth would, however, now have a much greater value.

On the Fal Estuary beds (excluding the River beds) oysters did not fatten generally appreciably in September in 1926 and 1927, but signs of fattening began to show on Parson's Bank (Sept. 20, 1927) and over most of the beds in October (1926–27), and became more evident in November and December (1924–27). But fattening on the Fal beds is apparently not usually good in comparison with the better fattening beds in the Thames Estuary, and certainly attains a maximum value normally later in the year—in late autumn or even in early winter—than on the beds off the East Coast.

In the samples analysed for Table VI only a little fattening had occurred. The types which are just beginning to show fattening and which will continue to fatten are 23a, 26b; these types have no developing gonad. Types 27, 14, and 14a, have a gonad developing in the early stages, and may or may not show fattening. Nos. 29 and 30 are very fat oysters with no developing gonad or with a quiescent male gonad. It is a striking fact that all categories of healthy individuals, including those showing early signs of fattening, show a high percentage of growth except categories 29 and 30, the very ones showing the highest degree of fattening. The total number of individuals in categories 29 and 30 is, however, small, being only 52.

There is therefore an apparent antagonism between excessive fattening and shell-growth, but none between gradual fattening and shell-growth. The antagonism between excessive fattening and shell-growth is shown in all those oysters which have been defined as dumps (Orton, **4**, pp. 201 and 203, and Orton, **1**, p. 69); but in these forms the condition of fatness is almost permanent, and even spawning individuals may remain relatively fat after extruding a normal batch of eggs. For these reasons the dumpy oysters are regarded as being physiologically pathological, and need not be further considered here.

On the Upper Fal Estuary—excluding the River—beds, therefore (in 1926 and 1927, and partly 1924 and 1925), shell-growth occurred simultaneously with only slight fattening, and the process of fattening was continued after the shell-growing period. The years and localities of observation are mentioned specially, as it is not improbable that variations may occur under special and unusual conditions.

On the Blackwater in 1927 the types which show early stages of fattening appeared on most of the beds about the middle of September and increased afterwards, during the shell-growing period. On one bed, namely, Thornfleet, however, on September 13, it was found that an extraordinary fattening had occurred throughout all the types of oysters indiscriminately. Previously on August 2 all types of oysters on this bed were found to be in very good condition for the time of the year with regard to food-reserves, and this was the case even in the male phases following recent female-spawning.

In this case therefore fattening had occurred clearly before the beginning of the shell-growing period and during the breeding period, as none of the individuals showed on September 13 any new growth; but a sample from the same bed on October 19 showed the same kind of fat fish with new but hardened shell-growth, and a confirmatory sample on November 23 showed the same features.

TABLE VII.

COMPARISON OF APPROXIMATELY SIMILAR OYSTERS FROM TWO R. BLACKWATER BEDS DREDGED ON THE SAME DAY, DEMONSTRATING DIFFERENT DEGREES OF FATNESS. SEPTEMBER 13, 1927.

	Thornfleet bed.	South Shore bed.
Number of oysters	21	22
Length of shell	63·1 mms.	64·8 mms.
Height of shell	65·0 ,,	65·0 ,,
Estimated age (average)	4·2 years	4·2 years
Weight of fish	8·56 grams	6·07 grams
Volume of fish*	7·52 c.cs.	5·32 c.cs.
Specific gravity (approx.)	1·14	1·14
Gonad condition of development	1st stage (G.D. St. A)	1st stage (G.D. St. A)
Potential Sex	Undifferentiated	Undifferentiated

* The mean approximate volume of the oysters was determined in the following manner: The flesh of each individual was carefully freed from the shell and dried quickly with a minimum loss of blood on good blotting-paper to remove the sea-water adhering to the surface of the body. Each individual was then dropped into a measuring cylinder containing a known amount of sea-water, and the cylinder shaken at the same time to release any adhering air bubbles. After all the oysters in the sample had been added to the water in this way the volume of the water and oysters was noted, and that of the oysters found by deducting the volume of water added in the first place. When weights of oysters were taken the rough-dried meats were first added to a weighed glass beaker and afterwards added along with the exuded blood to the cylinder containing sea-water. The mean volumes found will be low, owing to unpreventable loss of blood by the method adopted, which, in the circumstances, had necessarily to be one which could be quickly and easily performed.

Breeding records for Thornfleet in 1927 show that towards the end of August most of the population had passed their spawning stages, and only a few per cent of individuals remained with gonads in ripening phases, so that the condition of the population was similar to that of the Fal oysters in the middle of September, 1925 (see Orton, **6**, Fig. 3, p. 210). It is an interesting fact that breeding conditions were approximately similar at the same time on the other Blackwater beds, but nowhere was there any extraordinary fattening at this time except on the Thornfleet bed. In order to obtain a definite expression of the difference between the Thornfleet and other oysters, e.g. South Shore beds, a number of individuals in an equivalent state with regard to gonad development were measured, weighed, and their volume evaluated (see footnote to Table VII) with the following results, stated in averages. The same kind of difference in fatness as is demonstrated in Table V was, however, present in all types on these two beds at this time of the season.

It is clear, therefore, that (1) fattening occurred before shell-growth and in the final stages of the breeding season on the Thornfleet beds, and (2) that conditions were different and more favourable for fattening on the Thornfleet beds during August and early September in 1927 than on any other of the beds noted at the same time, namely, South Shore and North Shore (Flat ground) beds. An examination of samples in October, however, showed that the South Shore oysters had then fattened nearly as well as the Thornfleet individuals, but that the North Shore lot still lagged, as can be seen from the results given in Tables VIII and X, while shell-growth had occurred in the meantime on both these beds. On the South Shore grounds, therefore, fattening had occurred either contemporaneous with or—more probably—after shell-growth. It has been shown that all types of individuals may accumulate reserves of food, so that the average weights of equivalent individuals may be used as a rough index of fattening. The relative degrees of fattening on the Blackwater and Fal beds are shown in this way in Tables VIII, p. 407 ; IX, pp. 408–9 ; and X, p. 410.

In Table IX, p. 408, are given weights and other details of oysters examined from the Fal Estuary in October and November, 1924 and 1925 (samples 1–26), and for comparison samples from the Blackwater in September, 1927 (samples 28–31). The high weights of the dumpy oysters (samples 4, 5, 10, 16–21, 23, 24, and 26) are remarkable ; but as these individuals are not comparable with normal oysters, they need not be further considered here. Among the normal Fal samples only No. 2 of specially chosen large deep oysters, and No. 6, approach in average weights to those of the samples of similar age from the Blackwater, while No. 6 was taken in November, a month later in the season than any of

TABLE VIII.

COMPARISON OF THE RELATIVE FATNESS BY APPROXIMATE WEIGHT AND VOLUME OF EQUIVALENT CATEGORIES OF WELL-FATTENED *O. EDULIS* FROM THE BLACKWATER RIVER BEDS, OCTOBER, 1927, AND A SAMPLE OF *O. EDULIS* FROM HOLLAND RELAID OFF WHITSTABLE, MARCH TO NOVEMBER, 1927.

Number of Category[1]	South Shore. Oct. 12, 1927.				Thornfleet. Oct. 21, 1927.				Dutch, via Whitstable. Mar.–Nov., 1927.			
	Wt.[2]	Vol.[3]	Age.[4]	No.	Wt.[2]	Vol.	Age.	No.	Wt.[2]	Vol.	Age.	No.
4	–	–	–	–	13·9	12·2	5–6	1				
	–	–	–	–	13·3	11·7	4–5	1				
6	10·5	9·2	5–6	1	–	–	–	–				
8	15·0	13·2	7	1	8·8	7·7	5?	1				
	11·6	10·2	6	2	10·5	9·2	4–5	1				
14	9·3	8·2	6	1	9·7	8·5	4·8	17				
	7·3	6·4	5	8	–	–	–	–				
	5·9	5·2	4	5	–	–	–	–				
14a	10·1	8·9	6	4	17·9	15·7	6	1				
	10·8	9·5	5	3	11·5	10·1	5–6	5				
	–	–	–	–	8·0	7·0	4–5	6				
15	–	–	–	–	9·4	8·2	4–5?	1				
16	–	–	–	–	8·2	7·2	4–5?	1	6·5	5·7	4	1
17	10·5	9·2	5	1	–	–	–	–				
18	–	–	–	–	10·5	9·2	5?	1				
20	8·5	7·5	5	3	7·3	6·4	4–5	1	4·7	4·1	4	4
	5·6	4·9	4	2	–	–	–	–				
21	9·3	8·2	5	2	–	–	–	–				
	4·8	4·2	4	1	–	–	–	–				
23	9·3	8·2	5	3	7·1	6·2	4–5	1				
23a	8·2	7·2	4–5	2	7·3	6·4	4·5	5				
24	8·2	7·2	5	2	8·2	7·2	5	1	3·8	3·4	4	43
	5·9	5·2	4	2	–	–	–	–				
26	10·5	9·2	6	1	9·3	8·2	4·7	3	5·2	4·5	4	44
	9·3	8·2	5	2	–	–	–	–				
	5·6	4·9	4	13	–	–	–	–				
26b	8·6	7·5	5	11	10·3	9·0	4–6	20	7·7	6·7	4	1
	–	–	–	–	8·1	7·1	4–5	8				
27	11·9	10·4	6	6	10·3	9·0	4·8	13	5·4	4·8	4	7
	9·6	8·4	5	6	–	–	–	–				
	7·1	6·2	4	4	–	–	–	–				
29	13·9	12·2	6	1	15·6	13·7	6	1				
	14·1	12·4	5	3	9·9	8·7	5	4				
30	–	–	–	–	10·3	9·0	5	8				
	—	—	—	—	—	—	—	—	—	—	—	—
Averages	**8·7**	**7·6**	**4–6**	**90**	**9·85**	**8·55**	**4–6**	**101**	**4·65**	**4·1**	**4**	**100**

[1] The categories are the same as in Table VI, p. 401.
[2] Weights are approximate, in grams, and calculated on the volume from density=1·14.
[3] See page 405 for the method used for estimating the volume.
[4] In years, in range or averages.

TABLE IX.

COMPARISON OF THE RELATIVE FATNESS OF NORMAL AND DUMPY *O. EDULIS* FROM THE FAL ESTUARY, 1924 AND 1925, AND *O. EDULIS* FROM THE BLACKWATER RIVER, SEPTEMBER, 1927, AND FROM OTHER LOCALITIES.

No. of samples.	Date.	Locality.	No. of oysters.	Mean length in mms.	Estimated average length.	Mean height in mms.	Estimated age in years.	Wt. of flesh in grs.	Physiological State. v. fat or fattening.	Gonad dev.	Ripe ♀.	Ripe ♂.	Spents and resting stages.
	1924												
1	Oct. 24	Falmouth N. Bk.	31	66·2		67·0	4	5·3	–	–	–	–	mainly
2	,, 23	Vilt Bank	5	83·0		80·8	6 to 7	9·7	5	–	–	–	–
	1925												
3	Nov. 10	East Bk.	12		ca 70		5–6	7·36	2	5	–	–	5
4	,,	,, (D)	25			ca 62	>5	7·8	17	6	1	–	1
5	,,	,, (SlD)	12			ca 64	>5	8·2	4	7	1	–	–
6	,, 12	Mylor Bk.	37		ca 70		5–6	8·45	7	3	1	2	24
7	,,	,,	10		ca 68		5	7·76	3	0	2	1	6
8	,,	,,	27		ca 65		4–5	5·12	4	2	1	3	17
9	,,	,,	25		ca 60		3–4	4·2	2	4	3	1	15
10	,,	,, (SlD)	39			ca 62	>5	6·58	22	0	2	1	14
11	,, 17	Turnaware Bar Edge	20	73·1		73·0	5	7·1	3	5	2	–	10
12	,,	,, ,,	12	68·0		69·0	5	6·4	4	3	–	–	5
13	,,	,, ,,	12	68·0		66·7	5	7·2	5	3	1	–	3
14	,,	,, ,,	13	65·3		68·5	4	5·26	5	4	–	–	4
15	,,	,, ,,	47	56·2		61·4	3–4	4·67	14	15		1	17
16	,,	,, ,, (D)	10	53·9		62·7	>5	8·57	all	–	2	1	
17	,,	,, ,, (D)	12	57·0		64·0	>5	7·61	all	6			
18	,,	,, ,, (D)	12	50·2		60·7	5 or>5	6·17	all	4	–	2	–

19	,,	,, (SlD)	12	54·4		62·0	>5	7·39	5	4		1	2
20	,,	,, ,,	24	60·0		64·0	>5	7·29	9	11	1	1	2
21	,,	,, ,,	20	53·2		60·4	5 or >5	6·04	12	6	–	–	2
22	,, 25	East Bk.	7		72–77		4–5	7·91	2	4	–	1	–
23	,,	,, (D, M.O.)	2	84		112	>5	16·7	2	–	–	–	–
24	,,	,, (D)	7		45–55		>5	8·12	5	2	–	–	–
25	Dec. 2	Mylor Bk.	8		65 to 82		4–5	6·2	1	2	1	1	3
26	,,	,, (SlD, D)	11	60		70	>5	9·96	6	5	–	–	–
	1927												
28	Sept. 13	Thornfleet Blackwater	21	63·1		65·0	4·2	8·31	–	21	–	–	–
29	,,	South Shore ,,	22	64·8		65·0	4·2	5·83	–	22	–	–	–
30	Oct. 12	,, ,,	90	–		–	4–6	8·7	See Table VIII				
31	,, 21	Thornfleet ,,	101	–		–	4–6	9·85	,,				
32	Nov. 25	Dutch via Whitstable	100				4	4·65	,,				
	1919–1920*												
33	April 2	West Mersea	50	–		–	–	5·37	Unknown				
34	Aug.-Jan.	,, ,,	50	–		–	–	6·13 to 8·17	,,				
35	April 9	Whitstable	50	–		–	–	5·96	,,				
36	July-Dec.	,,	50	–		–	–	8·28 to 8·75	,,				
37	April 23	Burnham	50	–		–	–	3·56	,,				
38	Aug.-Jan.	,,	50	–		–	–	4·21 to 5·93	,,				
39	April 15	Ipswich	50	–		–	–	7·45	,,				
40	Sept.-Dec.		50	–		–	–	6·17 to 8·49	,,				

* By Government Chemist (see Russell, 1923, p. 22). The details of shell-size and age are not known, but the age of the oysters probably ranged mainly from five to six years.

D=dumpy; SlD=semi-dumpy; M.O.=mud oyster resembling the dumpy type.

TABLE X.

COMPARISON BY VOLUME[1] AND RELATIVE APPROXIMATE CALCULATED WEIGHT[2] OF EQUIVALENT CATEGORIES OF *O. EDULIS* FROM BEDS IN THE UPPER FAL ESTUARY AND THE BLACKWATER RIVER, SEPTEMBER–OCTOBER, 1927.

Category of oyster. No. of	Description of	Parson's Bank. Fal., Sept. 20, 1927. Wt. (grs.)	Vol. (c.cs.)	Age (yrs.)	No.	Turnaware Bar Edge. Fal., Sept. 21, 1927. Wt.	Vol.	Age.	No.	East Bank. Fal., Sept. 22, 1927. Wt.	Vol.	Age.	No.
4	Ripe ♀, ducts full	16·0	14·0	6	2	6·8	6·0	4–5	8	12·0	10·5	6	1
		7·2	6·3	4–5	3	4·57	4·0	4	1	8·55	7·5	5	1
		5·7	5·0	3–4	3	–	–	–	–	5·13	4·5	4	1
		–	–	–	–	–	–	–	–	4·57	4·0	3	1
6	Ripe ♀, ducts nearly full	9·1	8·0	5	1	5·7	5·0	4–5	3	12·5	11·0	6–7	1
		6·8	6·0	4–5	1	3·42	3·0	4	1	9·1	8·0	5–6	1
		–	–	–	–	–	–	–	–	6·8	6·0	5	1
		–	–	–	–	–	–	–	–	4·0	3·5	4	1
8	Ca. ripe ♀ ducts empty	12·5	11·0	5–6	1	–	–	–	–	–	–	–	–
		7·4	6·5	5	1	–	–	–	–	–	–	–	–
15	Fully developed ripe male	–	–	–	–	11·4	10·0	5–6	1	–	–	–	–
20	Almost spent ♂'s	–	–	–	–	5·2	4·4	4–5	7	5·93	5·2	4·7	8
		–	–	–	–	4·57	4·0	3–4	4	–	–	–	–
21	Post ♀-spawning ripe ♂'s	–	–	–	–	5·36	4·7	4–5	7	–	–	–	–
		–	–	–	–	4·9	4·3	3–4	3	–	–	–	–
23a	Spents with a trace of fattening	–	–	–	–	5·25	4·6	4	8	–	–	–	–
		–	–	–	–	4·0	3·5	3–4	2	–	–	–	–
24	Spents, tissues compact	–	–	–	–	4·27	3·75	4–5	8	–	–	–	–
		–	–	–	–	3·76	3·3	3–4	3	–	–	–	–
26	Spents, tissues loose	–	–	–	–	5·55	4·87	4–5	8	–	–	–	–
26b	As 26, beginning to fatten	–	–	–	–	–	–	–	–	7·64	6·7	5	3
		–	–	–	–	–	–	–	–	5·47	4·8	4	3
27	Recovering spent, dev. gonad, 1st stage	–	–	–	–	–	–	–	–	–	–	–	–

		North Shore. Blackwater, Sept. 17, 1927.				North Shore. Blackwater, Oct. 4, 1927.			
26	Spents, tissues loose	5·45	4·8	4	35	5·35	4·7	4·3	10
26b	As 26, beginning to fatten	–	–	–	–	6·95	6·1	4·5	20
27	Recovering spent, dev. gonad, 1st stage	–	–	–	–	7·05	6·2	4·6	10

[1] See page 405 for the method used for estimating the volume.

[2] The weights are calculated from observed volumes on the assumption that the specific weight is constant at 1·14.

the Blackwater samples. These results, along with those given in Table VIII, therefore show that fattening occurs later in the season on the Fal than on some of the Blackwater beds, namely, South Shore and Thornfleet.

The foregoing figures with regard to weights and volumes of oyster meats of different ages and conditions—with regard to gonad development—give some idea of the difficulty experienced in expressing fatness. There is no doubt that fattening is a process which occurs normally outside the breeding phase, nevertheless it is clear that under the special and peculiar conditions in Thornfleet in August–September, 1927, fattening began while breeding conditions were still favourable, but when most of the oysters had spawned and passed into various post-spawning phases. (The conditions in Thornfleet, 1927, are discussed more fully on pp. 420–423.)

The relation of the shell-growing to the fattening period can now be reviewed from the information available. In 1925–27, on the Upper Fal Estuary beds, it is certain that fattening—as a general phenomenon on the beds—occurred in November–December, after a general period of shell-growth at the end of September–October, and there is every reason to regard this as the normal sequence of events. In 1927, on the Blackwater beds, the sequence of general shell-growth and fattening was the same, except that on the Thornfleet beds fattening occurred in the period August to early September, and shell-growth during the period middle of September to early October. There is evidence that fattening is antagonistic to shell-growth, and some evidence that individuals which fatten well during a period of shell-growth do not grow shell during that period. Fattening may therefore begin at any time in the season towards the end of the breeding period, and continue into the early winter according to local conditions with an interrupted period for shell-growth about September.

(g) *Body-growth.*

There is very little information for a discussion of the relation between a period or periods of body-growth—apart from increase in size of gonad—and the periods of shell-growth. There are, however, indications that a period of body-growth may occur in the resting phases, especially after spawning as a female. In these phases the tissues take on a loose appearance to the naked eye, due to the occurrence of clear tissue between the resting or the developing gonad. This appearance may persist even in a well-fattened individual. A few comparative estimations of early with later post-female-spawning phases (namely, of category 24 with 26 and 26b), shown in Table VIII, p. 407, especially in the sample of Dutch oysters from Whitstable, and Table X, p. 410, prove that body-size does actually increase at this period, i.e. during the post-spawning resting

period, but this may be due entirely to the enlargement of the vesicular cells.

For instance, in the Dutch oysters mentioned, 43 oysters in the early resting phase had an average volume of 3·5 c.cs., while 44 similar individuals in a later resting phase had an average volume of 4·8 c.cs. It is possible that an increase in body size occurs in other phases, but there is as yet no means of analysing such meagre data on the question as exist. The shell-space increases only at periods of shell-growth and increase in size of the body will always be possible after shell-growth. Probably in most cases permanent increase of size of the body tissues occurs at least in the fattening period after the autumn shell-growth, but the Thornfleet oysters (see Tables VII, p. 405, and VIII, p. 407) may have increased their body size before the autumn shell-growth in 1927.

On the probable Cause of Shell-growth in *O. edulis*.

The view has already been advanced that in whatever situation *O. edulis* occurs, it may be postulated that shell-growth will be caused normally by similar or comparable conditions, that is, that shell-growth is an automatic response in certain general internal to certain general external conditions. This thesis is capable of discussion, but will be generally accepted as being applicable to a well-defined species.

In the foregoing observations it has been noted that oysters in the Fal Estuary exhibit rhythmic shell-growing spring and autumn periods which are normally well marked off from the breeding period. On other estuarine oyster beds the known phenomena are generally similar; but on beds where there is a very rapid rise in temperature in the spring the shell-growing period may overlap the beginning of the breeding period, but in the autumn in all localities so far as is known the shell-growing period *normally* begins at, or soon after, the close of the breeding period. It has been shown that in the localities of the Fal Estuary and the Blackwater an outburst of diatom and/or peridinian growths occur in spring and autumn at about the time of shell-growth, and there is every reason to believe that similar outbursts of growth of oyster food will occur in all estuarine situations comparable with those on the Fal and Blackwater. It has been shown that on the Fal in 1927 low salinities probably occurred in the spring, and did, in fact, occur in the autumn, but that significant observations are not available for other situations. But since good shell-growth occurs in seasons when rainfall has been low, when there is little reason to suspect the occurrence of low salinities at about the shell-growing period—especially in the autumn—it would appear that shell-growth is not dependent upon—but may be favoured by—low salinities, for example, by reducing the pH value of the water. Experimental

observations indicate that a change of some kind in the environment of an oyster may provide a stimulus for calcareous deposition, and in this respect salinity may be important.

It has been shown that both on the Fal and Blackwater beds categories of oysters in most diverse physiological states grow shell in high to fairly high proportion during the shell-growing periods, while fattening may occur before, or during, but generally after, the shell-growing period.

In all cases, however, so far as is known, shell-growth occurs at relatively low temperatures. In the spring, growth begins when the temperature rises above the level of about 50° to 52° F. and in an environment where temperature rises slowly growth is completed before the breeding season begins. In the autumn growth begins at the end of the breeding season when the temperature falls below the level of about 60° to 57° F., and may continue until a temperature of about 52° is reached. Thus shell-growth occurs mainly outside the breeding season. It would appear, therefore, that the internal constitution of *O. edulis* is such that if healthy individuals are supplied with abundance of food at temperatures ranging from about 50° to 60° F., in an environment in which the temperature is either rising or falling, a general physiological state is assumed during which a phase of shell-growth will occur. As it can be shown that significant breeding in *O. edulis* may occur so long as the temperature of the environment remains above the level of about 59° to 60° F., and ceases when the temperature falls below this level, it would seem that in this mollusc there occur two main antagonistic metabolic states, correlated with environmental conditions, the one concerned in breeding, i.e., the final stages of development of the gonad and spawning, and the other, mainly in shell-growth, the accumulation of food-reserves and preparation of the gonad for the purpose of breeding. The different times of the year when shell-growth and breeding begin in the two chief beds examined (see p. 385) confirm the conclusion set out above.

On this view of the causes of shell-growth low salinities are not regarded as necessary for good shell-growth, but they may, nevertheless, contribute to that effect by either providing a stimulus towards shell-deposition, or by altering the temperature and/pH and favouring the growth of estuarine vegetable organisms, diatoms, and/or peridinians. It is certain that peridinians form one of the most important forms of food—and probably the most important one on some beds—for oysters in estuarine situations. Orton (**18**), and Marshall and Orr (**19**) have noted that certain species of this group appear to attain a maximum of development in conditions of low salinity. It is, however, possible that the sequence during a season (i.e. shell-growth followed by breeding and then by fattening and/or autumn shell-growth and fattening) may be to some extent established in a time rhythm—apart from any other consideration—or that shell-growth may

depend—in addition to those factors mentioned above—upon some other undetected factor. With the exception, however, of particular light and special pH conditions, neither a mere time rhythm nor an undetected recondite condition are regarded as probable factors controlling shell-growth from the information at present available. Further observations on so-called deep-sea oysters, and on the variation in shell-growth phenomena in very abnormal seasons, may nevertheless be expected to provide additional critical information.

Thus the facts available with regard to shell-growth in *O. edulis* warrant the conclusion that a temperature between 50° and 60° F. and abundance of food are the *most important* factors concerned. It may be assumed that the internal economy of the oyster will require a certain interval of time to become adjusted to changed temperature—and perhaps correlated—conditions, and that such adjustment will be easier in certain physiological states than in others ; for example, in normal autumn states, as in post-spawning resting and recovering spents such as categories 27 and 14 in Table VI, p. 401. These conclusions will, however, need to be tested by definite *ad hoc* investigations on shell-growth in different hydrographical localities and in different seasons.

Comparison of Types of Environment on Oyster Beds (of *O. edulis*.)

The conclusion arrived at in the preceding pages with regard to the cause of shell-growth may be partially tested from known facts with regard to shell size in *O. edulis*.

It is known that in the English Channel, the North Sea, the Bristol Channel off Swansea, and in the Solway Firth, oysters attain a relatively great size, but nothing definite is known with regard to their age or rate of growth, so that size may be merely an indication of great age. If, however, shell-growth, as herein concluded, occurs automatically between about 50° and 60° F. provided abundance of food be available, the large size of the shells of individuals living in such habitats as mentioned above may be attained at ages which are not relatively great, and the nature of the shell-shoots on these large oysters supports this view. It will be important, therefore, in this regard to review the activities of the oyster individual during its seasonal cycles in different localities. Evidence has been accumulated to prove that *O. edulis* does not spawn in English waters in significant numbers below about 59°–60° F., and that if the temperature falls below this level during the normal breeding season, spawning becomes abortive (**22**). It has also been found, as will be shown in later communications, that whereas in such a situation as the Fal Estuary percentages as high as 10, or higher, may continue to spawn,

even late in September, on grounds like the Blackwater River, a maximum number of individuals spawn in early and mid-summer, and relatively few individuals *normally* remain to spawn at the end of August and in September. There can be little doubt that this difference is bionomical, and is due primarily to the range and rate of temperature change. It is, indeed, probable that the conditions on the beds in the upper part of the Fal River itself will be found to resemble Blackwater beds, but it has not been possible yet to investigate these beds. On the Fal Estuary beds the rate of temperature change is slow and the range low, on the Blackwater the rate is rapid and the range relatively high ; as a result oysters mature slowly on the former grounds and rapidly on the latter, and, in fact, mature at different overlapping times on the Fal (see Orton, **4**), but more collectively on the Blackwater in normal seasons.

Moreover, it has been shown (Orton, **6**) that there occurs after the female-spawning stage a distinct resting stage, and there is evidence of a similar resting stage after an efficient male spawning. After a resting period the body fattens, i.e. reserves are accumulated and development of the gonad may begin again either at the same time as fattening, in the autumn or in the following spring.

Shell-growth is therefore bound up with all these activities, and it is possible to draw up tentative diagrammatic representations of these activities in different bionomical situations.

Fig. 10, p. 417, depicts diagrammatically the relation of the variation in the main functional activities of *O. edulis* in three types of environment. The graph A depicts mean temperature conditions on insular estuarine beds, such as those in the Thames Estuary. (The graph is drawn from temperature records on the Blackwater and Whitstable beds and smoothed from the mean air records for these regions for a period of thirty-five years (**20**) and the established relation of mean sea-temperature in these situations to mean air (**4**).) Graph A gives type A of environmental conditions, and represents those existing on most of the important beds in the Thames Estuary, and approximately those on the main Dutch beds and the French beds at Arcachon. The graph B, giving type B, so-called deep-sea or insular deep-sea conditions, is drawn from surface temperature observations at the Varne Lightship, 1906–1923, from data supplied and published by courtesy of the Hydrographic Department of the Ministry of Agriculture and Fisheries, London, and Knudsen (**21**) has shown that only slight differences in surface and bottom temperatures occur in this part of the English Channel even in the months of February and August. The functional activities associated with this type of environment are in the nature of predictions and explanations, supported however by general observation. Such conditions as are shown in type B may be expected on the rare deep-sea beds

in the North Sea, English Channel, and off Ireland, and the fattening ponds in Norway.

The graph C, representing type C, gives curious conditions intermediate between the insular estuarine and insular deep-sea types, and may be called the open estuary type; it is drawn mainly from temperature observations on the East Bank, Upper Fal Estuary, in 1926, a year when warm sunshiny weather prevailed. The curious flattening of the curve in August has been retained, as a reduction of temperature in August has been observed on these beds for the years 1926–27, and was also suspected in 1925, and further, was associated in 1927 with high salinity water ($35{\cdot}2°/_{\infty}$), so that the feature may be normal, and due to a seasonal tidal influence of relatively cold Channel water (Orton, **22**).

The conditions represented by type C may be expected to occur on banks at equivalent insular situations in those open estuaries in Ireland and Scotland which are influenced by semi-oceanic tidal water with similar hydrographic properties to that in the west of the English Channel. Oyster beds in the River Shannon, in the lochs on the west coast of Scotland and parts of the Firth of Forth, may be expected to conform closely to this type after allowance for latitude is made.

The environment on most of the European oyster beds can probably be compared with one, or a combination, of the types A, B, and C, but careful local observations are needed before many important beds or parts of the beds can be definitely placed.

In comparing the three types of environments shown in Fig. 10, it is seen that in both the deep-sea (B) and the open estuary (C) types oysters have long periods for shell-growth, gonad development, and fattening in comparison with the insular estuarine (A) type, but that while types A and C give long potential breeding periods, that of type B gives a very short one. In addition, type A, which yields very low temperatures, also gives very high temperatures during the breeding season, while type C gives moderate and type B very low temperatures during the breeding season. The fluctuations of maximum temperature in type B in August and September, as represented by the conditions in 1911 and 1917 respectively, vary from 63·3° to 55·9° F., and the conclusion is reached that in this environment oysters do not spawn at all in the colder years, e.g. 1915–1918. In the environment A it has been seen that the long breeding period at high temperatures permits the maximum of sexual development in normal and warmer years by about mid-summer, and leaves a portion of this period available for resting, and, if conditions are suitable, for fattening also before the beginning of the shell-growing period, when the population moreover have attained a highly uniform degree of physiological condition. In environment C the moderate temperatures attained during the breeding season do not suffice—except in very hot seasons—to complete

the spawning of all the individuals which develop during the summer, so that the shell-growing period is entered with individuals in a great variety of physiological condition. In this environment the potential shell-growing period is long in both spring and autumn. In the environment B

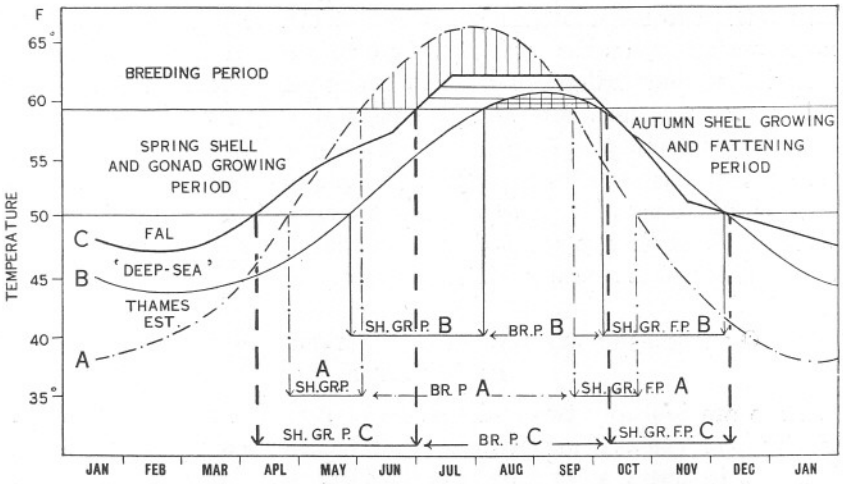

FIG. 10.—Diagrammatic representation of the varying periods of functional activities of *O. edulis* in three different types of environment controlled by rate and range of temperature variation.

Graph A represents mean sea-temperature over such *insular estuarine* oyster beds as occur in the Thames estuary. The graph is drawn from sea-temperature records on the Blackwater and Whitstable oyster beds, and is smoothed from mean air records for these regions for a period of thirty-five years (M.O. 214a, 1915) and the established relation of mean sea-temperature to mean air in these situations.

Graph B is drawn from surface sea-temperature records from the Varne Light-ship, English Channel, and represents the kind of temperature variation which occurs where so-called "*deep-sea*" oyster beds occur, e.g. English Channel, North Sea, Bristol Channel.

Graph C gives the temperature conditions obtaining in an *open estuary* influenced by sub-oceanic water. The graph is drawn mainly from temperature records made on the East Bank, Upper Fal Estuary, in 1926.

SH.GR.P.—A–B–C = Duration of spring shell-growing and gonad development periods respectively in A, B, and C types of environment.

BR.P.—A–B–C = Duration of breeding periods respectively in A, B, and C types of environment.

SH.GR., F.P.—A–B–C = Duration of autumn shell-growing and fattening periods respectively in A, B, and C types of environment.

The horizontal line at the level of 59° F. represents the approximate lower limit at which significant breeding, i.e. spawning, occurs; that drawn at the level of 50° represents the lowest limit at which shell-growth has been found to occur.

the breeding season is very short, and is preceded and followed by long periods, during which active and relatively uniform feeding may occur. In the warmer years in this type of environment it may be predicted that a heavy simultaneous spawning will occur, since a large proportion of

individuals will have had time to develop the gonad fully ; in the normal years a smaller proportion may spawn and leave a large proportion of the population fat and full of reproductive products. If these individuals in this type of environment do not experience a strong stimulus* to spawn abortively out of season (Orton, **22**), their metabolism will be such as will enable them to begin fattening at once ; and in the coldest years when no spawning occurs the spring shell-growing season will pass directly into the autumn shell-growing and fattening period, and all individuals will grow to a great size and become also very fat. It is, indeed, apparently the case that deep-sea oysters are generally large and generally unusually fat, as would be expected from the generalisations noted above. It has been noted that in type A the spring shell-growing period is a short one, and that so far as is known the spring shell-growth under these conditions is actually relatively slight.

On the probable Causes of Variation in Shell-size in *O. edulis*.

There are probably two main causes of variation in shell-size in *O. edulis* ; both causes being environmental, but one being due to situation in the environment, and the other to the nature of the environment itself. With regard to situation in the same or rather in approximately the same general environment, there can be little doubt that in the shallower situations, as on the Banks in the Fal Estuary and in the Fal River, or the upper parts of creeks as at Thirsleet, R. Blackwater, the shells of *O. edulis* of the same age are, on the whole, flatter and larger (in length and height) than in deeper situations near the same beds. In deeper water, individuals usually grow deeper and smaller shells than their neighbours in shallower water, e.g. Thornfleet as against Thirsleet (R. Blackwater) ; Parson's Bank Edge, and Trelissick Reach as against Parson's Bank (Fal Estuary and River). The difference is more obvious in the younger than in the older individuals. Definite measurements of inter-shell space are, however, needed to give, along with other measurements, mathematical expression to these differences. This difference in shape of shell must be due primarily to the manner in which the mantle is held during shell-growth. In shallow water the apparent tendency is to hold the mantle edges during shell-growth roughly parallel to the flat valve of the shell ; but in deeper water the left mantle is held so as to form a section of a hollow sphere which if produced would cut the plane of the flat valve ; so that whatever determines the way in which an oyster holds its mantle

* In estuarine situations proof has been accumulated that a maximum of spawning occurs at about the period of the spring tides. In such situations the variation in external conditions due to the tidal variation must be much greater than in deep-water situations, such as the English Channel. It is possible, therefore, that the tidal influence on spawning is weaker in the latter than in the former situations.

during shell-growth is the immediate cause of the shape assumed by the shell. To account for the manner of holding the mantle one probable factor may be suggested, namely, the rate of flow of the water over the shell. The habit of holding the mantle lobes nearly parallel is consistent with the adoption of a wide gape in feeding, and of holding the left mantle curved with a small gape in feeding. The more rapidly the water flows past an oyster the greater the amount of water brought in contact with it, and therefore where the food-content of the water is the same, the greater the amount of food brought into the immediate neighbourhood of the oyster—where the rate of flow is greater. Thus where other things are equal an oyster in more rapidly flowing water could obtain the same amount of food as one in less rapidly flowing water from a smaller amount of water, which can be obtained with a smaller gape of shell; therefore gape of shell may be related inversely to the amount of food in the water. Further, if the rate of flow of the water is great, there would be greater chances of large and unwelcome intruders being washed into the mantle cavity than if the rate of flow were small. In many shallow situations, as on the banks in a river or estuary, the rate of flow of water will be less than in the deeper water—in the channels, but in other shallow situations the mean rate of flow may be, but will usually not be, great. Thus the rate of flow of water over an oyster bed may determine the character of the shell-growth, and as a result the shell-size, but field observations in different environments correlated with shell measurements are required to obtain definite information. In this connexion it is interesting to record that on October 19, 1925, I obtained a *Gobius ruthensparri* in an oyster from the Falmouth North Bank. The fish had obviously been trapped and had had its tail cut off, or eaten off, after being gripped by the oyster in closing. Another oyster with a small Callionymus inside it was taken on the East Bank, Fal Estuary, on October 18, 1927. Both these cases prove that the oysters were gaping widely at the time these fishes entered the mantle cavity, but are nevertheless of little value for general consideration.

The second cause of variation in shell-size has been dealt with in the preceding section. An environment, such as the insular deep-sea environment, which in cold summers may permit growth throughout the spring, summer, and winter, or for long periods in the spring and autumn, will produce oysters of great size as compared with one having short periods only when shell-growth is possible.

On Physiological Antagonisms.

The observations on shell-growth and breeding on the Fal, supported by less definite work on other beds, point definitely to an antagonism in these two functions. There is also an indication, but less pronounced,

of an antagonism between fattening and shell-growth, and fattening and gonad development. It is suggested that the antagonism between growth and breeding may be a common phenomenon in marine animals (see Orton on Sycon and Grantia, **12**), and along with variation in the environmental conditions as herein indicated may go far towards explaining the variation in size exhibited by many marine animals in habitats in different situations and latitudes. It also follows that mean size of marine animals or mean weight of oysters at a given age may, and generally will, vary in different bionomical habitats, but would be expected to be the same in similar bionomical habitats, e.g. similar for oysters—and probably other forms—in environments corresponding to each of the types A, B, and C described in preceding pages.

It is hoped to discuss in a later paper the relation of the phenomena of shell-growth in *O. edulis* to growth in invertebrates in general.

A Note on Fattening in *O. edulis*.

The examination of frequent (mainly weekly) samples from the chief beds in the Blackwater River during 1927, as recorded in the preceding pages, led to the discovery that oysters on the Thornfleet beds began to fatten, i.e. to lay down food-reserves, as distinguished from gonad development, during August and early September, before the populations on neighbouring beds began to fatten. As the breeding conditions were approximately the same on all these beds, it would appear that some food factor was present on the Thornfleet beds and absent from the other relatively distant and somewhat differently situated beds. It would appear that food, or some special kind of food, was more abundant than elsewhere in the Thornfleet locality at that time, since the general environmental conditions over the whole of the beds were otherwise approximately the same. In a recent study, Savage (**15**) attributed fattening of *O. edulis* in Butley Creek (Thames Estuary) to abundant food in the form of diatoms, and particularly *Nitzschiella parva*. Unfortunately during 1927 no observations were made on the Plankton in the Blackwater locality, and no definite observations on stomach contents, but it is known that a form of Nitzschiella (**23**, and at other times) is often abundant on these beds. It is probably, however, of little importance what vegetable organisms are present in the water (Orton, **18**; Yonge, **24**) to produce fattening, provided they are present in sufficient abundance and the oysters are in a healthy condition, for the problem of fattening is undoubtedly definitely related to an *abundance* of vegetable organisms at the proper time of the season, namely, towards the end of the summer and in the autumn. We have therefore to find why vegetable organisms were more abundant on the Thornfleet than other beds in the locality

in August–September, 1927. Now abundance of diatoms is correlated with certain seasonal variations in the environmental physical conditions and is otherwise dependent, as Atkins (**25**) (1926) and Harvey (**26**) (1926) have shown, on a sufficient supply of inorganic substances in the sea-water, particularly of phosphates and nitrates, deficiency in which may limit the production of vegetable organisms in the open seas (Atkins, **25**). But as the environmental physical conditions were approximately the same over the Blackwater beds in 1927, where good fattening and no fattening occurred, it would appear that there was actually a deficiency of inorganic substances in the water circulating over these beds where no fattening occurred, but no deficiency in the waters circulating at the same time over the Thornfleet beds. It would seem, therefore, that the supply of inorganic food-substances was greater on the latter than on the former beds, and a cause may be looked for. Now on and near the Thornfleet beds great piles of Crepidula are thrown on the foreshore near high-water mark to die, and the products of their decomposing bodies are washed into the creeks. The decomposition products of these animals may therefore supply a possible deficiency at this time—August–September—in phosphates and nitrates, and may possibly offer an explanation of an abundant supply of inorganic food-substances in the adjacent waters over the oyster beds. This suggestion is made tentatively, since except at neap tides and in rough weather there is difficulty in accounting for a sufficient mixing of the upper stratum of water at high water with the bottom water which passes over the oysters, and for the limitation of the possible increase in concentration of phosphates and nitrates to the Thornfleet locality as against some other beds, particularly the North (Mersea) Shore beds.

The phenomena, however, indicate that in connexion with the problem of fattening in *O. edulis* it is advisable to obtain seasonal records of the phosphate—and probably nitrate—variation in concentration in the waters over beds where fattening does not always occur. It would appear that on the Whitstable beds the phosphates and nitrates derived from the sewage and effluents discharged into the Thames would rarely be reduced in sufficient amount to affect the production of vegetable organisms, and this may be the reason why the Whitstable beds are efficient and relatively constant in producing fat oysters. Nevertheless definite seasonal records of the variation in phosphate and nitrate content of the waters affecting the different Thames Estuary oyster beds might throw a flood of light on the much discussed and important economic problem of fattening. Observations on the phosphate and nitrate concentration in estuarine waters are rare, but Atkins (**27**, p. 449) gives a few analyses for phosphates in Plymouth Sound in 1925 (L1, L2), which show a diminution of phosphate in surface water during the

summer period, similar to that shown by offshore waters at greater depths in midsummer. Similar occasional analyses for nitrates at the same stations are given by Harvey (**26**, p. 188), which also indicate great reduction of nitrates in the summer period. The conditions off Plymouth may be regarded as approximately similar to those off the Fal Estuary. In the Thames Estuary no observations are known on the phosphate content, but estimations of nitrate and nitrite were made by Brady in the month of January in 1920 (see **13**a). Brady estimated nitrate by the method of distillation with sodium hydroxide and aluminium foil, which is now regarded as less satisfactory than a modification of the method devised by Denigès (Harvey, **26**). In the distillation determinations Harvey regards that the nitrate figures obtained are liable to be high—especially in coastal waters—due to the decomposition of organic compounds in the water. Brady obtained 0·015 parts to 0·064 parts of nitrogen as nitrate per 100,000 on respectively parts of the West Mersea and Ham Grounds, with similar or intermediate values for other parts of these beds and the Estuary. In 1919, however, the Government Chemist determined the albuminoid ammonia in seventy-six samples from the Thames Estuary oyster beds, and obtained 0·013 parts to 0·018 parts of nitrogen per 100,000 parts as albuminoid nitrogen in samples respectively from Whitstable and Burnham-on-Crouch with intermediate values for the River Blackwater and Ipswich ; thus if all the albuminoid nitrogen be deducted from Brady's results for the Whitstable beds especially, considerable quantities of nitrate alone still remain—in comparison with those obtained from the English Channel—e.g. 0·051 parts nitrogen as nitrate per 100,000 parts, or 510 mgrs. per cubic metre, as might perhaps be expected, but there is much less in the waters from the other beds. In estuaries which receive a large amount of sewage and general waste products, it seems unlikely that the available phosphates and nitrates could be consumed by vegetable organisms, more quickly than they are produced, but the matter is worth investigation ; on the other hand, in clean estuaries it seems probable from the recent work of Atkins and Harvey that these substances may actually be used up during the summer. If it be shown that phosphates and nitrates do disappear in summer on beds where fattening does not occur—and the oysters on the beds are otherwise healthy—one of the chief factors concerned in fattening will have been discovered, and Stanley Gardiner's prediction (**28**) that we shall in the future manure the seas with phosphates may become an economic proposition ; for the manuring of estuarine waters with phosphates and nitrates, or their substitutes, for the production of great crops of vegetable organisms for the purpose of fattening oysters is a possibility.

Fattening can now be recognised as a process which (1) occurs normally in the post-spawning resting phases, (2) requires an abundant or super-

abundant supply of vegetable organisms at the end of the summer and in autumn, and preferably before the shell-growing season begins, and in addition, as the sample of Dutch oysters from Whitstable (see Table IX, No. 32, p. 409) proves, cannot be expected to occur under the most favourable conditions in either a population whose physiological balance has recently been severely shaken, or in otherwise unhealthy individuals.

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Truro City Council Oyster Committee	Mr. E. Searle.
Yealm Oyster Company	Mr. J. Kingcome.
Falmouth Town Council Oyster Committee	Mr. C. May.
Saltash Council Oyster Committee	—
George Tabor, Ltd. (J. M. Tabor, Esq.)	—
Seasalter and Ham Oyster Company, Whitstable (Major Gardiner)	Mr. E. Luckhurst.

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SUMMARY.

Continuous observations on the Upper Fal Estuary oyster beds during the years 1925, 1926, and 1927 have established the fact that *O. edulis* exhibits on these beds two definite periods of shell-growth, i.e. increase in shell-area, in one year ; one period of general shell-growth occurs in the spring, beginning early in April, and the other in autumn at the end of September or early in October. There is some evidence—but as yet

incomplete—that internal shell-growth occurs solely and simultaneously with the deposition and thickening of the new shell-shoots in a period of one to two months.

These general bursts of shell-growth occur in the pre-breeding and post-breeding part of the season.

Similar periods of shell-growth occur on beds in the River Blackwater (West Mersea), and also occur mainly in the pre-breeding and post-breeding part of the season; but shell-growth begins in the spring in April–May on these beds, a few weeks *later* than on the Upper Fal Estuary, and in the autumn in August–September a few weeks *earlier* than on the Upper Fal beds.

Spring and autumn periods of shell-growth are also known to occur on many other estuarine beds.

Spring shell-growth begins on the Fal when the sea-temperature rises slightly above 50° F., but probably not greater than 52° F., and on the Blackwater also when the temperature rises above 50°, and when there is a probability on both sets of beds of an abundant supply of food.

Autumn shell-growth begins on the Fal and Blackwater when the temperature falls below 60° to 57° F.

The environmental factors correlated with shell-growth, namely, temperature variation, salinity, food, light, hydrogen-ion concentration, and tidal conditions are discussed.

An analysis of the oyster populations with regard to varying physiological condition is made, and the proportion of individuals growing new shell in all the different physiological states recognised is given.

It is found that shell-growth occurs in high proportions in very different states from spent individuals to ripe male and female individuals; but in only small proportion in well-fattening oysters. Female-functioning individuals actively developing at an almost ripe stage rarely occur during periods of shell-growth.

Fattening, i.e. the accumulation of reserve food-products mainly in the form of glycogen, occurs normally on the Fal after the autumn shell-growing period, and in 1927 also occurred mainly after the shell-growing period on the River Blackwater beds, except in one locality, Thornfleet, where fattening began in August towards the end of the spawning period.

The cause of shell-growth is discussed, and the conclusion arrived at that the internal economy of *O. edulis* is such that if food be abundant and a temperature of 50° to 52° F. be attained on a rising temperature, or a temperature of 60° to 57° on a falling temperature, a phase of shell-growth will occur. On the other hand, when temperature over the beds is maintained above about 59° to 60° F. physiological pre-spawning categories occur which are absent in the autumn and early spring shell-growing

periods. These facts indicate that at the higher temperatures the internal economy is modified for the immediate purposes of reproduction, and that this latter state is, on the whole, antagonistic to shell-growth. Low salinity, low hydrogen-ion values, and certain actinic rays may be contributory factors to shell-growth, but time itself does not appear to be a factor, since shell-growth begins earlier in the spring and later in the autumn on the Fal than on the Blackwater beds.

The variation in all the main functional activities of *O. edulis* in three typical and different environments is discussed.

The cause of variation in shell-size in *O. edulis* and the subject of physiological antagonisms are also dealt with briefly.

The cause of fattening on the Thornfleet beds in the River Blackwater in August–September, 1927, when fattening did not occur at the same time on other adjacent beds, is discussed. Good fattening occurs when the energies of the oyster individual are concentrated on transforming an abundant, or superabundant, supply of food-material into food-reserves, that is, when neither breeding nor shell-growth are taking place. It is regarded possible that a deficiency of inorganic food-materials, particularly phosphates and possibly also nitrates, occurred for a short period on the Blackwater beds except at Thornfleet, where dumps of decomposing Crepidula may have maintained the supply of phosphates and nitrates, and incidentally the vegetable crop in the neighbourhood of the oyster beds.

A deficiency in the supply of phosphates and nitrates on beds where fattening rarely occurs or occurs indifferently is regarded as a possibility, and further investigations are called for.

It is suggested that the relatively regular good fattening experienced on the Whitstable beds may be due to a continuous supply of inorganic food-materials from the Thames effluents, and that if these food-materials should be found deficient on oyster beds, it will be possible to manure the beds with phosphates and nitrates, or their substitutes, with the object of growing abundant crops of vegetable organisms, diatoms and peridinians, for the purpose of fattening not only *O. edulis*, but also other species of oyster.

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The Vertical Distribution of Marine Macroplankton. VII. Observations on the Behaviour of *Calanus finmarchicus.*

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With 6 Figures in the Text.

During the period April to September in 1926 a further series of observations on the vertical distribution of plankton were carried out with the stramin ring-trawl in a manner precisely the same as for those of 1925, the results of which have already been published (**12**). The present paper deals only with the results bearing on the behaviour of *Calanus finmarchicus* (Gunner.)

The collections were made at a position, A, about ten miles from land and two miles west of the Eddystone Lighthouse, in water of a depth of about 54 metres; one only (June 30th) being made at the International Station L4, which lies midway between Rame Head and the Eddystone. On all occasions the Admiralty depth recorder was in use. The full details of the log for all the hauls are not given here, but will be published in a later Report dealing either with the young fish or all the remaining plankton animals collected during the period under observation; the times at which the collections were made are given in Fig. 1, and each haul was of ten minutes' duration.

A sample of 100 Calanus from the catch at each depth was examined for separation into females, males, and young stages, and for making measurements. The total length of the body was measured, i.e. to the end of the caudal furcæ, the furcal setæ being excluded. Under the working conditions the divisions of the micrometer eyepiece corresponded to 0·055 mm. In the case of the males the measurements will not be quite so accurate as those of the females, owing to the habit of many males of dying with the caudal furcæ stretched widely apart; it is doubtful, however, whether this error is of much importance when compared with the differences in total length that occur during the season.

A further source of error may arise when sampling the Calanus, because many males die with their antennæ stretched out away from their bodies,

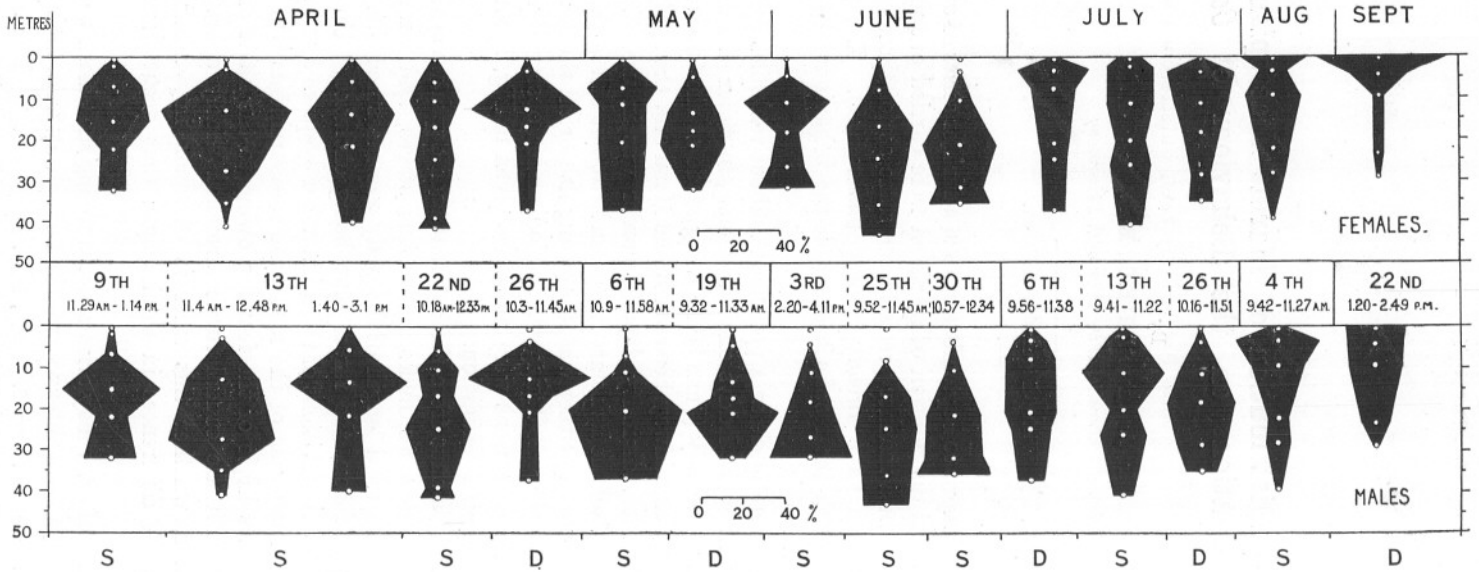


FIG. 1.—The percentage vertical distribution of adult females (top) and males (bottom) of *Calanus finmarchicus* in the daytime on the dates given, in 1926. The white spots and black circles indicate the average depths at which the hauls were made. The times given are Greenwich Mean Time and denote the time at which the first haul in a series was begun and at which the last haul was finished. S = Sunny. D = Dull.

and unless a very wide-mouthed pipette be used it will be found that females only are sucked up, the males sticking at the entrance. To overcome this difficulty the original collection of the Calanus were well mixed with plenty of water in a small vessel, and successive small samples were poured off and examined until 100 had been measured, whereby almost all the Calanus poured off where examined and there could be no selection by the pipette. By a thorough mixing with plenty of water the tendency for males to cling together by their outstretched antennæ was also prevented.

In Table I, p. 449, are given the total numbers of female and male Calanus in each catch and the average depths at which the collections were made, as shown by the depth recorder. Fig. 1 shows the vertical distribution of the females and of the males on each day, the numbers at each depth being expressed as percentages of the total number taken at all depths on the day in question.

In a previous publication (**11**) it was shown that there was a tendency for Calanus to move deeper in the water as the season advanced towards the end of June, and that there was a considerable rise towards the surface in July and August. A comparison of Fig. 4 on p. 422 of that publication with the present Fig. 1 shows that there is a striking similarity between the behaviour for the two years. We have once more a gradual descent from the beginning of April to the end of June, and again the very marked rise towards the surface in July and August, with a concentration at the surface in September. Furthermore, there is on certain days, again, a similarity between the actual vertical distribution diagram and the kite-shaped figure which would be theoretically possible if light intensity were the governing factor in controlling the behaviour of the animals (**11**, Fig. 3, p. 421).

Before proceeding attention must be called to the vertical distribution shown for June 25th in Fig. 1. When this diagram was first drawn it was found that on this day the Calanus were higher in the water than was to be expected under the clear sunny conditions that existed. The reason for this was not apparent until on going over the depth records it was found that on this day, for the only occasion in the season, the recorder was not working satisfactorily; the recording drum was not fully screwed down, so that it had considerable play. Fortunately on the same day samples had been taken at ten different depths with a coarse silk (58 strands to 1 inch) closing net of the dimensions of the international standard net (**9**). In Fig. 2, A shows the vertical distribution of female Calanus from the ring-trawl collections as first drawn in Fig. 1. C shows the vertical distribution of Calanus females, as shown by catches of the silk closing net. It is clear that they were considerably deeper in the water than the diagram A indicates.

Accordingly 4 metres was added to each depth of the ring-trawl catches, this being a little less than the full play that was allowed by the recorder drum not being fully screwed down. Fig. 2, B shows the vertical distribution of the Calanus in the ring-trawl collections with these revised depths,

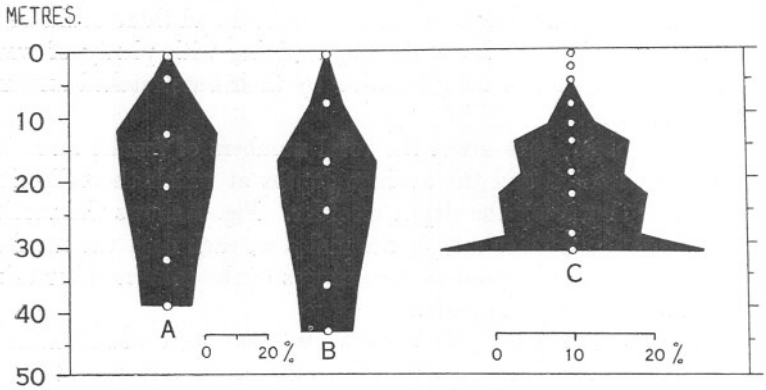


FIG. 2.—A, Vertical distribution of female Calanus caught in ring-trawl on June 25th, 1926, as first drawn in Fig. 1 (see text). B, Vertical distribution of female Calanus caught in ring-trawl on June 25th, 1926, corrected for error due to depth recorder. C, Vertical distribution of female Calanus on June 25th, 1926, as shown by silk closing net collections. The white spots and black circles indicate the average depths at which the hauls were made.

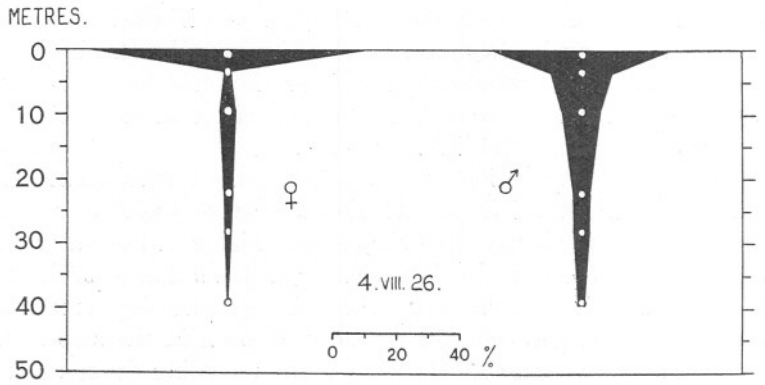


FIG. 3.—Percentage vertical distribution of female and male Calanus on August 4th, 1926, including first surface haul (see text).

and the writer feels that this diagram may be legitimately included, as it has been, in Fig. 1, seeing that it approximates so closely to that as shown by the silk closing net collections in Fig. 2, C.

The diagram in Fig. 1, recording the vertical distribution of Calanus on August 4th, also requires comment. On this day the surface haul

contained the largest catch of Calanus ever taken during the course of these researches, namely, 175,296 females and 15,936 males. Accordingly, after the full series of collections at the six different depths had been taken a further surface haul was made to see if the Calanus were really more abundant at the surface than in the deeper layers, or whether at that moment we had been steaming through an extraordinarily dense shoal. This second surface haul did not reveal anything like the numbers taken in the first haul, but at the same time it still produced a catch of females greater than at any other depth, showing that the Calanus were undoubtedly much more abundant in the upper layers than deeper down. In Fig. 1, on August 4th, the percentage vertical distribution is drawn, using the numbers from the second and smaller surface haul, as there was no room for the diagram which included the first surface haul. This latter has, however, been reproduced for both females and males in Fig. 3.

Seasonal Changes in the Vertical Distribution of Female Calanus.

A seasonal change in the vertical distribution of Calanus has been noticed by other workers. Bigelow (**2**, p. 202) found that the vertical distribution varied somewhat with the season of the year in the Gulf of Maine. In the spring, from February to May, Calanus occurred in all but one of the surface hauls irrespective of the time of day ; while " with the increasing intensity of the sunlight and progressive warming of the water which accompany the advance of the season, the surface stratum evidently becomes less favorable for Calanus, for in summer it is usually decidedly scarce or even wanting in the surface hauls, even at localities where it swarms a few meters down."

Nikitin (**8**) has also found a seasonal change in the vertical distribution of Calanus in the Black Sea. In a French summary to a paper written in Russian on work carried out from 1923 to 1925, he says : " *Calanus finmarchicus* Gunn. se tient depuis fin novembre jusqu'au commencement de mai (t° au dessous de 14°) depuis la surface jusqu'à la zone limitrophe (200–175 m.). Les individus jeunes se tiennent de préférence dans les couches supérieures. Vers la fin du printemps, au moment où la t° des couches supérieures remonte au dessus de 14°, *C. finmarchicus* descend vers les couches plus profondes et plus froides ; en été (juin–juillet) il n'apparaît point au dessus de 15 mètres ; au mois d'août—au dessus de 25 m. A la fin de l'automne au moment du refroidissement hivernal, il apparaît à nouveau dans les couches superficielles." Nikitin evidently regards temperature as a factor of great importance, and this may well be the case in the Black Sea, where the high average temperature of 24° is reached in the surface layers.

It has been mentioned above that the 1926 results (Fig. 1) agree very closely with those for 1925 in showing a gradual descent in the region of maximum abundance from about 10 m. on April 9th to 20 m. on June 30th, and a marked rise in July, August, and September. In 1925 the sudden rise towards the surface was explained (**11**, p. 427) by the fact that on the days in question the weather was very dull and foggy. An examination of the weather conditions in 1926, however, shows that while on July 6th and 26th and September 22nd the weather was dull, on July 13th and August 4th there was bright sunshine and a cloudless sky. The above explanation can apparently, therefore, no longer hold. On the days on which collections were made observations were taken on the transparency of the water by means of a Secchi's disc 20 cm. in diameter. This was lowered to the depth at which it disappeared, and the results on each day are given in the following table and are plotted graphically in Fig. 4, A (dotted curve).

SECCHI DISC RECORDS. 1926.

April 9th.	11.27 a.m.	10 metres.
	1.25 p.m.	12 ,,
,, 13th.	11 a.m.	12 ,,
	12.55 p.m.	10 ,,
	1.36 p.m.	9 ,,
	3.6 p.m.	9 ,,
,, 22nd.	10.12 a.m.	10 ,,
	12.40 p.m.	11 ,,
,, 26th.	10 a.m.	11·5 ,,
	12.45 p.m.	13 ,,
May 6th.	10.7 a.m.	9·5 ,,
	12.30 p.m.	9 ,,
,, 19th.	9.25 a.m.	13 ,,
	12 p.m.	11 ,,
June 3rd.	4.20 p.m.	10 ,,
,, 4th.	9.20 a.m.	10 ,,
,, 25th.	9.50 a.m.	19·5 ,,
	12 p.m.	20 ,,
July 6th.	11.47 a.m.	14 ,,
,, 13th.	11.30 a.m.	13 ,,
,, 26th.	12 p.m.	12* ,,
		11† ,,
August 4th.	12.55 p.m.	9‡ ,,

* Leeward side. † Windward side.

‡ The same on both sunny windward and shady leeward side.

On July 15th a series of observations were taken, showing how the transparency varies from place to place.

7.30 a.m.	Knap Buoy.	14 metres.
8 a.m.	L3	16·5 ,,
8.30 a.m.	L4	17·5 ,,
9.15 a.m.	L5	17* ,,
		15† ,,
10 a.m.	L6	12 ,,
10.35 a.m.	E1	12 ,,
1.30 p.m.	E1	13 ,,
1.55 p.m.	E1	13 ,,
3.40 p.m.	L4	15‡ ,,
		15·5§ ,,

On the same diagram, Fig. 4, A, is given a curve showing the depths at which the value of 20% could first be read off from the vertical distribution diagrams for female Calanus in Fig. 1 on each day, thus giving approximately the changes in depth distribution that occurred with the female Calanus from day to day (unbroken curve). It can be seen that the two curves follow one another very closely until the beginning of July. This is only to be expected, seeing that the greater the transparency of the water the greater the light penetration, apart from the fact that the light also increases in intensity after April. But in July and August, although the transparency of the water is once more much as it was in April and May, the Calanus are nevertheless very much closer to the surface.

The possibility suggested itself that the light at the end of the summer might differ somewhat in composition from that in the spring; that perhaps owing to the presence of much moisture in the upper atmosphere from evaporation at the sea surface there was an increased absorption of ultra-violet rays in July and August.

I have to thank Professor Leonard Hill, of the Medical Research Council's Laboratory at Hampstead, for kindly supplying me with figures for the amount of ultra-violet radiation measured at Lyme Regis on the Dorset coast, on the days on which the plankton collections were taken. The readings were as follows :—

LYME REGIS, 1926,

April 9th.	5	June 25th.	8
,, 13th.	6	,, 30th.	12
,, 22nd.	3·5	July 6th.	3·5
,, 26th.	2	,, 13th.	12·5
May 6th.	6·5	,, 26th.	2
,, 19th.	6	August 4th.	10
June 3rd.	9·5	September 22nd.	8·5

* On shady leeward side. † On sunny windward side.
‡ On sunny leeward side. § On shady windward side.

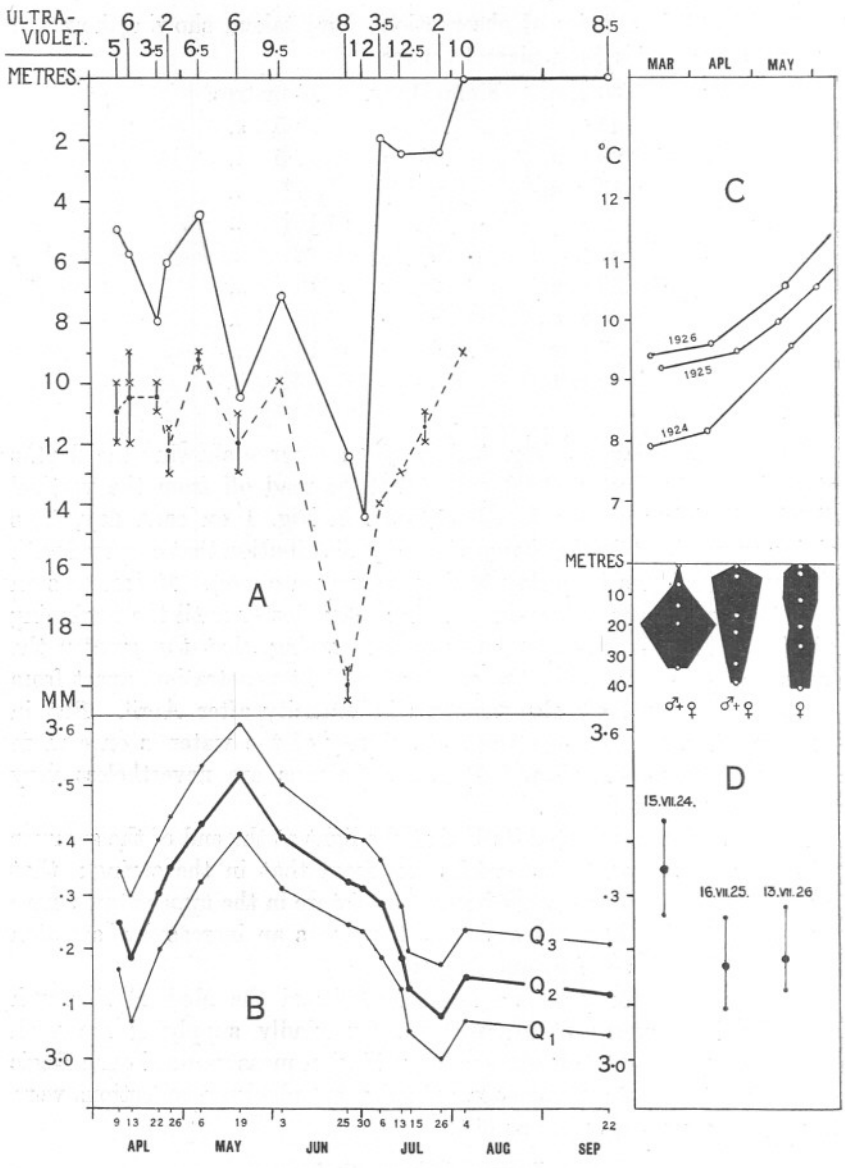


FIG. 4.—At top are given the ultra-violet radiations in 1926 for Lyme Regis on the dates indicated at the bottom of the figure. A, —— = curve showing depths at which female Calanus first reached 20% in abundance below the surface on the dates given; 1926 : – – – – – – – = depths at which the Secchi disc disappeared from sight. B, Median lengths and upper and lower quartiles in millimetres of female Calanus on the dates given, 1926. C, Curves showing temperatures recorded at 25 metres at the International Station E1 for March, April, and May in 1924, 1925, and 1926. D, Above are shown the percentage vertical distribution of Calanus on July 15th, 1924, July 16th, 1925, and July 13th, 1926, respectively; below are given the median lengths and upper and lower quartiles for the Calanus on these same dates.

These readings show a gradual increase in the radiation from April to June 30th, but there is no evidence of any decrease in July and August except on dull days; in fact, the highest record occurs on July 13th. We can therefore say that there is no evidence that the cause of the upward movement of Calanus lies in a decrease of the ultra-violet radiation.

In Table II* (p. 450) are given the measured lengths of female Calanus from all depths sampled on each day, and in Table V (p. 453) are the median lengths and upper and lower quartiles for each day calculated from Table II. (The median here approximates to the average length, and the upper and lower quartiles are the lengths within which 50% of the samples lie.) These results, Q_2 the median, and Q_3 and Q_1 the upper and lower quartiles, are plotted as a curve in Fig. 4, B. It can at once be seen that there is a marked seasonal change in length, the highest median length, 3·52 mm., being recorded on May 19th, and the lowest, 3·08 mm., on July 26th. The seasonal change in the size of copepods is a well-known phenomenon, and had already been noted for Calanus by Gran in 1902 (**6**, p. 60). Recently Adler and Jespersen (**1**) have studied it for three species of copepods, *Pseudocalanus elongatus*, *Temora longicornis*, and *Calanus finmarchicus*, in the North Sea and Cattegat. They found a regular seasonal change in size for Pseudocalanus and Temora over a period of nearly four years. For Calanus they only had records for a period of one year, and these results show well that this periodic change in size is a phenomenon exhibited by the copepodite stages as well as by the adults. For the adults, however, the numbers sampled were on many occasions very small, and there would therefore be no gain by comparing their measurements with mine.

This phenomenon of change of size with season appears to be closely related with the seasonal temperature changes (Fig. 5). The Calanus born in the early spring when the sea temperature is low give rise to a brood of large adults; these large adults probably spawn intermittently throughout the months of May and June when the temperature of the water is rising rapidly. Their offspring form a brood of small individuals making their appearance as adults in late June and early July, and predominating from then onwards. Although I have no winter observations the indications are that this summer brood of small individuals probably reproduce late in the summer when the temperature is still fairly high and give rise to a brood of small individuals, some of which tide over the winter months to form the original stock for the spring breeding

* In these and following tables data are given for 4 series on June 3rd–4th and 1 at E1 on July 15th, but the vertical distribution of Calanus on these occasions will not be dealt with in this paper.

in the following year. It can be seen from the curve that early in April the Calanus were small.

It is a striking fact that when the brood of small adults begins to predominate in the collections early in July the change appears in the behaviour of the Calanus and they move nearer the surface. The suggestion at once presents itself that this summer brood may be physiologically different from the brood of large individuals which precedes them in the spring. While the brood of large Calanus prefer a somewhat low intensity of light and live deep in the water, gradually going deeper as the strength

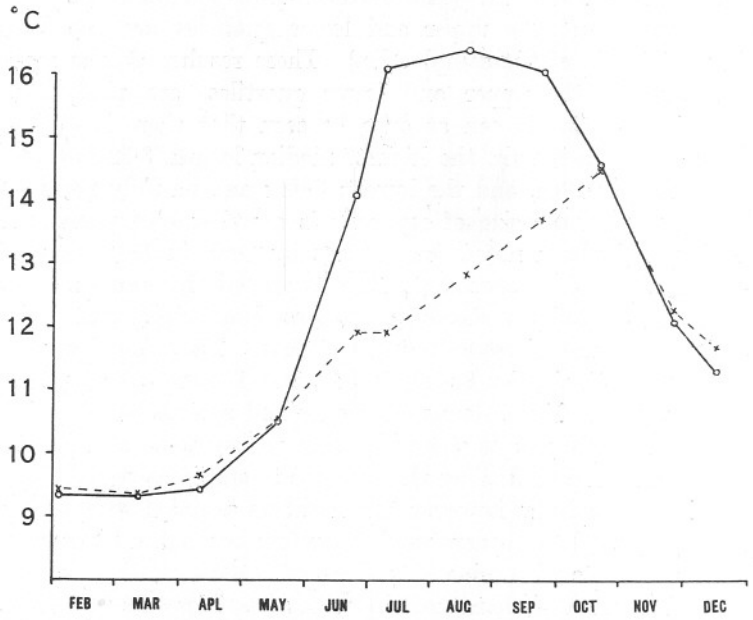


FIG. 5.—Temperatures at International Stations L5 (surface), continuous line, and E1 (25 metres), broken line, in 1926.

of light increases with the season, the "small" summer brood perhaps prefers a higher intensity of light and lives considerably nearer the surface.

This suggestion receives support from a totally unexpected direction. In Fig. 4, D, are given the vertical distribution diagrams for Calanus on the 15th, 16th, and 13th of July in 1924, 1925, and 1926, respectively. It will be noticed that while in 1925 and 1926 the Calanus were high up in the water and close to the surface, in 1924 they were much deeper in the water, having their region of maximum abundance at 20 metres. But if the sizes of the Calanus on these three days be examined it will be found that while the 1925 and 1926 Calanus do not differ appreciably,

the 1924 specimens were very much larger. The medians, and lower and upper quartiles on each day, are given in Fig. 4, D, below the vertical distribution diagrams to which they refer, and the figure shows clearly the difference in size between the 1924 Calanus and the 1925 and 1926 specimens. Also on comparing these with Fig. 4, B, we see that while the 1925 and 1926 Calanus lie within the size range of the small summer brood, those of 1924 lie well outside this range and tend towards the average size of the large spring individuals.

The actual data are given below; the 1924 and 1925 measurements include both males and females, but the 1926 are only females. This will not, however, upset the general result, because males are always slightly smaller than females and the tendency would be to make the 1924 measurements smaller if anything than they should be.

Mm.	June 15th, 1924. ♀ + ♂	July 16th, 1925. ♀ + ♂	July 13th, 1926. ♀
2·86	–	–	1
2·915	–	6	5
2·97	–	8	11
3·025	4	20	14
3·08	2	20	21
3·135	4	22	53
3·19	9	24	27
3·245	14	15	29
3·3	17	18	24
3·355	15	4	9
3·41	15	1	5
3·465	9	–	1
3·52	2	–	–
3·575	2	–	–
3·63	1	–	–
3·685	1	–	–
Q_1	3·264	3·082	3·12
Q_2	**3·348**	**3·174**	**3·18**
Q_3	3·435	3·260	3·27

In Fig. 4, C, are given the temperature curves of the sea in March, April, and May in the three years 1924, 1925, and 1926. It shows that for March and April the temperature was fully a degree lower in 1924 than in the other two years, and in May it was half a degree lower than in 1925 and a whole degree lower than in 1926.

The temperatures at 25 metres at the International Station E1 were as follows :—

1924.		1925.		1926.	
Feb. 15th.	8·70° C.	Feb. 17th.	10·01° C.	Feb. 3rd.	9·40° C.
Mar. 10th.	7·90°	Mar. 14th.	9·18°	Mar. 11th.	9·37°
April 8th.	8·15°	April 22nd.	9·44°	April 10th.	9·65°
May 20th.	9·59°	May 13th.	9·96°	May 17th.	10·55°
June 17th.	10·49°	June 3rd.	10·55°	June 24th.	11·92°
July 9th.	11·54°	July 8th.	11·85°	July 8th.	11·90°
Aug. 7th.	12·01°	Aug. 5th.	12·02°	Aug. 16th.	12·86°
Sept. 3rd.	12·34°			Sept. 22nd.	13·76°

The large size of the Calanus in July, 1924, may have been caused by the low temperature at which they were born, and it is easily conceivable that physiologically they would approach more nearly in their reactions and behaviour to the brood of large individuals which predominated in the spring in 1926 than to the brood of small Calanus which followed later. This would perhaps explain why in 1924 the Calanus were much deeper in the water in the daytime in mid-July than in either of the two years 1925 and 1926.

The above suggestion of physiologically different broods appearing during the year might be tested in another way. Fig. 4, B, shows that in the spring the size of the Calanus increases gradually until a maximum size is reached in May, it then decreases gradually until by July the small size becomes more or less stable with only slight variations. The most obvious explanation is that the gradual increase in size is due to a mixture of small and large individuals, i.e. the small adults of the previous summer's brood now spawning and the large adults resulting from this spawning. The proportion of large to small increases gradually, the small dying off, and more and more large reaching maturity, until at the peak of the curve the population consists almost homogeneously of large individuals. The gradual downward slope of the curve until July can be explained in a similar but reverse manner, the large ones dying off until the small summer adults predominate.

If such were the case we should expect that on May 19th the population consisted homogeneously of Calanus of the brood of large individuals, and from July onwards to early April of the " small " brood. But at the periods between early April and May 19th and the latter date and July the populations would not be homogeneous, but would consist of mixtures of " large " and " small " individuals. If these two types of broods truly differ in their reactions towards external conditions a comparison of depth distribution with size might show a tendency for a segregation of the smaller individuals to the upper layers and the larger

individuals to the deeper layers at those times when the population was mixed, a differentiation which should not be apparent when the populations are homogeneously " large " or " small." Owing to the wide range of size of both the " large " and the " small " types it is impossible to show whether a population is homogeneous or not by size measurements alone, since the two ranges overlap to such an extent as to form a unimodal curve which may be truly unimodal or consist of the addition of two little-separated modes on a bimodal curve.

Unfortunately the numbers of females measured at each depth on any single day are not sufficiently great to allow any calculations to be made. I have attempted to arrive at a solution by grouping several days together. For instance, one might group together all the days from July 13th to September 22nd inclusive, during which period the population should be homogeneously " small," and one could take together April 22nd and 26th and May 6th, when the population may be a mixture of " large " and " small " broods. But while in the former case the method may be fairly legitimate, in the latter the results would be severely vitiated by the fact that there is a relatively enormous difference in average size between the individuals from day to day. No evidence of any difference in size with depth could be found from July 13th onwards, but a very slight tendency for the large forms to congregate in the deeper layers was shown for April 22nd and 26th and May 6th. No such tendency, however, was shown on June 25th and 30th and July 6th, when one expects the population to have become once more heterogeneous. On the whole, the data do not warrant such minute examination, and we must await the time when a large number of measurements can be made on any single day. It might be remarked that with a homogeneous population, although the actual range of size is large, calculation of a number of days lumped together (July 13th to September 22nd) showed no evidence of changes in size with depth. This, perhaps, is to be expected, seeing that all were presumably born under the same conditions and have reached the same stage of development. Segregation by size is shown by many plankton animals, notably Sagitta, but it must be remembered that with Sagitta size is a criterion of age rather than of development, corresponding actually to the various growth stages of a moulting crustacean, and segregation by growth stages has been shown for Calanus.

Although some evidence has been put forward to support the suggestion made above that the summer and spring broods of Calanus are physiologically different, we must not lose sight of the fact that so little is as yet known of the actual seasonal changes in light conditions beneath the sea surface that we cannot say that this apparent seasonal change in the behaviour and reactions of Calanus is not due entirely to changes in external conditions and not to any physiological differences at all.

Seasonal Changes in Vertical Distribution of Male Calanus.

Fig. 1 shows that the males differ in their behaviour from the females, being always slightly deeper in the water than the latter. This is shown clearly in Fig. 6, A, in which are plotted the depths below the surface

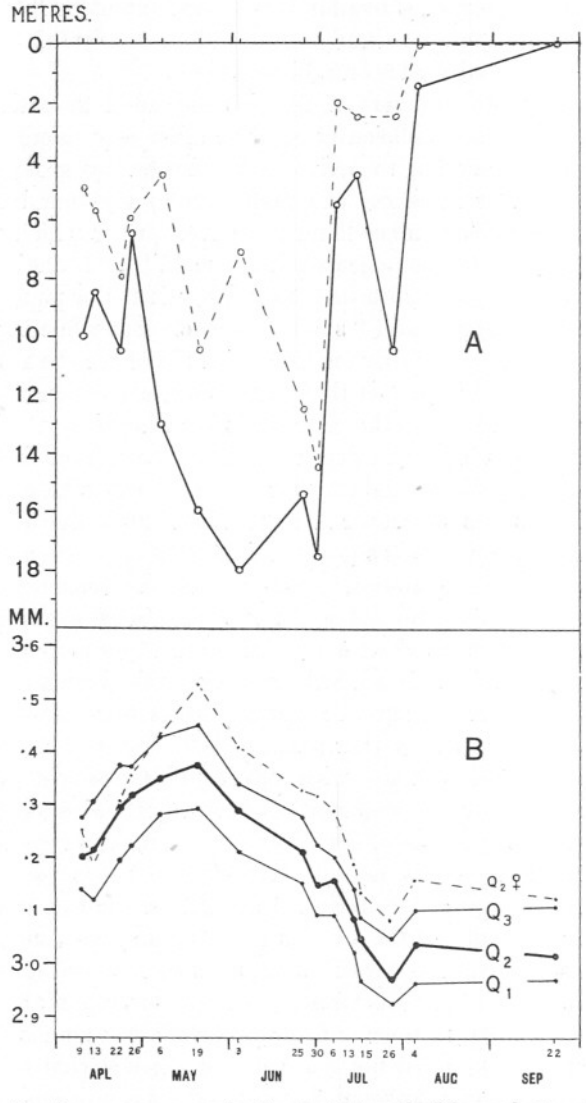


Fig. 6.—A, ———— = depths at which male Calanus first reached 20% in abundance; – – – – – – = ditto for females. B, Median lengths and upper and lower quartiles in millimetres for male Calanus on the dates given; – – – – – – – = median lengths for females.

at which the male Calanus first reach 20% in abundance on each day. For comparison the similar curve for the female Calanus has been reproduced from Fig. 4, and is shown as a dotted curve in Fig. 6, A. Indications of this difference in behavour between Calanus males and females have already been noticed by other workers (Paulsen, **10**, p. 16).

Fig. 6, B, shows the measured lengths of the male Calanus as shown for the females, viz. the median and upper and lower quartiles. For comparison the median for the females is shown as a dotted curve. It can be seen that in essentials the males show a similar seasonal change in size to that of the females, the only difference being that the males were always slightly smaller than the females, except early in April when they were about the same size. Full details of the measurements of the males are to be found in Tables III and V. The highest and lowest median lengths of the males were 3·37 mm. on May 19th and 3·01 mm. on September 22nd as opposed to 3·52 mm. for the females on May 19th and 3·08 mm. on July 26th. It is to be noticed that while the females approach very nearly to the smallest limits of the males, the males never reach anything like the largest sizes of the females.

The Presence of Swarms of Calanus at the Surface.

It has been hard to reconcile the fact that the sun's light is the main factor in causing Calanus to avoid the surface layers in the summer with the occasional occurrence of vast swarms of this copepod at the surface itself. The results of this present research appear, however, to afford an explanation.

During my observations I have never yet met with Calanus in great abundance in the surface layers in the daytime after April except in the months of July, August, and September. In the following extract from a work by H. B. Bigelow, who finds indications of a seasonal change in the vertical distribution of Calanus in the Gulf of Maine (**2**, p. 203), it can be seen that July and August are again the only months mentioned in which swarming at the surface in sunlight occurred : " I have already pointed out that its absence on the surface in the regions where it swarms in deeper water is not caused altogether by sunlight, for while it probably does tend to descend during the most brilliantly illuminated hours, on several occasions we have made rich catches on the surface when the sun was high in the sky. Such was the case off the entrance to Gloucester harbor on July 22, 1912 (Station 10012), when nearly a litre was taken in the 4-foot net on the surface at about 3 p.m. Again, on August 14, 1914 (Station 10251), we made a rich surface catch of Calanus at about 2 p.m. off Cape Elizabeth ; in July, 1916, a month when *C. finmarchicus* was notably abundant, surface hauls yielded considerable numbers off Cape

Cod at 4 p.m. (Station 10345), and off Martha's Vineyard at 5 p.m. (Station 10351). Willey (**13**, p. 181) records the "presence *en masse* of *C. finmarchicus* at the surface between 3 and 4 p.m. under a bright sun." This occurred on September 14th, but there was a possibility that this may have been a forced swarming caused by hydrographical conditions, since Dr. A. G. Huntsman observed a stirring up of the water by tidal currents.

If it is a general rule that these swarms are only met with on the surface in the months of July, August, and September, and not in May and June, their presence ceases to contradict the light intensity theory, for all my observations so far point to the conclusion that it is the rule and not the exception for Calanus to be high up in the water in these months.

On the Life-History of Calanus in the Plymouth Area.

A certain amount of information on the life-history of Calanus in this region is given by the measurements and calculations in Tables II, III, and V and Figs. 4, B, and 5, B.

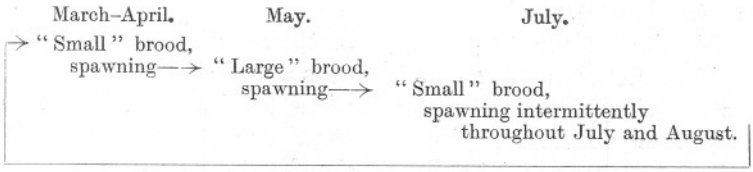
Crawshay (Lebour, **7**) has shown that the complete development of Calanus from egg to the last copepodid stage (V) may be passed through in the Laboratory within two months. At this rate then it appears probable that the brood of large individuals which is beginning to predominate at the end of April may have developed from eggs hatched early in March. The brood of small adults appearing in June, July, and August must have arisen from this brood of large individuals. Table II shows that practically all the females of a size less than 3·1 mm. had disappeared from the catches by the middle of May, presumably having died off. Any adults of this small size that appear in the catches two months after this date must therefore be the offspring of the brood of large individuals prevailing in May. Seeing that we have direct evidence that all the Calanus below a size of 3·1 mm. have died off, it is quite reasonable to presume that the whole brood of small adults predominating early in April has died off by the middle of May, and that the July brood is an entirely new brood arising from the spawning of the large individuals which predominate in the middle of May.

Furthermore, by the end of June almost all the adult females of a size greater than 3·5 mm. had disappeared from the catches. If this means that they have died off, as it surely must do, it indicates that their length of life cannot have exceeded much more than three months, presuming that they were the offspring of the small adults which spawned in March. If, again, all those above 3·5 mm. have died off it seems probable that the whole of this brood of large individuals may have died by July.

At the same time it seems very probable that the small adults present in the summer will spawn intermittently throughout the months of July

and August, and perhaps September, giving rise to a brood, some of which will tide over the winter months to spawn early in the following spring, and produce once more a brood of large individuals.

Schematically this will give us :—



An examination of the numbers of females carrying spermatophores shows that the percentage was always very low during the months under observation. The following table, which shows the percentages, at all depths combined, on each day indicates that there is a slight increase in the middle of April, which soon falls off and is followed by a similar increase towards the end of July and beginning of August.

	%		%
April 9th.	·6	June 3rd.	·7
,, 13th(i).	1·5	,, 25th.	1·2
,, 13th(ii).	3·5	,, 30th.	0·0
,, 22nd.	3·4	July 6th.	1·4
,, 26th.	·5	,, 13th.	1·5
May 6th.	·4	,, 26th.	2·6
,, 19th.	·9	August 4th.	3·3
		September 22nd.	0·0

Farran (**4**, p. 85) records the presence of females bearing spermatophores on the south coast of Ireland in February, May, and August.

This outline of the life-history of Calanus in this region agrees in essential with that given recently by Farran (**5**) for the south coast of Ireland deduced from the abundance of the different stages of development. He says : "In April there is a sudden outburst of reproduction, of which indications have already appeared in March, but then on such a small scale as not to cause any appreciable increase in stock. . . . Reproduction goes on irregularly all through the summer. . . . The adults of the previous year probably do not live beyond April or May, their places being taken by specimens hatched earlier in the year, which have rapidly gone through their metamorphoses."

On the Occurrence of the Last Copepodid Stage (Stage V) in the Ring-Trawl Catches.

In a previous publication I stated that " a catch of *Calanus finmarchicus* made by the stramin ring-trawl consists nearly always of over 80% adults " (**12**, p. 605).

In Table VI are given the percentage abundance of females, males, and Stage V in each catch. It shows that this statement held good for 51 catches out of 59 up to and including June 30th, and on three of the eight occasions, when Stage V were present to the extent of more than 20%, the numbers were too small to be significant. But in the remaining catches, from July 6th to September 22nd, out of 30 there were 20 in which Stage V occurred as more than 20% of the catch, even reaching 60% and 70% in August and September. This probably indicates that in these latter months the Stage V Calanus were actually so very much more abundant than the adults that even those that were retained in the net outweighed the number of adults caught. Farran (**5**, p. 141) says for the south coast of Ireland that in September " the majority of specimens are now definitely in Stage V."

Owing to the obvious fact that the stramin ring-trawl cannot be regarded as an efficient instrument for the capture of these last copepodid stages, because it probably allows many to pass through the meshes, I have not attempted to express diagrammatically their vertical distribution. The actual numbers caught are, however, given in Table VII.

Although we do not know to what extent the full range of size of the Stage V are sampled, the measurements of total lengths and the calculations of median and upper and lower quartiles based on them given in Tables IV and V are of interest. They show the seasonal change in size in the same manner as do the adults. From the small length of 2·76 mm. on April 22nd the median rises to a maximum of 3·04 mm. on May 19th, falling again to a minimum of 2·69 mm. on July 29th. This shows that the increase in the numbers of Stage V in the July, August, and September catches cannot be put down to an increase in size.

SUMMARY.

1. The vertical distribution of *Calanus finmarchicus* adults in the daylight in the Plymouth region as shown by stramin ring-trawl catches is described for the period April to September in 1926. The general results confirmed the indications given in 1925* that there is a gradual descent of the region of maximum abundance from about 10 metres in April to

* In the summary to the paper recording these results (**12**, p. 605) there is a misprint—1926 should read 1925.

20 metres in June, with a definite rise towards the surface in July, August, and September.

2. The rise towards the surface was evident on sunny days as well as dull, indicating that the suggestion that dull weather and low light intensity was its cause in 1925 may possibly have been incorrect.

3. Measurements of the total lengths of Calanus were made which showed a seasonal change, a brood of small adults occurring in July, August, and September, as opposed to a brood of large adults which dominated in the spring.

4. It is suggested that possibly these two broods are physiologically different, and that the small type of adult prefers a higher light intensity and lives nearer the surface than the large type.

5. The males and females differed in their behaviour, the males being always slightly deeper in the water than the females.

6. Some indications are given of the course of the life-cycles of Calanus in the Plymouth area.

7. While from April to the end of June the abundance of the last copepodid stage (Stage V) rarely exceeded more than 20% of the total Calanus in any one catch, they became very much more abundant in July, August, and September, reaching even 60% and 70%.

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TABLE I.

AVERAGE DEPTHS OF EACH HAUL (*D*) IN METRES AND NUMBERS OF CALANUS FEMALES AND MALES IN EACH CATCH.

	April 9th.			April 13th (i.)			April 13th (ii.)			April 22nd.			April 26th.		
	D	♀	♂	*D*	♀	♂	*D*	♀	♂	*D*	♀	♂	*D*	♀	♂
	S.	60	5	*S*	1	–	*S.*	13	2	*S.*	211	–	*S.*	144	14
	2	812	31	*2·8*	70	–	*5·8*	431	43	*5·9*	1,527	74	*3·2*	589	23
	7	2,456	55	*13*	2,175	140	*13·8*	916	181	*10·4*	2,198	345	*12·6*	5,088	1,696
	15·5	2,738	438	*27·6*	1,115	207	*21·6*	561	34	*16·9*	1,245	266	*16·7*	1,885	649
	22·4	958	146	*35·4*	316	30	*40·1*	213	61	*24·6*	1,798	534	*20·8*	1,030	200
	32·4	1,047	225	*41*	175	18	–	–	–	*39*	829	215	*37·1*	738	258
										41·3	1,390	290	–	–	–
Totals.		8,071	900		3,852	395	–	2,134	321	–	9,198	1,724	–	9,474	2,840

	May 6th.			May 19th.			June 3rd.			June 25th.			June 30th.		
	D	♀	♂	*D*	♀	♂	*D*	♀	♂	*D**	♀	♂	*D*	♀	♂
	S.	3	–	*S.*	–	–	*S.*	117	6	*S.*	5	–	*S.*	20	–
	7·3	4,897	59	*4·6*	1,032	323	*4·3*	2,000	43	*8·2*	1,113	12	*3·5*	10	10
	11·2	3,245	299	*13·4*	4,382	1,587	*10·8*	40,437	3,145	*16·9*	3,607	1,219	*10·4*	909	493
	20·4	3,264	1,360	*17·6*	5,306	1,842	*18*	10,876	6,296	*24·6*	2,776	1,607	*21·4*	2,759	1,549
	37·1	2,656	747	*21·1*	5,545	3,824	*26·6*	16,585	10,120	*36*	2,227	1,306	*31·6*	1,760	1,654
		–	–	*32*	1,601	1,104	*31·5*	26,441	12,591	*43·1*	1,901	1,162	*35·2*	2,332	2,047
Totals.		14,065	2,465	–	17,866	8,680	–	96,456	32,201	–	11,629	5,306	–	7,790	5,753

	July 6th.			July 13th.			July 26th.			Aug. 4th.			Sept. 22nd.		
	D	♀	♂	*D*	♀	♂	*D*	♀	♂	*D*	♀	♂	*D*	♀	♂
	S.	235	78	*S.*	270	–	*S.*	20	–	*S (i.)*	175,296	15,936	*S.*	3,317	121
	3·3	2,781	876	*2·3*	572	260	*3·9*	756	85	*S (ii.)*	11,679	916	*4·4*	1,467	116
	7·9	1,698	1,455	*11·2*	584	701	*11·5*	614	307	*3·5*	4,895	5,402	*9·6*	254	109
	20·9	1,190	1,459	*20·1*	377	234	*18·5*	428	469	*9·5*	9,590	3,563	*23·5*	250	58
	24·7	1,084	1,112	*26·4*	509	403	*28·7*	223	347	*22·2*	5,641	1,410	*28·7*	106	20
	37·2	874	713	*40·7*	302	190	*35·1*	264	216	*28·2*	4,362	1,670	–	–	–
										39·4	640	461	–	–	–
Totals.		7,862	5,693	–	2,614	1,788	–	2,305	1,424	–	–	–	–	5,394	424
											200,424 or 36,807	28,442 or 13,422			

* Depth corrected for error due to depth recorder (see text, p. 431).

TABLE II.

Measurements of Total Length of Female Calanus in Millimetres.

Mm.	April 9th.	13th (i).	13th (ii).	22nd.	26th.	May 6th.	19th.	June 3rd (i).	3rd (ii).	3rd (iii).	4th (iv).	4th (v).	25th.	30th.	July 6th.	13th.	15th.	26th.	Aug. 4th.	Sept. 22nd.
2·695	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
2·75	2	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–
2·805	–	2	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–	6	3	–
2·86	3	6	1	2	5	–	–	–	–	–	–	–	1	–	1	1	4	4	2	5
2·915	5	12	4	3	5	1	–	–	2	1	1	–	–	1	1	5	6	14	5	6
2·97	10	20	11	9	10	4	–	–	1	1	3	–	6	2	4	11	11	20	21	13
3·025	26	32	28	20	10	2	3	6	3	5	8	7	11	6	7	14	15	32	41	28
3·08	19	33	22	24	18	3	4	6	8	13	9	7	14	9	16	21	19	20	39	23
3·135	45	34	29	40	26	14	8	15	14	15	18	10	13	18	25	53	24	23	55	20
3·19	59	38	22	54	29	18	16	23	24	26	27	20	38	23	27	27	11	20	45	15
3·245	52	27	20	40	27	8	12	48	35	34	29	28	55	41	34	29	7	6	37	14
3·3	70	30	26	101	65	45	15	66	51	52	55	59	62	40	38	24	5	2	17	7
3·355	31	19	11	45	60	32	20	67	55	54	72	52	55	28	33	9	3	3	5	1
3·41	23	10	15	50	57	44	31	77	58	53	70	54	34	28	11	5	1	–	5	–
3·465	9	6	5	22	34	36	50	53	51	64	59	42	23	10	4	1	1	–	–	–
3·52	3	1	3	17	20	28	46	47	27	30	29	26	15	8	7	–	–	–	–	–
3·575	2	2	1	6	14	28	52	24	16	21	36	22	5	3	2	–	–	–	–	–
3·63	1	–	1	1	2	11	32	12	11	12	8	10	1	1	–	–	–	–	–	–
3·685	2	–	–	3	2	6	19	8	2	5	6	2	1	–	–	–	–	–	–	–
3·74	–	–	–	1	–	5	10	4	–	1	1	2	–	–	–	–	–	–	–	–
3·795	–	–	–	–	2	–	3	–	1	–	2	–	–	–	–	–	–	–	–	–
3·85	–	–	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–
3·905	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–
3·96	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4·015	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Totals.	362	275	199	443	388	286	323	456	359	387	433	342	334	218	210	200	107	152	276	132

TABLE III.

Measurements of Total Length of Male Calanus in Millimetres.

Mm.	April 9th.	13th (i).	13th (ii).	22nd.	26th.	May 6th.	19th.	June 3rd (i).	3rd (ii).	3rd (iii).	4th (iv).	5th (v).	25th.	30th.	July 6th.	13th.	15th.	26th.	Aug. 4th	Sept. 22nd.
2·75	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	3	–	–
2·805	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	1	–
2·86	–	–	–	3	–	–	–	–	–	–	–	–	–	2	1	6	2	6	5	–
2·915	–	–	–	2	–	–	1	–	2	4	1	–	3	2	4	9	3	23	23	5
2·97	–	–	3	2	1	–	1	1	–	1	1	–	4	13	9	18	2	14	18	6
3·025	2	4	3	4	3	–	1	3	1	4	3	3	7	17	18	30	7	13	22	2
3·08	8	4	2	2	6	2	4	9	4	6	8	7	10	27	30	31	3	8	22	3
3·135	9	4	2	7	5	3	4	8	13	24	13	23	27	36	37	21	1	2	7	2
3·19	13	4	4	10	11	4	10	22	28	20	22	23	31	33	34	9	–	–	2	–
3·245	5	4	6	12	7	6	20	18	40	23	14	29	20	12	12	2	–	–	–	–
3·3	2	3	4	16	28	12	24	21	34	26	17	41	15	11	6	1	–	–	–	–
3·355	3	1	2	9	8	10	33	15	17	14	25	12	4	1	1	–	–	–	–	–
3·41	–	2	1	12	6	8	23	9	11	8	10	8	1	–	–	–	–	–	–	–
3·465	–	–	1	1	5	1	18	4	2	4	4	4	–	–	–	–	–	–	–	–
3·52	–	–	–	–	1	2	5	2	1	–	3	–	–	–	–	–	–	–	–	–
3·575	–	–	–	–	1	3	6	–	–	–	–	1	–	–	–	–	–	–	–	–
3·63	–	–	–	–	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Total.	42	26	28	80	83	51	151	113	153	134	121	151	122	154	152	128	18	76	100	18

TABLE IV.

Measurements of Total Length of Calanus Copepodid Stage V.

Mm.	April 9th.	13th (i).	13th (ii).	22nd.	26th.	May 6th.	19th.	June 3rd (i).	3rd (ii).	3rd (iii).	4th (iv).	4th (v).	25th.	30th.	July 6th.	13th.	15th.	26th.	Aug. 4th.	Sept. 22nd.
2·31	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
2·365	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1
2·42	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	1	4	5
2·475	3	1	3	1	1	–	–	–	–	–	–	–	1	–	3	2	3	5	3	13
2·53	–	3	1	–	1	–	–	1	–	1	–	–	3	–	4	–	1	4	10	11
2·585	5	5	6	2	–	–	–	–	2	–	1	1	–	–	6	2	3	12	25	21
2·64	2	3	4	6	1	1	1	–	4	1	2	–	3	1	8	2	2	15	34	25
2·695	7	7	5	7	–	1	1	1	5	1	2	1	5	1	20	9	11	13	41	25
2·75	9	4	13	11	8	10	3	1	8	6	8	2	8	2	24	11	8	13	81	53
2·805	2	6	5	9	11	5	1	1	7	8	4	1	9	4	25	15	–	5	59	30
2·86	17	2	6	7	17	7	1	4	10	15	3	8	5	11	36	3	5	2	55	23
2·915	9	6	15	20	15	10	1	11	17	15	10	4	6	7	17	–	–	–	19	14
2·97	4	2	1	12	16	7	3	2	12	22	8	7	2	4	12	–	–	–	2	2
3·025	2	1	3	12	29	10	7	5	17	4	5	5	2	1	1	–	–	–	–	–
3·08	1	1	–	8	22	9	3	2	6	3	1	2	–	–	–	–	–	–	–	–
3·135	–	–	–	3	13	5	1	1	–	2	–	–	–	–	–	–	–	–	–	–
3·19	–	–	–	–	3	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3·245	–	–	–	–	1	2	2	–	–	–	–	–	–	–	–	–	–	–	–	–
3·30	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Total.	61	43	62	98	139	72	24	29	88	79	45	31	44	31	156	44	35	70	334	223

TABLE V.

LENGTHS OF FEMALE, MALE, AND STAGE V CALANUS IN MILLIMETRES AS MEDIAN (Q_2), AND UPPER (Q_3) AND LOWER (Q_1) QUARTILES.

	Females.			Males.			Stage V.		
	Q_1	Q_2	Q_3	Q_1	Q_2	Q_3	Q_1	Q_2	Q_3
April 9th	3·16	3·24	3·34	3·14	3·20	3·27	2·74	2·87	2·92
,, 13th (i)	3·06	3·18	3·30	3·11	3·21	3·30	2·59	2·76	2·92
,, 13th (ii)	3·09	3·20	3·32	3·11	3·25	3·37	2·71	2·80	2·93
,, 22nd	3·20	3·31	3·39	3·19	3·29	3·37	2·79	2·93	3·02
,, 26th	3·23	3·35	3·44	3·21	3·31	3·37	2·90	2·97	3·10
May 6th	3·32	3·43	3·53	3·28	3·34	3·42	2·87	2·99	3·05
,, 19th	3·41	3·52	3·61	3·29	3·37	3·44	2·87	3·04	3·09
June 3rd (i)	3·31	3·40	3·49	3·20	3·28	3·33	2·87	2·95	3·04
,, 3rd (ii)	3·33	3·39	3·48	3·22	3·28	3·34	2·83	2·94	3·03
,, 3rd (iii)	3·30	3·40	3·49	3·17	3·26	3·33	2·87	2·94	3·00
,, 4th (iv)	3·31	3·40	3·43	3·20	3·29	3·38	2·78	2·93	3·00
,, 4th (v)	3·31	3·39	3·49	3·20	3·28	3·33	2·88	2·96	2·97
,, 25th	3·24	3·32	3·40	3·14	3·20	3·27	2·74	2·82	2·91
,, 30th	3·23	3·31	3·39	3·09	3·14	3·22	2·81	2·90	2·95
July 6th	3·18	3·28	3·36	3·09	3·15	3·20	2·75	2·84	2·90
,, 13th	3·12	3·18	3·27	3·02	3·08	3·14	2·73	2·79	2·83
,, 15th	3·04	3·13	3·20	2·96	3·04	3·08	2·59	2·73	2·78
,, 26th	3·00	3·08	3·17	2·92	2·97	3·04	2·62	2·69	2·76
Aug. 4th	3·07	3·16	3·23	2·95	3·03	3·09	2·70	2·78	2·85
Sept. 22nd	3·04	3·11	3·21	2·96	3·01	3·10	2·65	2·76	2·83

TABLE VI.

PERCENTAGES OF FEMALES, MALES, AND STAGE V CALANUS IN EACH CATCH.

		April 9th.	,, 13th (i).	,, 13th (ii).	,, 22nd.	,, 26th.	May 6th.	,, 19th.	June 3rd.	,, 25th.	,, 30th.	July 6th.	,, 13th.	,, 26th.	Aug. 4th.	Sept. 22nd.
Surface	♀	92	100	62	88	41	33	–	95	50	100	48	100	100	44 51	55
	♂	8	–	9	–	4	–	–	5	–	–	16	–	–	4 4	2
	V	–	–	29	12	55	66	–	–	50	–	36	–	–	52 45	43
II	♀	91	94	70	83	77	83	67	93	92	50	54	55	62	29	38
	♂	4	6	7	4	3	1	21	2	1	50	17	25	7	32	3
	V	5	–	23	13	20	16	12	5	7	–	29	19	31	39	59
III	♀	89	77	71	70	60	76	69	90	71	59	35	40	48	36	21
	♂	2	6	14	11	20	7	25	7	24	32	30	48	24	13	9
	V	9	17	15	19	20	17	6	3	5	9	35	12	28	61	66
IV	♀	75	72	66	75	61	60	72	57	57	57	31	58	42	44	26
	♂	12	13	4	16	21	25	25	33	33	32	38	36	46	11	6
	V	13	15	29	9	18	15	3	10	10	11	31	6	12	45	68
V	♀	72	82	56	64	79	64	58	59	58	50	39	48	36	47	20
	♂	11	8	16	19	14	18	40	36	34	47	40	36	56	18	4
	V	16	10	26	17	7	18	2	5	8	3	21	14	8	35	76
VI	♀	65	76	–	58	60	–	58	63	54	49	38	54	44	25	–
	♂	14	8	–	15	21	–	40	30	33	43	31	34	36	18	–
	V	21	16	–	27	19	–	1	7	13	8	31	12	20	57	–
VII	♀	–	–	–	72	–	–	–	–	–	–	–	–	–	–	–
	♂	–	–	–	15	–	–	–	–	–	–	–	–	–	–	–
	V	–	–	–	13	–	–	–	–	–	–	–	–	–	–	–

TABLE VII.

ACTUAL NUMBERS OF CALANUS COPEPODID STAGE V TAKEN IN EACH HAUL.

	April 9th.	13th (i).	13th (ii).	22nd.	26th.	May 6th.	19th.	June 3rd.
	"	"	"	"	"		"	
S	–	–	6	29	193	6	–	–
II	47	4	131	239	153	944	185	107
III	249	10	193	597	1,696	726	371	1,338
IV	474	267	255	149	556	816	222	1,908
V	199	39	106	478	200	747	191	1,405
VI	338	37	–	386	234	–	55	2,938
VII	–	–	–	250	–	–	–	–

	June 25th.	30th.	July 6th.	13th.	26th.	Aug. 4th.	Sept. 22nd.
	"	"		"	"		
S	5	–	177	–	–	207,168 10,205	2,592
II	85	–	1,493	208	379	6,583	2,277
III	254	138	1,697	175	259	13,497	847
IV	487	532	1,191	39	123	5,769	652
V	307	106	584	148	50	3,248	404
VI	457	341	713	68	20	1,459	–

Further Photo-electric Measurements of the Penetration of Light into Sea-Water.

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With 1 Plate and 4 Figures in the Text.

Introduction.

Descriptions have been given in previous papers (**1** and **2**) of some measurements, carried out during the autumns of 1924 and 1925, on the penetration of light into sea-water near Plymouth; a review has also been given by one of us (**3**) of previous work on submarine illumination with special reference to plant distribution. Various circumstances combined to prevent the carrying out of any further work at sea until the autumn of last year (1927). In the interval, considerable modifications, which our previous experience had shown to be desirable, were made in the apparatus, and tests were carried out on the colour-sensitivity of the cells employed. Before giving details of the most recent marine measurements, a brief account will be given of the various modifications introduced and the laboratory tests which they involved.

For a detailed description of the apparatus reference must be made to the previous papers (**1**) and (**2**). The method consists in passing the current which flows through a photo-electric cell, under the influence of the light to be measured, through a known high resistance, and balancing the pressure drop across the latter against a potentiometer. A telephone is used as a detector, the current due to lack of balance being rendered intermittent by means of a special interrupter, and amplified by means of a 2-valve amplifier. By this means it is possible to measure currents down to about 10^{-9} ampere even when the steam trawler, on board which the work is done, is rolling heavily.

A general idea of the apparatus may be gained from Plate I, Figs. *A* and *B*. *A* shows the apparatus lying on the port side of the counter. The

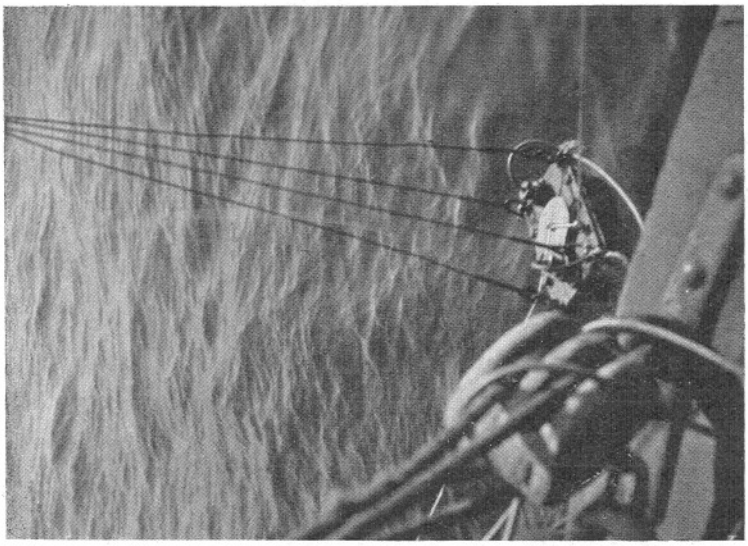
box projecting into the top left-hand corner contains the submarine photometer (K) lying under its coiled cable ; lower down is seen a portion of the deck photometer (G), mounted on gimbals ; near this is submarine photometer L, recognised by its thicker cables. The negative leads from all the photometers are attached to a 'bus bar on the positive terminal of the potentiometer in the large box, the positive terminals of the cables being plugged into the high-tension battery held in position by the bands and paraffin wax blocks seen on the left side of the large box. Note the arrangement of the strings for opening and closing the lid of L, also the loop attachment of the cable to avoid a sharp bend due to sagging. On the near left-hand corner of the large box is the rheostat for the valve filaments, next to it being the switch. Below these lies the 100,000 ohms resistance. The front portion of the box is occupied by the potentiometer, under which lie the two dry cells for the valves, also the condenser used to increase the sensitivity. On the back wall of the box the amplifier may be seen, with telephones attached to the right-hand corner, next to which is the high-tension battery for the amplifying valves. Below this the standard cell is secured, but it is in the shade ; next it the potentiometer accumulator may be seen, and then the interrupter, showing vanes, counterpoise piece, winding key, and lever. For use, the box of apparatus was conveniently placed and lashed down on a shelf in the deck-house a few feet forward from the counter. In damp weather "dark currents" were minimised by opening a door communicating indirectly with the engine-room and by keeping a Primus stove, also lashed down, burning on the floor of the cabin.

The G photometer, mounted on gimbals, was placed on the deck-house roof, so as to be as clear as possible from all obstructions ; the cables enter on the A azimuth of the photometer (see later). It was most convenient to turn this aft, so, as the ship's stern was always turned as nearly towards the sun as the wind allowed, the sunlight always fell within the 180° of azimuth D, A, B.

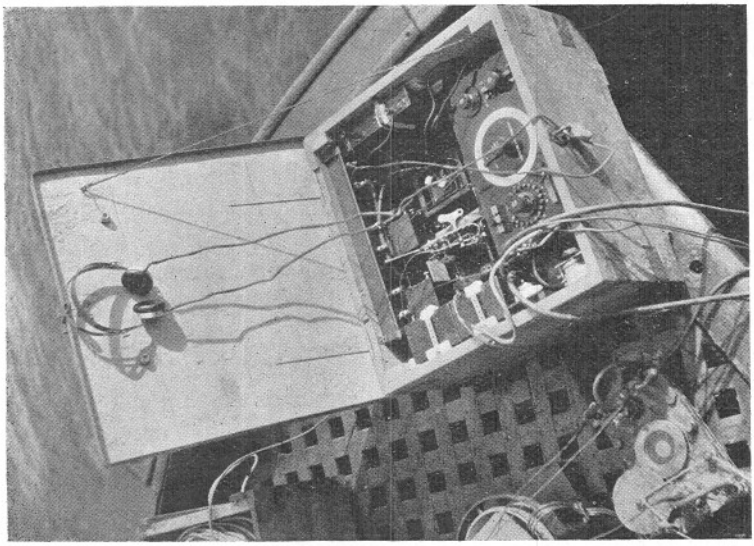
Figure *B* shows one of the photometers being lowered, from a short pole lashed on to the boom, by a steel cable. The cables are being paid out amidships, the opening and closing strings being worked from starboard and port respectively. The raised centre bolt-head, seen more clearly in plate, *A*, acts as a stop when the closing string is pulled taut.

Modifications in the Current-measuring Apparatus.

The original interrupter proved to be rather delicate, and, as already mentioned, had to be kept at a distance from the rest of the apparatus, otherwise the current working the electric buzzer, which operated it, induced currents in the main circuits, and thus prevented the attainment



B.



A.

of a sharp balance. Similar effects upon the wires connecting the interrupter were occasioned by the electric lighting and power circuits in the laboratory, so that the apparatus was most conveniently used when all were switched off, or in a shed at Cawsand remote from external currents, or at sea. Accordingly, a new interrupter was made, which, being actuated by a clock spring, did not cause any induced currents, and, thus, could be mounted in the box with the rest of the apparatus. This eliminated the interference caused by electric light mains.

This interrupter is constructed almost entirely of Meccano parts, and consists of a spring motor driving a short train of gear wheels, the last spindle of which carries an aluminium air vane to reduce the speed of rotation to a suitable value. The same spindle carries a ratchet wheel, on which a smooth wheel rolls. The axle of the latter supports a light framework which is pivoted on an insulated fixed axle and counterpoised, so that there is only very light contact between the smooth and ratchet wheels. The current to be interrupted is led in to this insulated axle, and passes from that through the pivoted frame and the wheels to the main frame of the motor. As the smooth wheel only touches the tops of the teeth of the ratchet wheel and breaks contact in the intervening spaces, the circuit is broken once for every tooth. It is found best to arrange that the speed of rotation of the ratchet wheel is comparatively slow, say a few revolutions per second. The variation in speed, caused by the running down of the clock spring, does not appreciably affect the sensitivity. Winding, which is required about every five minutes, is facilitated by a ratchet gear.

The interrupter is mounted on rubber buffers and felt pads in the box containing the rest of the apparatus. The rubber insulates it from the box, and helps to deaden the noise made by the wheels. This is further assisted by the felt pads which are interposed between the rubber and the box.

As this interrupter does not cause any induced currents a rather sharper balance is attainable. This renders it advantageous to increase the resistance across which the potential difference is measured. Moreover, the resistance previously used had to be discarded, as its very fine wire broke somewhere inside the vitreous insulation, causing the resistance to become almost infinite. Accordingly, it was replaced by a well-insulated bobbin-type variable resistance. This can be increased in steps of 10,000 ohms from 0 to 100,000 ohms. For the small currents available with photo-electric cells it was always used at its maximum value. This makes one potentiometer scale division represent 10^{-9} ampere. Under favourable circumstances a measurement could be made to within about 0·5 scale division, or 5×10^{-10} ampere. For these measurements the potentiometer was used on its lower range, namely, with the one-tenth multiplier plug in position.

Modifications in the Old Photometers G and K.

It was found that the matt varnish used for obtaining a diffusing surface on the photometer windows darkened with time. In addition, it caused a large loss of sensitivity even when new. Accordingly, it was discarded, and windows of glass, ground on the inner face, substituted on both the photometers. Unfortunately, the diffusing properties of ground glass are very poor, so that the effect of obliquity of illumination is quite different for such a photometer from that for a perfectly diffusing surface. Moreover, even if the photometer window is horizontal (the usual working position), the effect of illumination by a beam light of a given altitude generally varies considerably with the azimuth of the beam relative to the photometer. Thus it was necessary to calibrate the photometers for the effects of the altitude and the azimuth of the illumination, as described later.

The new window of the air photometer (denoted henceforth by the letter G) is 12 cm. in diameter. It is surrounded by thin sheet zinc, so that there is no appreciable screening of low angle light. The potassium vacuum photo-electric cell is mounted just below the centre of the window. As no diaphragm is introduced between the cell and this large window, it is possible that some light enters the cell through apertures in the metallic coating, in addition to what comes in through the actual pupil of the cell. This may account for some of the differences in sensitivity found for beams of the same altitude, but of different azimuths. This view is supported by the fact that, in the two submarine photometers, which have small windows, and are fitted with reflecting collars to direct all light entering the window into the pupil of the cell, the effect of azimuth is much less important. Moreover, when a thin sheet metal diaphragm of about 5 cm. aperture was placed over the window of the air photometer, not only was the average effect of altitude changed, but, in addition, the relative sensitivities at different azimuths was entirely altered. It is accordingly proposed to try the effect of fitting a diaphragm tightly round the cell pupil, so as to prevent the entry of any light except through the pupil itself.

The sensitivity of the submarine photometer (K) (which contains a gas-filled potassium-hydride cell of the Kunz type) to oblique light could not be increased by increasing the size of the window, in view of the pressure which it must bear. Some improvement in the oblique sensitivity was effected by the use of a cylindrical collar, of sheet aluminium, about 3 cm. diameter by 0·75 cm. deep, the surface being matted and coated with celluloid varnish. This fits closely round the rim of the pupil of the cell and fills up the space between this rim and the rim of the window in the gun-metal case. Thus, most of the oblique light which,

if it passes through the marginal parts of the window, might otherwise not enter the cell, is reflected so as to do so.

The loss of light is much less in this ground-glass window than in the matt-varnished one previously employed ; the window is somewhat larger, the mirror reduces internal losses, and, finally, the sensitivity of the current-measuring apparatus is nearly twice as great, so the light sensitivity has been so much increased that it has been possible to extend the measurements to almost twice the depth. This has necessitated the fitting of connecting cables each about 90 metres long. In order to prevent these from being unduly heavy they have a lesser thickness of rubber insulation than those used previously, being only about 7 mm., over-all diameter, instead of 11 mm.

New Vacuum Submarine Photometer L.

As it was considered that more reliance could be placed on the results if they were not entirely dependent on the readings of a gas-filled cell, a new submarine photometer (L) has been made. The case is similar to the old one. A modified form of shutter, which can be more readily opened and closed by two strings, has been fitted to both photometers.

A large vacuum cell, specially made by the General Electric Co., is fitted in this photometer in place of the Kunz cell. Apart from the difference between the cells, the chief optical difference between the photometers lies in the fact that in L the reflecting collar is conical, and made of polished silver, widening from 2·0 cm. internal diameter, where it is in contact with the rim of the window, to 2·7 cm. where it meets the rim of the pupil of the cell. This conical mirror is more effective than the cylindrical one in increasing the relative sensitivity to oblique light. The reduction of the effective aperture from 3 cm. to 2 cm. reduces the sensitivity to direct light ; but, for the diffuse light occurring in the sea, the reduction caused by the mirror is small. This L photometer is fitted with the 11 mm. cables, which had previously been used on the K photometer. The length (45 metres) of these cables is, perhaps, sufficient, as, owing to the relative insensitiveness of the vacuum cell, this photometer can only be used at lesser depths than can the K photometer. It has, however, been used down to 40 metres, which is 5 metres deeper than the greatest depth at which the K photometer was worked in 1925. The latter has now been used down to 65 metres.

Standardisation of Photometers.

As before, an open carbon arc lamp was used for standardising the vacuum photometers, but the process has been simplified by making use of the work of Forrest (**4**) and Allen (**5**). The former has shown that

the luminosity perpendicular to the face of the positive carbon is about 173 candle-power per square mm., and the latter found that under the conditions of his work the current was 0·746 ampere per square mm. Combining these two we get 232 c.p. per ampere in a direction perpendicular to the face of the positive carbon.

The carbons (7 mm. solid) were vertical, the positive being above, and a magnified image of the arc was thrown on a screen by means of a lens. This enabled us to ensure (*a*) that the end of the positive carbon was maintained in the same position, (*b*) that the end was very nearly horizontal, and (*c*) that the arc was sufficiently long to ensure that, at an angle of 45° to the vertical, no part of the positive carbon was blocked out by the negative one. The photometer to be tested was fixed at a measured distance (15 to 20 cm.) from the positive crater, the line joining the crater and the centre of the pupil making an angle of 45° with the vertical and being perpendicular to the window of the photometer. The candle-power of the arc along this line was obviously $0{\cdot}707 \times 232$ times the current in amperes. Thus, by measuring this current with a good ammeter, when the conditions were steady, the illumination on the photometer was found. About eight to ten readings of the photo-electric current were taken, the extreme readings deviating about 5% from the mean.

In this way it was found that a current of 10^{-9} ampere through the air photometer G represented an illumination of 69·5 metre candles. The same current through the new submarine photometer L corresponded to 17·8 metre candles. There was obviously no use in standardising the old submarine photometer in this way, as its sensitivity varies from day to day. Both of these standardisations were made with an anode potential of 60 volts. Tests of the effect of anode potential on the sensitivity of G showed that for voltages between 60 and 120 the sensitivity increased about 0·39% of its value at 60, per volt. For L the corresponding figure was 0·36%, the characteristics of the two photometers being very similar over a range of voltages 12 to 120.

In the previous standardisations the line of illumination made an angle of 63° with the axis of the carbons, the current being 10 amperes. This should, on the above assumptions, have given a candle-power of 1053, if the face of the carbon was at right angles to its axis. The candle-power actually measured was 1250 on one occasion and 953 on another. The variation may have been partly due to slight obliquity of the carbon face, and partly to differences in the positive carbons, which in these earlier measurements were 12 mm., cored. The general agreement between the two methods of finding the candle-power of the arc is, however, quite satisfactory. Tests of G by this method, with the old matt-varnished window darkened with age, showed a sensitivity of 10^{-9} amp. per 200

metre candles. The sensitivity found by the old method, when the window was new, was 150 m.c.

Test Lantern for Detecting possible Changes in Sensitivity.

Although there is no evidence of any change in the sensitivity of the G cell in the course of some years, a test lantern has been constructed as a check on possible changes.

It consists of a large white enamelled iron tumbler, through the bottom of which a circular hole is bored large enough to take a small lamp-holder which carries a 6-volt, 18-watt vacuum lamp. The flexible leads are soldered to the lamp contacts, so as to eliminate the possibility of errors due to variations in the resistance of the lamp-holder contacts. When this lantern is placed standing on its rim centrally on the photometer window the lamp is at a fixed distance from the cell. The voltage applied to the ends of the lamp leads was varied from 5·0 to 5·6, and the corresponding relative changes of illumination measured by the L photometer. In this way it was found that small variations of voltage in the immediate neighbourhood of 5·50, which was taken as the standard, caused a change of illumination of 80% per volt.

The lantern was standardised for each photometer shortly after the latter had been standardised with the arc, and the illumination in metre candles recorded. This illumination will generally differ for different photometers. Thus with G, the test lantern gave an illumination of 3000 m.c., while with L it only gave 2100 m.c. This difference is to be ascribed to the facts that (*a*) with L the lantern stands on the brass rim and not directly on the window, and the window itself is thicker, so that the lamp is over a centimetre further from the cell, (*b*) L is relatively less sensitive to the oblique light reflected from the white enamel, and (*c*) L is relatively less sensitive to yellow and green light than G.

As this lamp is only used occasionally for a few minutes, and at a reduced voltage, its candle-power should remain approximately constant for years. Tests of photometer G made in Dublin and Plymouth, respectively, with an interval of nearly five months, gave almost exactly the same sensivity.

Effect of Obliquity of Illumination.

A 12-volt, 48-watt gas-filled lamp (head-lamp type) was mounted on a circular brass scale, divided in degrees, so that the filament of the lamp could be placed anywhere on a vertical semicircle 14·5 cm. radius, at the centre of which the pupil of the photometer was placed with the window

horizontal. In this way the effect of obliquity was found for four rectangular azimuths for each photometer. The results are plotted in Fig. 1, which shows the relative effect of a beam of parallel light of variable altitude for four rectangular azimuths A, B, C, and D with photometer G, and the mean effects for K and L. In the latter cases the differences between the various azimuths were very much smaller than with G.

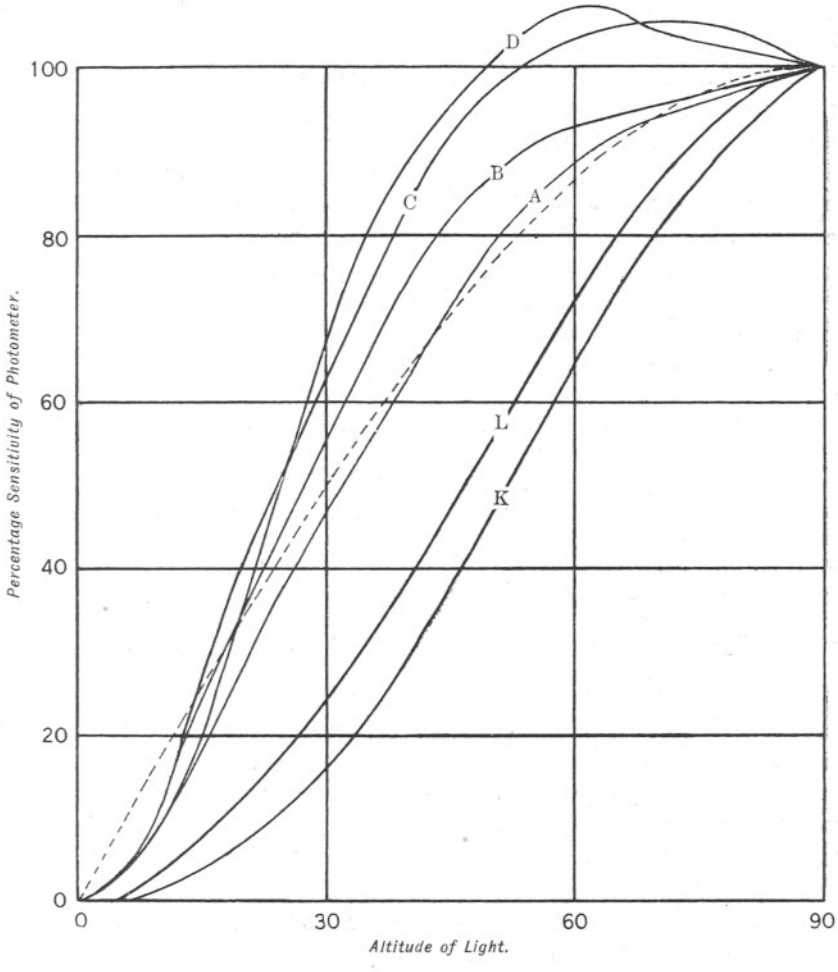


FIG. 1.—The ordinates are percentage sensitivities of the photometers and the abscissæ the altitude of the light source in degrees. Curves A, B, C, and D show the relative effects of a beam of parallel light of variable altitude for four rectangular azimuths on photometer G. Curves K and L show the mean effects for each of the four azimuths for these photometers, the differences between the various azimuths were very much smaller than with G. The dotted sine curve shows what the effect would be with a perfect diffusing surface and no reflection losses at the front surface of the window.

The dotted sine curve shows what the effect would be if the diffusing surface were perfect, and reflection losses at the front surface of the window absent. It will be observed that K and L are both very insensitive to oblique light. G, except at very low altitudes, is, for most azimuths, more sensitive to oblique light than it would be if the diffusing properties of the window were perfect. The ratio of the sine of the altitude to the ordinate of the given obliquity curve at that altitude gives the factor by which the reading of the photometer must be multiplied to obtain the vertical illumination V_a when the photometer is used in air. This corresponds to the factor f (**2**, p. 184), which effected the correction for the reflection loss, since in these earlier experiments the diffusing surface itself was almost perfect. The value of the obliquity factor for diffuse light is found, as before, by dividing the sky into 9 zones.

The water photometers K and L were tested with their windows covered with water. This is their usual condition when they are being calibrated at sea. This thin layer of water increases the sensitivity by 1·7% for vertical light and rather more for oblique light, but the effect is small compared with other sources of error, so that its presence or absence is of little importance. When a photometer is in use under water it is the light *in the water* that we are interested in, but when it is being calibrated above water by comparison with the G photometer it is the light *in the air* that is the same for both, the light in the water covering the photometer window being less in the ratio $\frac{V_w}{V_a}$ (**2**, p. 184) since the surface of this layer is unruffled. Thus to obtain the submarine vertical illumination we must multiply the submerged reading by the value of $\frac{V_w}{V_a}$ for the given conditions. The most convenient method is to combine this factor with the obliquity factor, so that for a given photometer we have different obliquity factors according as the photometer is used in air or in water.

As will be seen later, there is good reason to think that, except, possibly, within a few metres of the surface, the average obliquity of the submarine illumination is almost independent of that in the air above. It apparently does not differ greatly from the value found by calculation for a smooth water surface and a uniform sky. Thus all submarine readings of either photometer have been multiplied by the obliquity factor of that photometer, for these conditions.

Colour-Sensitivity of the Photometers.

A simple form of spectrum projector was constructed as follows. A Pointolite lamp, run off an 84-volt storage battery, was mounted on the

carriage of an old vernier microscope, so that it could be moved at right angles to the axis of a Grubb portrait lens of about 22 cm. focus and 6 cm. aperture. Behind this was a 60° carbon disulphide prism of 6 cm. edge, forming a rather impure, but very bright, spectrum at a distance of nearly a metre behind the lens. This was thrown on a very wide " slit " about 5·5 mm. wide, behind which the photometer could be placed. Thus, by screwing the carrier holding the lamp along its scale the band of the spectrum entering the cell could be changed. Special precautions were taken to reduce stray light as much as possible. The apparatus was standardised by covering the " slit " with tissue paper and observing the diffused, emergent light with a direct vision spectroscope. This enabled the mean wave length, and the total width of the spectrum band corresponding to any given setting of the lamp, to be found. This width varied from about 500 Å.U. for the red end of the spectrum to 300 in the green and 200 in the blue-violet.

The energy in this band was measured with a Moll vacuum thermopile and a very sensitive Kipp und Zonen Type Z galvanometer. Although the low resistance of this galvanometer renders it more suitable for thermo-electric than for photo-electric work, it was found to be quite sensitive enough to measure the photo-electric currents flowing in this test. Accordingly, it was used for both thermopile and photometers, and the ratio of the photo-electric to the thermo-electric current, for any given lamp setting, was taken as the relative sensitivity of the cell for light of the wave length corresponding to the centre of the spectrum band used.

The curves obtained for the three photometers, and also for three other photometers, H, N, and C, used in light measurements on shore, are shown in Fig. 2. H contains a vacuum potassium cell, similar to G, but somewhat larger and considerably more sensitive. N contains a vacuum sodium cell, and C a gas-filled cæsium cell.* The impurity of the spectrum probably has the effect of rendering the values given for the sensitivity near the red end of the range somewhat too high. It is hoped to modify the arrangement so as to increase considerably the purity of the spectrum, without rendering the quantity of energy transmitted towards the blue end of the spectrum too small for accurate measurement.

The results show good general agreement with those of other workers. The three photometers, G, H, and L, employ potassium as an active element. Even these show appreciable differences in colour sensitivity. K contains a Kunz gas-filled cell, and, we believe, has a potassium hydride kathode. This, as is known, is relatively more sensitive to green light than cells with pure potassium kathodes. The slight difference between the colour sensitivities of K and L should be remembered when considering the results obtained with them under water. Its effect

* Obtained from the Cambridge Sci. Inst. Co.

was apparently small, as the absorption coefficients obtained with the two photometers generally agreed closely.

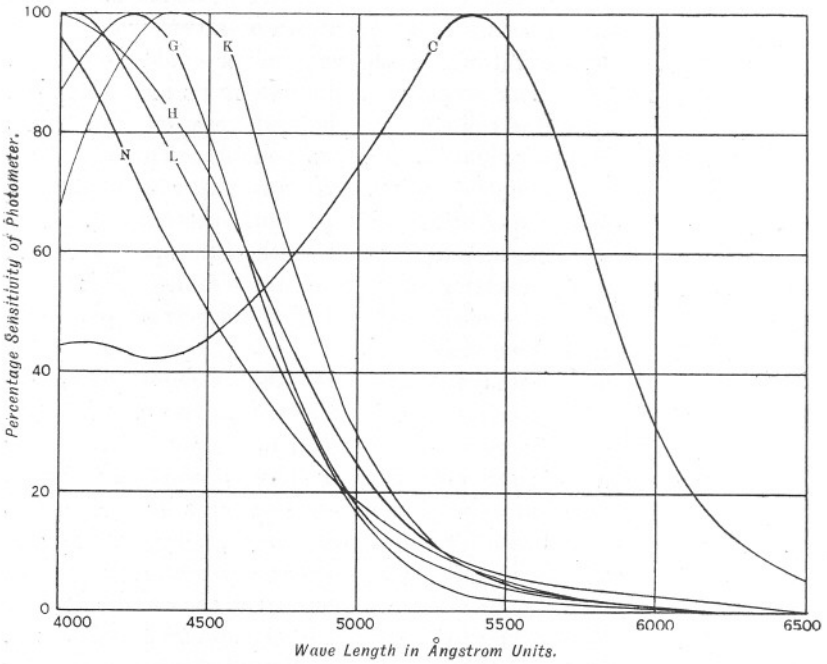


FIG. 2.—The ordinates show the percentage sensitivity of the photometers for various wave lengths as plotted in Ångstrom units on the abscissæ. The photometers contain photo-electric cells as follows: C, a gas-filled cæsium cell; K, a gas-filled potassium-hydride cell; G, H, and L, vacuum potassium cells; N, a vacuum sodium cell.

SUBMARINE MEASUREMENTS, 1927.

The greatly increased sensitivity of K rendered it expedient to reduce further the anode potential when making the above-water calibrations at the commencement and end of each series.

In the first 1927 measurements 12 volts was used. As this gave a very large current (5×10^{-6} amp.) with strong sunlight, it was subsequently reduced to 7 and, later, to 3 volts. The latter voltage is quite sufficient, as it generally renders K more sensitive than G, and will be used in future.

The anode potential of the standard photometer G was always about 67 volts, small corrections being made for the effect of small voltage changes on the sensitivity. L, which was not used as a standard, can safely be used in any light with anode potentials up to at least 120 volts, but the increase in sensitivity caused by raising the voltage above 60 is small, and it was generally used with a potential of 60–70 volts.

In the open sea it is only under exceptional circumstances that the light within a few metres of the surface is steady enough to be measured by our method. Accordingly, the usual procedure during 1927 was to make the shallowest submarine set of readings at 5 metres below the surface, and further sets at intervals of 5 metres down to the limit imposed either by the depth of the water or by the sensitivity of the photometer.

For comparatively shallow readings and bright surface light L is superior to K, owing to its freedom from the troublesome changes of sensitivity to which the latter is liable. It is, however, not suitable for measuring illuminations much below 100 m.c., so for the deeper readings K must be used.

When using K the anode potential needed to be raised, at a depth of 15 or 20 metres, in order to increase its sensitivity. The voltage used for these intermediate depths was usually either 39 or 67, these sockets in the high tension batteries being conveniently placed for plugging in the wander plug attached to the positive lead. A comparison of the readings with the different potentials enabled the voltage factor, correcting for increase in sensitivity, to be ascertained. At a depth of 25 to 40 metres the sensitivity was further increased by raising the anode potential to 120 volts. Time seldom permitted of a complete series of ascending readings after the greatest depth had been attained ; but sets of readings, at both anode potentials, were taken at those levels at which the voltage had been changed on the descent.

Further determinations were thus made of the voltage factors. The ascending and descending factors generally differed slightly, and the mean was used. The series terminated with a calibration reading. This, with K, might show a variation of sensitivity as high as 30% during the series. The sensitivity was assumed to have changed uniformly with time during the series, and a suitable correction applied to each set of readings. " Dark currents " were rather more troublesome than before. This was partly due to the increased sensitivity of the apparatus and the smallness of the photo-electric currents at the greater depths now attained. The fact that the insulation of the cables of the K photometer is much thinner than formerly probably explains the occurrence of appreciable " soakage " currents, which were now observed for the first time. These become of importance when the anode potential is large and the true photo-electric current small. Under these conditions the values found during the first couple of minutes after connecting the anode potential are appreciably larger than those obtained subsequently. These sources of error were eliminated by keeping the anode potential on continuously and taking alternate readings with the photometer shutter open and closed. Readings of G may be taken with the shutter of K closed, without cutting off the anode potential from the latter.

Calculation of Illumination from Photometer Readings.

It may be as well to collect the various factors, already mentioned, by which the photo-electric currents must be multiplied in order to obtain the vertical illumination. In the case of the standard photometer G, we must multiply by the obliquity factor, as estimated for the given altitude of the sun, its azimuth relative to the photometer, and the relative proportions of sunlight and diffuse light. This factor generally does not differ much from unity.

The vertical illumination in metre candles is then found by multiplying the result so obtained by the number of metre candles corresponding to 10^{-9} ampere for the given value of the anode potential.

In general L was not used as a standard, as its sensitivity had not been checked with the testing lantern since it was standardised some months before, and its relative insensitivity to oblique light, as compared with the perpendicular illumination used in standardisation, rendered it somewhat unsuitable for the direct measurement of daylight. The ratio of its reading at any depth multiplied by the diffuse obliquity factor for water, to its reading in air multiplied by the air obliquity factor for the given conditions, gives the ratio of the submarine vertical illumination at that depth to the surface vertical illumination, which is found from the simultaneous reading of G.

The readings of K are treated in the same way, except that, in addition to the obliquity factor, the submarine reading may require to be multiplied by an anode voltage factor, to allow for increase in sensitivity caused by increase of anode potential, and by a time factor, to compensate for the variation of sensitivity with time.

As an example of the method of calculation we give the figures for Series 22. On this occasion all three photometers were in use, as the weather was so bad that photometer L was used on deck as a substandard instead of G, which was only used at the conclusion of the series for standardising L.

Taking this standardisation first, the anode potential for photometer G was 112·0 volts, which corresponds to a sensitivity of 57·6 metre candles per 10^{-9} ampere. The standardisation was made at 3.45 p.m., at which time the altitude of the sun (α) was 4°. The conditions were such that the direct sunlight was negligible compared with the diffuse light, i.e. $\beta=1$, where β is the ratio of the total vertical illumination to the illumination with the direct sunlight screened off. Hence the obliquity factor for G (f_g) was that for diffuse light, which had been calculated to be 0·915. If sunlight had been present it would have been necessary to interpolate between this diffuse value of f_g and the value for pure sunlight of the proper altitude and relative azimuth (**2**, p. 183). The means

of several alternate readings of photometers G and L were 98×10^{-9} ampere for each photometer. Hence the vertical illumination was $98\times0{\cdot}915\times57{\cdot}6=5{\cdot}16\times10^{3}$ metre candles.

Now the value of the L obliquity factor f_1 for diffuse light in air is 1·56, so the corrected reading of L becomes $98\times1{\cdot}56=153$. Dividing this into 5160 we find that for L one scale unit [10^{-9} ampere] of the corrected reading corresponded to 33·7 metre candles. The anode potential used with L was, on this occasion, only 10·6 volts. The sensitivity deduced for this voltage from the laboratory tests done 8 months before is about 32·5 metre candles, so the agreement is quite satisfactory.

TABLE I.

MEASUREMENTS AT INTERNATIONAL HYDROGRAPHICAL STATION E1, ON DECEMBER 14, 1927.

T	α	ß	d	L	K_3	K_{43}	f_1	f_K	t	V_a	V
1.5 p.m.	15°	1·5	g	482	536	–	1·89	2·31	1·08	30·8	30·8
1.30 ,,	14	1	5	280	162	–	1·56	1·60	1·07	14·7	6·4
1.52 ,,	13	,,	10	321	102	–	,,	,,	1·06	16·9	4·0
2.0 ,,	,,	,,	,,	–	126	630	,,	,,	,,	–	4·9
2.8 ,,	12	,,	20	232	(26·2)	131	,,	,,	1·05	12·2	1·01
2.29 ,,	10	,,	30	266	(12·0)	60	,,	,,	1·04	14·0	0·46
2.44 ,,	9	,,	35	233	(8·4)	42	,,	,,	1·03	12·25	0·32
2.58 ,,	8	,,	20	226	(29·0)	145	,,	,,	1·02	11·9	1·09
3.10 ,,	7	,,	10	185	(77)	385	,,	,,	1·01	9·75	2·86
3.16 ,,	6	,,	,,	–	75	372	,,	,,	,,	–	2·78
3.30 ,,	5	,,	g	134	180	–	,,	1·71	1·00	7·05	7·05

The remainder of the readings constituting Series 22 are shown in Table I. Here T is the clock time (G.M.T.) and d the depth in metres of photometer K, the letter g in this column denoting that it was on the raised stern grating beside the substandard L, whose readings are shown under column L. The columns K_3 and K_{43} show the mean readings of K with anode voltages 3 and 43 (nominal), respectively. It will be noticed that readings at both voltages were made at a depth of 10 metres, both on the descent and on the ascent. The two values found for $\frac{K_3}{K_{43}}$ were 0·200 and 0·201, respectively. The agreement was seldom, however, as good as this, and the usual practice is to take the mean of the descending and ascending values. In this way we get the voltage factor—0·200 in this case—by which the deeper readings must be multiplied to correct for the increased sensitivity caused by the increase in

anode potential. The reduced values obtained in this way are entered in brackets in the K_3 column. For very weak illuminations a further increase in anode voltage up to about 120 would be necessary, the voltage factor being found by comparison of the readings with high and intermediate voltages, respectively. The voltage factor found at 120 volts in another series was 0·029, i.e. raising the potential had multiplied the sensitivity of the photometer by 34.

The obliquity factors for L and K are given under f_l and f_k. During the first set of readings there was appreciable sunlight, β being estimated at about 1·5. Later, owing to clouds and the declining altitude of the sun, β became sensibly equal to unity. Accordingly the first values of f_l and f_k differ from all the others. The first and the last values of f_k are the air factors, the other entries being the value of the diffuse light water factor. The vertical illumination in air, V_a, is equal to $33{\cdot}7 \times f_l \times L$. The unit adopted in the table is 1000 metre candles.

The initial value of the product $f_k K_3$ is 1240, V_a being $30{\cdot}8 \times 10^3$ m.c., this corresponds to an initial sensitivity for K_3 of 24·8 m.c. per unit. The corresponding figures obtained at the conclusion of the series are 308 units, $7{\cdot}05 \times 10^3$ m.c., and 22·9 m.c. per unit. This apparent increase of sensitivity in K by about 8% may be partly due to differences between the actual light distribution and the ideal distributions for which the obliquity factors were calculated, or to the slight difference in colour-sensitivity of the two photometers, K being relatively more sensitive to the longer wave lengths. As, however, a change of sensitivity of K, amounting occasionally to over 30%, commonly occurs during a series, the usual practice is here followed of assuming that the sensitivity changes uniformly with the time, and introducing a time factor t, which makes the two calibrations agree. The product $22{\cdot}9 \times t f_k$ K then gives the vertical illumination V recorded by photometer K, the first and last values, of course, being identical with those for V_a.

The vertical absorption coefficient λ measures the relative reduction of illumination per metre. It is defined by the well-known equation, $V = V_0 e^{-\lambda d}$. If V_1 and V_2 are simultaneous values of V at two points differing in depth by δ metres, evidently $\lambda = \frac{2{\cdot}3}{\delta}\left(\log_{10} V_1 - \log_{10} V_2\right)$. Since, however, we do not measure V_1 and V_2 simultaneously, we must allow for variations in the surface light. The most convenient way of doing so is to record the illumination at any depth as a percentage p of the simultaneous value of the surface light V_a. Then $\lambda = \frac{2{\cdot}3}{\delta}\left(\log_{10} p_1 - \log_{10} p_2\right)$.

Values of p and λ are given in Table 2.

The Results.

The results of the 1927 measurements are given in Table II, the serial numbers being consecutive with those in the last paper. λ, the vertical absorption coefficient of the water, is obtained from the ratio of the values of p for the two depths immediately above and below the given one. In a few cases the mean of these two depths differs somewhat from the depth opposite to which λ is entered. An asterisk in this column indicates that the upper reading used in finding λ is the above-water reading, a surface loss of 15% being assumed. The letter a in the depth column indicates that the photometer was slung just above the water. This was not practicable except in fairly smooth water, as the photometer swayed violently with the rolling of the ship. Under rough conditions the photometer was placed on the fender at the extremity of the counter, on the broad rail of the bulwarks, or on the grating inside the bulwarks. These positions, which are indicated by the letters f, r, and g, respectively, involve less shading by the ship than position a. The effect of this shading is seen in Series 13, where raising the photometer a metre above the surface increased the reading by 20%. The shading effect must also affect the submarine readings by varying amounts, but the errors so introduced are small compared with the large variations in illumination which occur.

If the photometer were suspended from a long spar so as to reduce the shading effect, larger errors would be caused by its greater vertical motion, which would also impose excessive strains on the gear. For the same reason it was found to be absolutely necessary to suspend the photometer on the centre line of the ship, so as to eliminate the effect of rolling.

It will be noticed that the illuminations recorded at a few levels with an ascending photometer usually exceeded those found at the same depth during the previous descending series. The discrepancy is only serious in Series 16, where it is so large as to suggest that an error may have been made in the depth. The cable was marked off in 5-metre lengths, and it is possible that a miscount may have occurred in hauling up, which would explain most of the discrepancy. In other cases the increase can only be explained by assuming that the ship was drifting into clearer water, or that there was a general tendency for the water to clear as the day advanced. In either case the deeper readings would be increased relative to the earlier shallow ones causing an apparent decrease of λ with depth. The effect is generally small, and sometimes absent, or reversed ; but it is worth noting, since it may explain some part of the difference between the 1927 and the 1925 results. The latter were mostly obtained in ascending order, so that the effect of progressive

TABLE II.

Date, Remarks, etc.	T G.M.T.	α	Light	ß	d metres	V_a m.c. $\times 10^3$	V m.c. $\times 10^3$	p %	λ
SERIES 7. 2.9.'27.	11.33 a.m.	46	Bright Sun	4	a	109·5	109·5	100	
L Photometer. About 4	11.47 „	47	„	„	4·9	103	31·4	30·5	0·168*
miles S.W. of Mewstone.	11.54 „	47	„	„	10·0	107	16·9	15·8	0·395
Drifting slowly inshore.	12.2 p.m.	47	„	„	16·3	108	0·00	0·00	
Depth at start 50 m.	12.24 „	47	„	„	14·6	107	0·72	0·67	
(Sounding). Light air S.	12.29 „	47	„	„	12·7	109	3·0	2·75	0·62
Very slight swell. Surface	12.36 „	47	„	„	11·1	108	6·2	5·85	0·48
almost glassy. Cloudless	12.42 „	47	„	„	10·0	107	10·8	10·1	0·241*
sky. High water 8.55 a.m.	12.47 „	46	„	„	a	107	107	100	
SERIES 8. 2.9.'27.	1.52 p.m.	43	Bright Sun	4	a	90	90	100	
L Photometer. Posi-	1.57 „	43	„	„	4·7	88·5	46·0	52	0·147*
tion and conditions ap-	2.2 „	42	„	„	7·6	87	24·0	27·6	0·175
prox. as in Series 7.	2·6 „	42	„	„	10·6	86·5	15·9	18·4	0·130
	2.15 „	41	„	„	12·8	83	11·6	14·0	0·191
	2.22 „	41	„	„	14·7	80	6·7	8·4	0·443
	2.28 „	40	„	„	17·1	78	1·62	2·08	0·500
	2.35 „	40	„	„	19·0	78·5	0·77	0·98	0·509
	2.43 „	39	„	„	20·9	74·5	0·22	0·30	
SERIES 9. 5.9.'27.	12.36 p.m.	—	Sun invisible	1	a	34·7	34·7	100	
K Photometer. At El.	12.44 „	—	most of time	„	5	43·7	5·69	13·0	0·350*
10 miles S.W. of Eddy-	12.54 „	—	„	„	10	44·7	1·14	2·56	0·268
stone. Approx. depth	12.59 „	—	„	„	15	43·6	0·386	0·89	0·215
70 m. (Chart). Light	1.8 „	—	„	„	20	28·8	0·085	0·295	0·151
breeze S.E. Surface al-	1.13 „	—	„	„	25	29·6	0·058	0·196	0·106
most glassy. Uniform grey	1.16 „	—	„	„	30	34·3	0·035	0·102	
sky. High water 10.5 a.m.									
SERIES 10. 5.9.'27.	1.56 p.m.	—	Dull	1	a	30·4	30·4	100	
L Photometer. At El,	2.0 „	—	„	„	1·2	27·9	15·4	55	0·349*
Conditions approx. as in	2.2 „	—	„	„	5	28·6	4·24	14·8	0·318
Series 9.	2.5 „	—	„	„	10	37·2	1·25	3·35	0·266
	2.9 „	—	„	„	15	48·9	0·50	1·03	0·212
	2.18 „	—	„	„	20	36·4	0·146	0·400	0·168
	2.26 „	—	„	„	25	25·3	0·048	0·191	
	2.32 „	—	„	„	20	18·4	0·073	0·396	0·170
	2.38 „	—	„	„	15	17·2	0·243	1·41	0·217
	2.42 „	—	„	„	10	20·7	0·73	3·52	0·232
	2.44 „	—	„	„	5	22·2	3·17	14·3	0·294
	2.48 „	—	„	„	1·2	20·6	9·6	46·5	0·356*
	2.54 „	—	„	„	a	18·6	19·1	102·5	
SERIES 11. 7.9.'27.	1.18 p.m.	44	Bright Sun	4	a	92	92	100	
K Photometer. At El.	1.22 „	44	„	„	1·2	93·5	54·5	58·5	0·318
Light breeze W. Blue	1.26 „	44	„	„	5	100	17·3	17·3	0·308*
sky with light clouds.	1.28 „	44	„	„	10	94·5	3·69	3·90	0·295
High water 1.34 p.m.	1.32 „	43	„	„	15	93·5	0·865	0·925	0·267
Secchi disc, 8 m. at 12.15	1.38 „	43	„	„	20	99·5	0·271	0·272	0·206
p.m.	1.45 „	42	„	„	25	90	0·106	0·117	0·179
	1.52 „	42	„	„	30	89·5	0·0405	0·045	0·148
	1.56 „	41	„	„	35	85·5	0·023	0·027	0·128
	2.5 „	40	„	„	40	83·5	0·0105	0·0125	0·128
	2.12 „	39	„	„	45	83	0·006	0·0075	0·082
	2.16 „	39	„	„	50	80	0·0045	0·0055	0·051
	2.23 „	38	„	3·5	55	79	0·0035	0·0045	0·061
	2.28 „	38	„	„	60	79	0·0025	0·003	
	2.38 „	37	„	„	35	76·5	0·0275	0·036	
	2.46 „	36	„	„	25	75·5	0·182	0·231	
	2·53 „	35	„	„	15	78	1·15	1·47	
	3.1 „	34	„	„	f	74	74	100	

Date, Remarks, etc.	T G.M.T.	α	Light	ß	d metres	V_a m.c. $\times 10^3$	V m.c. $\times 10^3$	p %	λ
SERIES 12. 7.9.'27.	3.10 p.m.	32	Bright Sun	3	f	67	67	100	
L Photometer (without reflecting collar). Conditions approx. as in Series 11.	3.12 „	32	„	„	1·2	65	22·0	34	0·523*
	3.16 „	31	„	„	5	66	4·10	6·2	0·387
	3.19 „	31	„	„	10	65	0·735	1·13	0·306
	3.24 „	30	„	„	15	62	0·180	0·29	0·208
	3.28 „	30	„	2·5	20	58·5	0·083	0·14	0·175
	3.32 „	29	„	„	25	59	0·030	0·05	
	3.39 „	28	„	„	10	60	1·00	1·67	
SERIES 13. 9.9.'27.	2.35 p.m.	—	Dull	1	−1	27·2	32·3	120	
L Photometer. Anchored in Cawsand Bay. Depth 15·5 m. (Sounding). Light breeze N.W. Water fairly smooth. High water 3.39 p.m.	2.40 „	—	„	„	a	33·0	33·0	100	
	2.42 „	—	„	„	1·2	31·8	15·75	49·5	0·722*
	2.46 „	—	„	„	2	32·3	6·47	20·0	0·671
	2.49 „	—	„	„	4	31·4	2·37	7·55	0·387
	2.52 „	—	Light rain	„	6	28·2	1·20	4·25	0·307
	2.56 „	—	„	„	8	28·6	0·634	2·21	0·282
	3.2 „	—	„	„	10	33·9	0·451	1·37	0·280
	3.10 „	—	Rain	„	12	26·0	0·188	0·72	
SERIES 14. 9.9.'27.									
K Photometer. L used on deck instead of G, owing to probability of rain. Other conditions approx. as in Series 13.	3.42 „	—	Dull	„	a	11·0	11·0	100	
	3.49 „	—	„	„	1·2	15·3	9·3	60·5	0·685*
	3.54 „	—	„	„	2	23·9	5·18	21·6	0·565
	3.57 „	—	„	„	4	15·8	1·96	12·4	0·290
	4.5 „	—	„	„	6	17·8	1·20	6·75	0·296
	4.18 „	—	„	„	8	12·4	0·47	3·79	
							H	p_h	$\frac{p_h}{p}$
SERIES 15. 12.9.'27.	12.32 p.m.	44°	Weak Sun	1·5	a	65·2	54·0	83	0·83
K Photometer with window vertical so as to measure horizontal illumination (H). About 6 miles S.W. of Rame Head. Drifting S.E. towards Eddystone. Fresh breeze N.W. High water 6.21 p.m.	12.40 „	—	Dull	1	5	52·5	2·53	4·82	0·14
	12.45 „	—	„	„	10	48·7	0·96	1·97	0·14
	12.49 „	—	„	„	15	45·3	0·566	1·25	0·21
	12.55 „	—	„	„	20	38·6	0·122	0·316	0·115
	1.0 „	—	„	„	25	33·0	0·042	0·127	0·11
	1.4 „	—	„	„	30	30·9	0·022	0·071	0·14
	1.14 „	—	„	„	35	29·4	0·009	0·033	0·145
	1.21 „	—	„	„	40	32·5	0·005	0·015	0·145
							V	p	λ
SERIES 16. 12.9.'27.	1.42 p.m.	—	Dull	1	r	40·0	40·0	100	—
K Photometer in usual position. Other conditions approx. as in Series 15. Secchi disc 9·5 m. at 3 p.m.	1.49 „	—	„	„	5	45·6	15·7	34·3	0·180*
	1.52 „	—	„	„	10	46·8	6·53	13·9	0·173
	1.54 „	—	„	„	15	47·1	2·83	6·0	0·163
	1.59 „	—	„	„	20	48·7	1·34	2·75	0·166
	2.2 „	—	„	„	25	45·9	0·524	1·14	0·170
	2.10 „	—	„	„	30	45·9	0·228	0·50	0·156
	2.15 „	—	„	„	35	45·7	0·104	0·227	0·157
	2.21 „	—	„	„	40	45·8	0·047	0·103	0·150
	2.28 „	—	„	„	45	41·4	0·022	0·052	0·163
	2.33 „	—	„	„	50	33·2	0·007	0·020	—
	2.41 „	—	„	„	30	37·7	0·492	1·30	0·200
	2.54 „	—	„	„	20	45·8	3·70	8·1	0·139
	2.58 „	—	„	„	r	41·8	41·8	100	—
							U	p_u	$\frac{p_u}{p}$
SERIES 17. 12.9.'27.	3.10 p.m.	—	Dull	1	a	39·3	1·73	4·4	0·044
K Photometer inverted so as to measure light travelling vertically upwards (U). Other conditions approx. as in Series 15 and 16.	3.18 „	—	„	„	5	30·5	0·117	0·382	0·011
	3.26 „	—	„	„	10	30·8	0·053	0·172	0·012
	3.33 „	—	„	„	15	27·4	0·021	0·077	0·013
	3.37 „	—	„	„	20	25·8	0·010	0·038	0·014
	3.53 „	—	„	„	30	29·3	0·000	0·000	0·000
	3.56 „	—	„	„	25	30·6	0·006	0·021	0·018
	4.0 „	—	„	„	20	27·8	0·012	0·042	0·015
	4.3 „	—	„	„	15	25·8	0·020	0·077	0·013
	4.6 „	—	„	„	10	22·5	0·041	0·182	0·013
	4.10 „	—	„	„	5	22·6	0·088	0·389	0·011

Date, Remarks, etc.	T G.M.T.	α	Light	ß	d metres	V_2 m.c. $\times 10^3$	V_1 m.c. $\times 10^3$	p %	λ
SERIES 18. 3.10.'27.	1.26 p.m.	33°	Bright Sun	4	r	73·3	73·3	100	
K Photometer at E1.	1.47 ,,	31	,,	3·5	5	71·0	18·2	25·6	0·166*
Light breeze N.E. Long	1.52 ,,	31	,,	,,	10	71·8	11·5	16·0	0·099
swell from S.W. Clear	1.59 ,,	31	,,	,,	15	71·2	6·78	9·5	0·115
sky. Depth 73 m. Water	2.5 ,,	30	,,	,,	20	69·5	3·52	5·1	0·149
column almost isother-	2.19 ,,	29	,,	,,	25	66·5	1·42	2·14	0·121
mal, t = 13·8°. High water	2.25 ,,	28	,,	,,	30	65·3	0·99	1·51	0·063
9.26 a.m. Secchi disc	2.30 ,,	28	,,	,,	35	63·4	0·725	1·14	0·080
15 m. in shadow of ship	2.42 ,,	26	,,	3	40	60·3	0·411	0·68	0·089
at 5 p.m. Disc appeared	3.0 ,,	24	,,	2·5	45	55·2	0·257	0·465	0·127
green.	3.5 ,,	24	,,	,,	50	55·6	0·119	0·214	0·108
Interval. Cloud over sun.									
	3.39 ,,	20	Bright Sun	2	50	37·0	0·064	0·173	0·108
	3.54 ,,	18	,,	,,	55	32·9	0·053	0·161	0·068
	4.2 ,,	16	,,	,,	60	30·5	0·030	0·098	0·129
	4.8 ,,	15	,,	,,	65	27·2	0·012	0·044	—
	4.20 ,,	13	,,	1·5	40	22·6	0·123	0·545	0·104
	4.33 ,,	12	,,	,,	20	17·4	0·84	4·85	0·119
	4.47 ,,	10	,,	,,	10	13·9	2·70	19·4	—
SERIES 19. 5.10.'27.	12.34 p.m.	35°	Bright Sun	4	c	70	70	100	
L Photometer. About	12.47 ,,	,,	,,	,,	5	70	21·1	30·1	0·172*
1 mile N.W. of Eddy-	12.53 ,,	,,	,,	,,	10	70	10·6	15·2	0·146
stone. Drifting slowly	1.1 ,,	34	,,	,,	15	71	5·0	7·0	0·135
inshore. Depth at start	1.18 ,,	33	,,	,,	20	64	2·52	3·94	0·138
57 m. (Sounding). Light	1.24 ,,	,,	,,	,,	25	64·5	1·14	1·76	0·133
breeze N.E. Considerable	1.30 ,,	32	,,	,,	30	62	0·65	1·05	0·111
swell. High water 11.39	1.37 ,,	31	,,	3·5	35	61·5	0·356	0·577	0·141
a.m.	1.51 ,,	30	,,	,,	40	59·5	0·150	0·253	
SERIES 20. 5.10.'27.	2.15 p.m.	28	,,	3·5	c	55	55	100	
L Photometer used for	2.59 ,,	24	,,	2·5	20	44	0·74	1·68	
first three sets of read-	3.4 ,,	23	,,	,,	15	43	1·35	3·14	0·196*
ings. K Photometer used	3.27 ,,	20	,,	2	15	32·8	1·03	3·14	
for last three sets. p	3.47 ,,	18	,,	,,	30	28·3	0·143	0·505	0·123
assumed to be the same	3.57 ,,	17	,,	,,	40	24·2	0·034	0·143	
for both sets at 15 m.									
Other conditions as in									
Series 19. Secchi disc,									
16 m. at 4.15 p.m.									
SERIES 21. 6.10.'27.	9.22 a.m.	24°	Sun through	2	40	27·7	0·183	0·66	0·121‡
K Photometer. Same	9.36 ,,	26°	haze	,,	20	28·2	1·76	6·25	0·130‡
locality as Series 19 and	10.21 ,,	30	,,	,,	20	34·0	1·96	5·76	0·134‡
20. Calm. Moderate	10.28 ,,	31	,,	,,	40	34·5	0·228	0·66	0·121‡
swell. High water 0.31	11.22 ,,	34	,,	,,	10	45·2	7·80	17·2	0·160‡
a.m. Secchi disc 20 m. in	11.34 ,,	,,	,,	,,	g†	45·3	38·3	84·5	
shadow of ship, 16 m. in	11.50 ,,	35	,,	,,	20	44·5	2·48	5·58	0·137‡
sun at 9.50 a.m.	12.6 p.m.	,,	,,	,,	40	43·5	0·252	0·58	0·124‡
	12.21 ,,	,,	,,	,,	g†	41·5	33·7	81·2	
	12.29 ,,	,,	,,	,,	g	40·8	40·8	100	
SERIES 22. 14.12.'27.	1.5 p.m.	15	Variable	1·5	g	30·8	30·8	100	
K Photometer. L used	1.30 ,,	14	,,	1	5	14·7	6·4	43·5	0·128*
on counter, where it and	1.52 ,,	13	,,	,,	10	16·9	4·0	23·5	0·110
K were compared side by	2.8 ,,	12	,,	,,	20	12·2	1·01	8·3	0·098
side. L used thus, instead	2.29 ,,	10	,,	,,	30	14·0	0·46	3·3	0·077
of G on deck-house roof,	2.44 ,,	9	,,	,,	35	12·25	0·32	2·6	
owing to risk of rain and	2.58 ,,	8	,,	,,	20	11·9	1·09	9·15	
rough sea. Same locality	3.10 ,,	7	,,	,,	10	9·75	2·86	29·5	0·111*
as Series 19 and 20.	3.30 ,,	5	,,	,,	g	7·05	7·05	100	
Wind S.W. veering to W.									
about 2 p.m. Sea rough.									
High water 9.23 a.m.									
Secchi disc 13 m. in									
shadow of ship, 11 m. in									
sun, at 3.55 p.m.									

‡ In this 21st series of readings separated by considerable time intervals the value of λ given is the mean for the layer extending from the surface to the given depth.

† In these two readings the photometer was not quite level.

clearing of the water would be reversed, and indicated generally a small increase of λ with depth.

It is possible that the vertical movements of the plankton, shown by Russell (**6**) to be due to variations in illumination, may explain these rather puzzling results. It seems probable that the algal microplankton are most largely concerned in cutting down the light—and they move but little—but the movements of copepods, etc., seem bound to have some effect.

The results are shown graphically in Fig. 3, where the percentage illumination is plotted, unsmoothed, on a logarithmic scale against the depth. Series obtained with photometer L are shown dotted. There is no evidence of any dependence of the form of the curve on the photometer used. Series 10 is plotted from the means of descending and ascending readings which, in this case, agreed closely. The other series only represent the descending readings, the few ascending ones being omitted for clearness. The relative insensitivity of the photometers with ground-glass windows to oblique light renders them quite unsuitable for the accurate measurement of the loss of light at the sea surface, as the scattering of the light by the surface must alter the average obliquity, and so render the obliquity correction rather uncertain. Moreover, the light just below the surface was generally too unsteady to measure, as the 1927 measurements were for the most part made when there was an appreciable swell. The mean surface transmission recorded in 1925 with a diffusing photometer window was 85%, as measured by the vertical illumination. This value has been assumed in every case in plotting the 1927 results.

It is worth noting that variations in the surface loss are of negligible importance compared with the variations in the absorption coefficient at all depths below 10 metres. Thus if $\lambda=0{\cdot}15$ the absorption in 20 metres of water reduces the illumination to 5% of its value, while if $\lambda=0{\cdot}20$ the light is reduced to 1·8%. Much larger variations in opacity are common in the sea.

Series 7 and 8, obtained comparatively close inshore, differ from all the later ones in showing very clear surface water and a very large increase in λ with depth. It is worth noting that Series 5, which showed a similar effect, was obtained in 1925 in about the same locality. One may suspect an abundant phytoplankton—or possibly water from Plymouth Sound and its rivers or from the R. Yealm, which is exceptionally rich in fine particles from the china clay works on Dartmoor. This water would probably be above the denser water of the open sea, but the particles in suspension, clumped by the action of the divalent ions present in sea-water, might have settled to an appreciable depth, carrying down some of the microplankton and leaving a surface layer of very clear water.

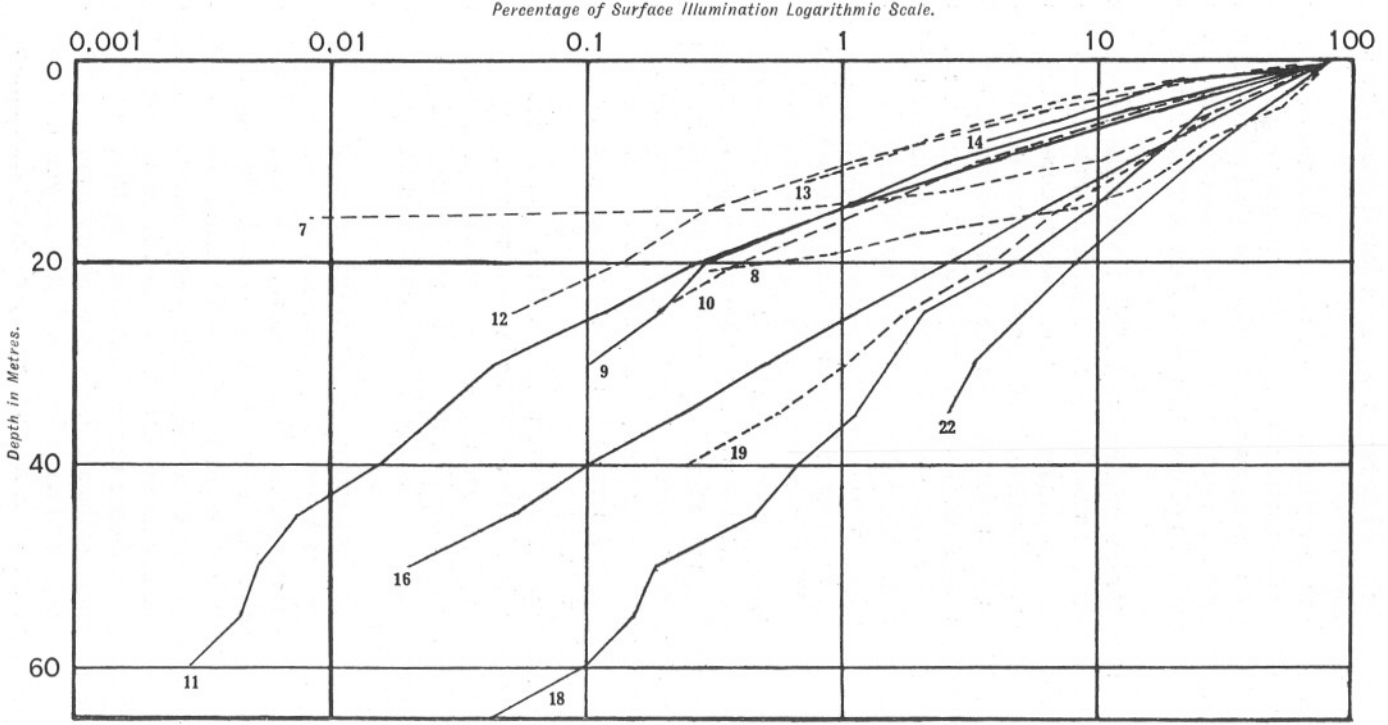


FIG. 3.—The ordinates show depths in metres. The percentage of the surface illumination is shown (logarithmic scale) on the abscissæ. The series numbers are given beside each curve. Where photometer L was used the line is dotted, a full line being used for K. Note the increased steepness of the curves as the serial numbers rise—showing the progressive clearing of the water from September to December.

Series 9 to 12 were obtained on September 5th and 7th at E1. They agree well, except that Series 12 shows somewhat greater absorption than the others in the surface layers.

There was a temperature break at 20 metres, temperature 15·1, with 13·83 at 25 m. and 13·36 at 70 m. At 15 m. it was 15·76 and 16·1 at the surface.

Series 13 and 14, obtained in Cawsand Bay with a flood tide, agree fairly well with each other and with the surface results found two days before at E1. Series 14 could not be carried below 8 metres, since at 10 metres the photometer apparently became intermittently shaded by weeds. This is rather surprising, as it was still 5 or 6 metres above the uneven rocky bottom; but as it occurred shortly after high water it is possible that the slackness of the tide enabled long streamers of Laminaria spp., or perhaps Chorda, to reach up to this level.

Series 15 to 17 were obtained with a strong offshore wind. The temperature at 5 m. was 15·2° C., falling to 14·3° at 25 m., and 14·2° at 45 m., showing that at this site vertical mixing had already taken place, though it is not noticeable at E1 till later, as a rule. This is shown in the approximate uniformity of the absorption coefficient in 16, which closely resembles some of the 1925 series.

These three series enable some idea to be obtained of the angular distribution of the submarine light. A comparison of Series 15 and 16 shows that the reading of the photometer with the window vertical averaged about 0·14 of the reading at the same depth with the window horizontal.

This ratio was approximately independent of the depth, the variations being no larger than would be expected, since there was no means of insuring that the azimuth of the photometer remained constant in Series 15. The photometer in the above-water set was facing towards the sun, so the value of p_h in air is about what one would expect. In deducing the submarine illumination from the photometer readings in Series 15 and 17 the same obliquity factor has been used as in the other series. This certainly gives too low results for both the horizontal and the upward illuminations, since, in both cases, the average obliquity of the light, relative to the photometer window, must considerably exceed that for the normal position.

We can calculate the horizontal illumination just below a smooth water surface, lit by a uniform sky, by a method similar to that already described (**2**, p. 183) for finding the vertical illumination under these conditions, remembering that, as the horizontal illumination is equally distributed in all azimuths, a plane vertical surface will only receive $\frac{1}{\pi}$ of the whole. We find that the illumination on a vertical surface comes out as 0·19 of

the vertical illumination on a horizontal surface. We have seen that the average ratio recorded by the photometer is 0·14, and that the photometer certainly under-estimates the horizontal light. Probably the photometer reading represented rather more horizontal light than that given above for the ideal case.

It appears, then, that the angular distribution of the submarine light does not differ very greatly from that for the above conditions, and that we may use the obliquity factor appropriate to them in finding the vertical illumination, without introducing any large error. Moreover, since the distribution seems to be almost independent of the depth, any such error will affect all the submarine readings equally, so that it will not affect the value of λ. It will, however, seriously affect our estimate of surface loss, so that, to find this, a photometer with a perfect diffusing window, as used in our earlier measurements, appears to be essential.

Since, in the various series, λ seems to be almost independent of the altitude of the surface light,* we may assume that the angular distribution of the submarine light (which evidently affects the value of λ) is also almost independent of the altitude of the surface light.

The fact that the average angle of illumination appears to be almost independent of the depth is readily explained. The effect of absorption is to enhance the proportion of high-angle light, while that of scattering is just the reverse. At a moderate depth the average obliquity should attain a value such that these effects balance. Below this the obliquity should remain constant, unless the ratio of the scattering and absorption effects altered with depth.

In Series 17 the upward illumination was about 1·3% of the downward at the same depth in Series 16, showing a tendency to relative increase with depth.

The remaining series show clearly the great increase in the clearness of the water which occurred with the approach of winter. If we except the remarkably clear surface water found in Series 7 and 8 the effect is most marked in the upper layers.

The effect of this reduction in opacity is also shown in Table III, where the illuminations recorded at different depths on four different dates are given in metre candles. As the surface light generally varies considerably during a series, the submarine illuminations have all been reduced to the value corresponding to the mean surface light for the series which is shown opposite to the letter a in the depth column.

* Series 21 was specially carried out to test this point.

TABLE III.

Series No.	11	16	18	22
	September 7.	September 12.	October 3.	December 14.
Depth in metres.	Vertical Illumination in Metre Candles.			
a	88,000	45,000	56,000	14,000
5	15,200	15,400	14,300	6,100
10	3,430	6,250	9,000	3,280
15	815	2,700	5,300	—
20	239	1,240	2,850	1,160
25	103	513	1,200	—
30	39·5	225	845	460
35	24	102	640	364
40	12	46·5	380	
45	6·5	23·5	260	
50	5		108	
55	4		90	
60	2·5		55	
65			24·5	

The variation in opacity is shown in Fig. 4, where λ is plotted against the depth. The curves are numbered to correspond with the series from which these are derived. Some of them represent the means of two or more series obtained under approximately similar conditions of time and place.

Comparison with the 1925 Results.

Series 2 and 5 were obtained just before, and just after, low water on September 2 and 3, 1925, in about the same locality as Series 7 and 8. The latter were obtained during the last three hours' ebb on September 2, 1927. The opacity of the surface water was very similar in the four series, but in Series 2 this remained almost constant down to at least 30 m., while in Series 5, 7, and 8 it showed large, and comparatively sudden, increases at about 25 m., 5 m., and 10 m., respectively. In the case of Series 5, which was obtained on a rough day, this was attributed to material derived from the bottom, but this could not be the explanation of the effects found in Series 7 and 8. It is possible that the effect may, in all cases, have been due to the presence of harbour or river water, though, if so, it is rather surprising to find it underlying a layer of very clear water. A suggested explanation has already been given.

Series 13 and 14 showed considerably greater surface opacity than

Series 1, 3, and 4, which were also obtained in Cawsand Bay, though under somewhat different conditions.

Series 9 to 12 are not comparable with any of the 1925 results, as the first obtained at E1 was Series 6, on October 1, 1925. This may be compared with Series 18 (October 3, 1927), which gave about the same surface opacity, but differed from the earlier series in showing a decrease

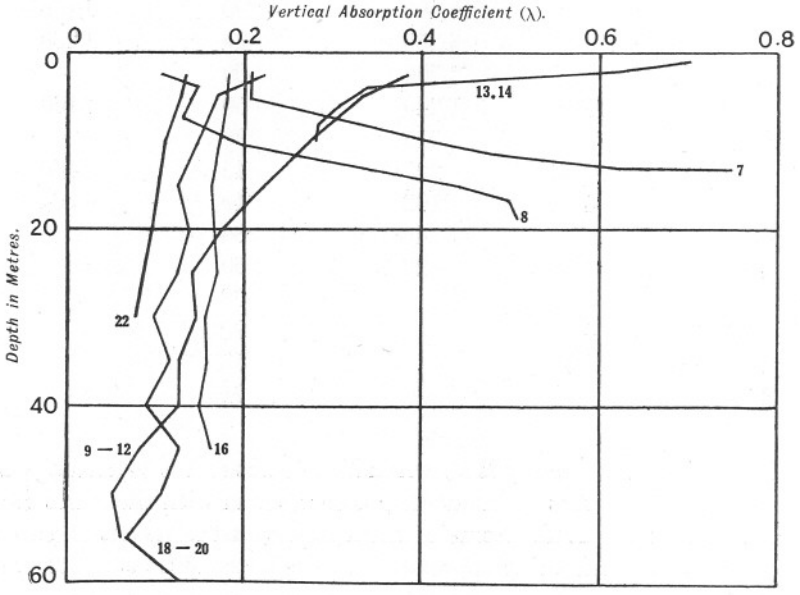


FIG. 4.—The ordinates show depths in metres against which values of the vertical absorption coefficient, λ, are plotted on the abscissæ.

with depth, instead of a slight increase. The differences are probably due to variations in the distribution of the phytoplankton—or even of the zooplankton.

The other series are not comparable, as regards conditions, with any of the earlier ones.

OBSERVATIONS WITH THE SECCHI DISC.

Table IV gives an attempt to correlate some observations made with a Secchi disc at about the same times as some of the series. Here d is the depth in metres at which the disc was just visible. Where observations were taken in the shadow of the ship they are indicated by an asterisk in the depth column. V_a is the estimated value of the surface illumination in thousands of metre candles, and p the percentage illumination at the limit of visibility as estimated from the corresponding series. V is the corresponding illumination on the disc at that depth.

TABLE IV.

Series.	Date.	T	d	V_a m.c. $\times 10^3$	p m.c. $\times 10^3$	V
11	7/9/27	0.15 p.m.	8	100	8	8
	,,	,,	8*	,,	,,	,,
16	12/9/27	3.0 p.m.	9·5	40	14·5	5·6
18	3/10/27	5.0 p.m.	15*	10	9·5	0·95
20	5/10/27	4.15 p.m.	16	20	3	0·6
21	6/10/27	9.50 a.m.	16	30	8	2·4
,,	,,	,,	20*	,,	6	1·8
22	14/12/27	3.55 p.m.	11	4	21	0·8
,,	,,	,,	13*	,,	17·5	0·7

It is evident that both the absolute and the percentage values of the illumination at which the disc was just visible varied widely. This was probably due to variations in the surface which would probably have a greater effect on the visibility of the disc than on the illumination. It seems probable that the use of a water telescope might lead to more consistent results.

SUMMARY AND CONCLUSIONS.

Further measurements have been made of the penetration of daylight into the sea near Plymouth, photometers containing both vacuum and gas-filled photo-electric cells being used. The effect of obliquity of illumination on the sensitivity of these photometers was large, and has been allowed for as far as possible. The sensitivity of the vacuum cell used in the sea attained its maximum at a wave length of about 4,050 Å.U., that of the gas-filled cell at about 4,350. The sensitivity of both to wave lengths greater than 5,500 was small.

The following tentative conclusions have been reached :—

1. For depths down to about 40 metres, in clear water, the vacuum type is the more convenient, owing to its constancy.

2. When suitable corrections are applied the results obtained with the gas-filled cell approximate closely to those found under similar conditions with the vacuum cell. Its much greater sensitivity enables measurements to be made at greater depths. By altering the voltage applied a very wide range of illumination can be measured, the maximum found being 109,500 metre candles, and the minimum read at 60 metres being 2·5 metre candles.

3. The effect of the variations in the surface loss of light is apparently negligible compared with that of variations in opacity.

4. The altitude of the surface light has but little effect on the penetrating power of the light in the water, since the average altitude of the latter depends chiefly on a balance between the opposing effects of absorption and scattering. There is some evidence that the average altitude of the light in the water at depths below 10 metres is between 50° and 60°.

5. The opacity of the water generally decreases with increase of depth, though the opposite is sometimes true, as was found in the earlier experiments. It is suggested that the variation is due to the different horizontal distribution of the phytoplankton, and to the zooplankton ascending or descending according to the movement of the optimum light intensity for each species.

6. The opacity decreased with the advent of winter to such an extent that measurements in December showed more light at all depths below 10 metres than was found on several occasions early in September. Correspondingly, the sea is far poorer in plankton in December than in September.

The absorption coefficients found varied from 0·62 to 0·051 in the open sea at various seasons, places and depths.

7. Attempts to correlate the maximum depth of visibility of a Secchi disc with either the absolute or the percentage illumination at that depth were unsuccessful.

The authors desire to acknowledge their indebtedness and to express their thanks as follows: To the Marine Biological Association for the greater part of the apparatus used at sea, also for laboratory and sea-going facilities; to the Royal Dublin Society for laboratory facilities; to Prof. W. E. Thrift for the loan of apparatus used at sea and for apparatus from the Physical Laboratory, Trinity College, Dublin, used in standardising; to Prof. J. Joly for the loan of the amplifier; and to the Government Grant Committee of the Royal Society for apparatus, especially photo-electric cells also used in work on illumination in relation to plant distribution ashore, for which the grant was given. The authors also desire to express their thanks to Capt. V. Lord and the crew of the *Salpa* for their whole-hearted assistance in the handling of the gear, without which the work could not have been carried out. Our thanks are also due to the Staff of the Research Laboratories of the General Electric Co., Wembley, for preparing a special photo-electric cell and for their advice.

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Studies on Conditioned Responses in Fishes. Part I.

By

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With 19 Figures in the Text.

CONTENTS.

(A) General Introduction.

The present work is an attempt to supply objective information upon fish behaviour in its relations to animal behaviour generally, and also has a second application as a contribution to our knowledge of the relative importance of the factors affecting the lives and migrations of fish.

Words of introduction are needed for both sides.

It may be said that out of the mass of data concerning the senses,

movements, and reactions of fishes, almost the whole of it is of a subjective nature, and thereby open to conscious or unconscious bias. When rigidly applied there appears to be no sound reason to doubt the validity of subjective methods, but it is clearly more satisfactory to study any nervous reaction in an objective manner, if suitable methods can be found. It does not seem necessary for our purpose to take up any definite stand upon the psychological or philosophical implications involved, as they are discussed elsewhere by numerous writers. Washburn (**1**) gives a very readable account of most of the current views upon these points. For the various ways of approaching the problem of Behaviour generally, Driesch (**2**), E. S. Russell (**3**), and McDougall (**4**) may be consulted for the " vitalistic " or " hormic " standpoint ; J. B. Watson (**5**) for the attitude of the American school of Behaviourists ; Pavlov (**6**) and Bechtereff (**7**) upon the purely objective physiological " conditioned reflex " method. H. Cason (**8**) gives a very good summary of the literature on conditioned responses—which is an indispensable guide, for this literature is very scattered. C. J. Herrick (**9**) gives an account, with bibliography, of the relations between structural and functional evolution in the nervous system, which must be considered in conjunction with one another. These books are mentioned merely as an introduction—the literature is voluminous.

Now, the work of Pavlov and his collaborators, and the work of the American Behaviourists is fundamentally alike, although they differ considerably in their mode of experimentation. It seems, indeed, that the method of " conditioned reflex " formations in studying the higher nervous activities opens up to us, at last, a sound way of investigating the finer discriminatory sense of the analysers (the receptor centres) in the mammalian brain. Moreover, the method is such that the question of consciousness, which plays so large a part in current psychological discussion, does not in any way affect the results when considered solely in regard to the discriminating power of the sense receptors. Herein lies its value as applied to the study of environmental factors in their effect upon animals generally, or upon fishes, if it can be used satisfactorily with them.

With the exception of some experiments carried out recently by J. P. Froloff (**10**)*, there have been, so far as I know, very few investigations upon fishes or lower vertebrates definitely from this point of view. There has been, however, a good deal of work, mainly by American and German investigators, upon the sensory reactions of fishes and amphibians, which,

* Hulsey Cason (**8**) states that Westerfield used the conditioned response method in studying the ability of 9 mud minnows (*Umbria limi*) to form associations with sounds. (*J. Comp. Psych.*, 1922, vol. 2, p. 187.) The minnows were able to distinguish between vibrations of 288 and 426 per second, on a ukulele, when the low tone was associated with food and the high one with a distasteful flavour. MacDonald (same ref.) showed the same in *Pimephales notatus*. I have not yet had access to these papers.

if we could know how the experimental conditions were controlled, would probably fit in quite well. This applies particularly, of course, to training and learning experiments, similar to my own.

Before the main functional units—" unconditioned " and " conditioned " reflexes—are finally regarded as playing the enormous part in purposive behaviour assigned to them by Pavlov and by the Behaviourists, it seems imperative that their evolutionary development should be worked out and understood. It is plain that structural and functional evolution in the nervous system have gone hand in hand in phylogeny.

The physiological findings of to-day must therefore be in reasonable agreement with the anatomical findings in order to make this understanding complete ; otherwise all is confusion. At present, the exact relationships between the two are not really clear, although Herrick (**9**, p. xi), who has done so much to correlate them, states that " the evidence is biologically adequate that mind (awareness), as we know it phenomenally, is a function of a particular configuration of bodily organs." This statement seems to me still premature, unless he means it in a very broad sense, when it appears to be justified. Thus, Pavlov (**6**) regards the cerebral cortex as almost certainly the sole portion of the mammalian brain concerned in the final elaboration of conditioned reflexes, a fact which finds expression in the alternative title of his chief book. This belief is held by many others. No well-differentiated cortex is present in fishes, however ; although certain regions,—the " cortical primordia "—represent fairly definitely the places where the cerebral cortex appears in higher forms. These regions are most clearly seen in the brains of Dipnoians, and are still similar and present in almost as primitive a condition in Amphibians. (Papers by G. Elliot Smith (**11**), J. B. Johnston (**12**), Holmgren and Van der Horst (**13**).) Yet it is obvious from even a casual acquaintance with fish that they can, and do, form associations which are apparently quite comparable in nature with the conditioned responses of mammals,—certainly with those of the lower forms. It would appear, then, that subcortical regions are involved, and according to Kalischer's experiments (**14**) this takes place in dogs also, but Johnson (**15**) and others criticise his results. (See Herrick (**9**), for discussion of some of these points.)

Hence the Ichthyopsid type becomes one of the most important stepping-stones in any general study of the higher nervous activities, particularly in regard to associative memory and intentional control of behaviour and their relationships with the brain-centres.

On the other hand, and of more immediate importance to the marine biologist, it is believed that investigations on the lines here presented will offer a sounder basis for the discussion of migratory influences. Nearly all the available information relating to factors exerting an influence on fish migrations has been summarised by F. E. Chidester (**16**).

His general conclusions may be regarded as forming a summing up of the position as it now stands. After a careful examination one is forced to conclude that the foundation upon which our knowledge of the reactions of fishes to their environment rests is very slender.

Fish migrations may be divided into intentional journeyings and passive driftings. The latter do not present the peculiar difficulties to the minds of those who attempt to understand them as do the former. The denatant drift of many fish larvæ, for instance, will be completely understood when the physico-chemical conditions in the oceans are thoroughly known—a knowledge which is swiftly growing. But purposive migration, such as is undoubtedly undertaken by large numbers of fishes, will never be adequately explained, of course, until some degree of unification is achieved amongst physiologists and psychologists upon the vital questions of consciousness and biological memory. This is a reservation to be borne in mind. Certain physiological sequences are nevertheless essential in the fulfilling of any conscious or unconscious act. These, at least, can be investigated with hope of immediate practical results, and without undue insistence upon their philosophical aspect with which I am not competent to deal.

(B) An Introductory Account of Conditioned Reflex Formations.

It is necessary to give a brief account of the methods and particulars concerning conditioned reflex formations, in order that the nature of the present experiments may be more clearly understood. These details are compiled in the main from Pavlov's work on dogs (**6**). Introductory accounts are also given by Hogben (**17**), Lovatt Evans (**18**), Anrep (**19**), and others. Podkopaew (**20**) describes the practical methods in more detail.

It must be borne in mind that the whole of this literature refers solely to work on mammals, and that we are as yet ignorant of the extent to which the phenomena will be found to apply elsewhere.

Starting with Descartes' idea of the reflex, our knowledge has expanded to such a degree that it is now said we are justified in regarding all the elementary motor activities of an animal as essentially reflex. Pavlov (**6**, p. 7) summarises the idea of the reflex in the following words :—

" An *external* or *internal* stimulus (my italics) falls on some one or other nervous receptor and gives rise to a nervous impulse ; this nervous impulse is transmitted along nerve fibres to the central nervous system, and here, on account of existing nervous connections, it gives rise to a fresh impulse which passes along outgoing nerve fibres to the active organ, where it excites a special activity of the cellular structures. Thus, a stimulus appears to be connected of necessity with a definite response, as cause with effect."

In addition to the reflexes making up the sum-total of their motor activities, animals possess a limited number of inborn species reflexes, upon which their whole nervous activity primarily depends. That is to say, an animal responds from birth (or earlier) by a definite reaction when given certain stimuli, and any other individual of that species, under similar external and internal conditions, will give a like response, unless some other extraneous factor inhibits it. (Instincts, for example, may possibly be explained briefly as a whole chain of reflexes for which an inherent organisation is provided in the structure of the animal.) An example of such an inborn reflex is to be found in the mammalian salivary reflex. If food is introduced into the mouth, a secretion of saliva results. This is an inborn, elemental, or "*unconditioned*" *reflex*, due to the reaction of the stimulatory substance with the mucous membrane of the mouth. But in a normal adult animal, the sight or smell of food or of innumerable other stimuli, after sufficient association with the giving of food or of the other stimuli, will also of themselves produce a secretion of saliva, although they had previously had no such effect. These stimuli (such as sight or smell) are said to have acquired " conditioning " or " signalling " properties, and are called "*conditioned*" *stimuli*. They evoke a "*conditioned*" *reflex*. Training and education appear to be essentially the processes of formation of new conditioned reflexes, or, as Herrick, Lloyd Morgan, and others prefer to express them—*conditioned responses*. By Bechtereff they are called " combined " or " associated " reflexes, and the science of their study—reflexology.

An example of training in fishes which illustrates these points is that of Dr. Allen's experiment in which he trained fishes in the Plymouth aquarium to associate the sound of a submerged buzzer with the introduction of food. As this work was incidental to war investigations no detailed records are available, but the case is cited and interpreted by Lloyd Morgan (**21**).

The experimental formation of conditioned reflexes may be brought about in several ways. A most important general condition of the experiments is that all extraneous stimuli, other than the one undergoing investigation, should be excluded. Under such stabilised conditions the formation of conditioned reflexes proceeds with a sureness and definitiveness quite comparable with the results obtained with the spinal animal.

In building up conditioned reflexes experimentally it is necessary that the unconditioned stimulus should bring about an easily registerable response—such as a secretion of fluid—or defensive movement of a limb —or movement of the body as a whole. Food is such a stimulus, and involves both a secretory and motor reaction, either of which may be used for registration. An electric shock evokes a definite defensive motor reaction. These are thus two suitable stimuli with which to build up

conditioned reflexes. An essential point is that the presentation of the *conditioning* stimulus should be applied in rigid synchrony with the *unconditioned*; this may mean either simultaneously or at any definite interval *before*, but, so far as is known at present, not after.

Conditioned reflexes are divisible into three types, depending upon their mode of formation, and upon the time relationship existing between the unconditioned and the conditioned stimuli:—(1) Simultaneous; (2) Delayed; and (3) Trace—reflexes. These derive their name from the time allowed to elapse before the unconditioned stimulus follows the conditioned stimulus. With *simultaneous* conditioned reflexes the conditioning stimulus is given at the same instant as, or within less than 2–3 seconds from, the unconditioned. In *delayed* reflexes the conditioning stimulus is presented from a few seconds to several minutes before the unconditioned stimulus, and is allowed to act for the whole of the intervening time. *Trace* reflexes are variants of delayed reflexes. Instead of allowing the conditioned stimulus (say, a buzzer used as a signal for food) to act continuously until the unconditioned stimulus is given, it is allowed to act for a period of $\frac{1}{2}$ to 1 minute, then stopped and the unconditioned stimulus is not given until after a further definite interval of 1 to 3 minutes. Under any of these conditions, conditioned reflexes appear in dogs or in man after relatively few trials, from 1 to 30.

Conditioned reflexes after they have become firmly established may be caused to disappear by many methods—that is, they are subject to *extinction*, experimental or otherwise. This may be of the nature of an *external* or *internal*, *temporary* or *permanent inhibition*. Any strong extra stimulus falling on the animal at the time of experimentation may also cause an inhibition of the reflex then undergoing investigation. The effect may be of short or of long duration, but is usually temporary. An inhibition of this type is called by Pavlov *indirect* or *external* as it originates in a part of the brain remote from that where the reflex has its centre. Instances of this type of inhibition will be frequently revealed in the present paper.

The first type of *direct* or *internal* inhibition occurs when the positive conditioning stimuli are themselves given inhibitory properties. This may be brought about by the method of *experimental extinction*. After a conditioned reflex has become firmly established, by giving the conditioning stimulus repeatedly in succession without association with the unconditioned—the reflex becomes gradually extinguished. The exact mechanism involved is doubtful.

The second type of internal inhibition is called *conditioned inhibition*. When a previously neutral stimulus is applied repeatedly in combination with a positive conditioning stimulus and never in this combination associated with the unconditioned, it acquires inhibitory properties;

although the positive conditioned stimulus, occasionally reinforced, retains its properties when applied singly.

The third type is rather unsatisfactorily defined as *inhibition of delay*; it is involved in trace and delayed reflexes.

The fourth type, which is of the greatest interest for the investigation of sensory discriminations, is *differential inhibition*. It is brought about as follows :—A musical tone, for example, is used as a conditioned stimulus ; at first, any other tone serves also as a positive stimulus, though generally with weaker effect. This is called *generalisation of stimuli*. By continuing to apply the tone first used always in association with the unconditioned stimulus and presenting any other allied tone invariably without reinforcement, the latter speedily becomes ineffective—if, of course, the animal is capable of differentiating between them. It will appear obvious that this provides a good physiological means of investigating the sense analysers.

Many more complex phenomena relating to conditioned reflexes have been investigated by Pavlov and others, but as they are outside the scope of the present article they need not be described here.

It is becoming more and more stressed that inhibition is one of the main functions of the cerebral cortex. What performs this most necessary function in fishes ?

(c) Representation of the Results Obtained in the Present Investigation.

A uniform graphical method of recording the results has been adopted throughout the paper for the sake of brevity. Each record (cf. Figs. 3 and 4) indicates the number of associations made, their nature, and their distribution in time. Days and months are marked off with small vertical lines on the base line—the number of experiments made daily is thus seen at once. This diagrammatic picture of the progress of " conditioning " has many limitations, for it is obviously impossible to record all details in this way.

A positive conditioned response is shown by a + (plus), no response by a − (minus sign). It may be taken for granted that the conditioned stimulus was invariably reinforced by the unconditioned stimulus (food, shock, or touch, as the case may have been) except where otherwise indicated, or in tests where experimental extinction was investigated. With many of the fish, proof of their capacity to differentiate between allied stimuli was attempted. This necessitates differential indication on the graph. It has been done by the use of dots, triangles, circles, or crosses, but it has not been possible to keep the meaning of these uniform for all the records, wherefore the legends or the correlated text should be carefully

noted. The " original " or " primary " conditioned response is always denoted by a plain dot whether or not differentiation was attempted. Time records—that is, of the time interval between presentation of stimulus and performance of the conditioned response—are of great interest for comparison with the learning curves of other animals, apart from their bearing on the phenomenon of the " delayed response." These are the most important omissions from the graphical records and an endeavour will be made to bring out these relationships in the text. Important intervals or events having a direct influence on the behaviour of the fish are indicated by bold arrows at the appropriate point. These are lettered, and their effect, together with any inferences to be drawn from it, is also discussed in the text. Some of the experiments lasted several months and the records are lengthy ; where one line is not sufficient they are continued in the line or lines below. This is clearly indicated in the figures, and they should be consulted carefully and constantly when reading the paper which amplifies what the records show.

SECTION A. FOOD AS UNCONDITIONED STIMULUS.

(A) The Formation of a Conditioned Response in *Blennius gattorugine* Bloch, towards an Increase in Temperature of the Surrounding Water.

There is much diversity in the type of environment which fishes naturally frequent, and a very great difference in their mode of living. The blenny, *Blennius gattorugine*, was chosen for this investigation partly because of the readiness with which it adapts itself to aquarium conditions, partly because it feeds readily in captivity, but mainly because of its own particular habits. It is a natural habit of the blenny to live in a suitable hole or crevice in the rocks, about low-water mark. For this reason, if a specimen is placed in an aquarium containing any empty pots or jars it will very soon make such a pot its permanent home and only leave it when attracted by food, etc. This at once suggested to me the possibility of using a pot in which the fish could live permanently and of utilising as a registerable response its habit of coming out when it saw food placed before it. The method of doing this in the present investigation was as follows :—

The Apparatus.

This is shown in general perspective as a diagram in Fig. 1. The heavier unbroken lines indicate the part visible to the observer—mainly screening arrangements. The screen surrounds a glass aquarium (Fig. 1, A), 30 cm.$\times$45 cm.$\times$15 cm., which together with its component and

contained accessories is shown in the same figure in thin dotted lines, as it is hidden from view. The aquarium rested on a wooden bench, from which it was separated by a layer of felt to lessen vibrations, if any. The box B, Fig. 1, projecting towards the observer, was the compartment from which observations were made, and was sufficiently large to take my head and shoulders. This was completely covered in by black cloth, thus forming a darkened chamber. The side of the aquarium away from the observer was close up to a north window and was not screened in any way. The whole of the aquarium and apparatus within the screen could be surveyed through the telescopic lens (C, Fig. 1), placed at a distance of 26 cm. from the thermometer T, mentioned later. Food could be introduced through

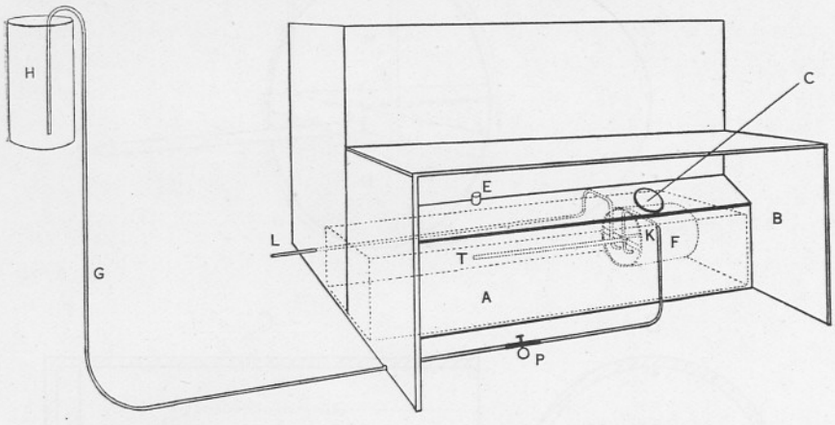


FIG. 1. General view of the apparatus used in the formation of conditioned responses in *Blennius gattorugine* towards *temperature* stimuli. Explanation in text.

the small tube (E, Fig. 1) and dropped upon a platform in the aquarium, about 20 cm. from the opening of the pot F (Fig. 1).

The pot (Fig. 1, F) and its component fittings is the essential part of the apparatus. The general arrangement is shown by dotted lines in Fig. 1, and details are given in Fig. 2 (A) in perspective, (B) in elevation and (C) in plan. It is an ordinary 2 lb. earthenware jam jar divided longitudinally into upper and lower portions (Fig. 2 (A), M, N), separated from each other by a glass plate 1 cm. in thickness. There are two narrow gaps 0·7 cm. wide in this partition, marked *a* and *b* in Fig. 2, C. These permit of a free communication of water in the upper and lower portions. A piece of glass tubing 0·6 cm. diameter (Fig. 1, G) leads down from a small vessel (Fig. 1, H) containing hot water, placed about 200 cm. above the bench and 150 cm. away from the screen. This tube passes through the observation compartment, where it is provided with a pinch-cock (Fig. 1, P), connects with a piece of lead tube of the same bore which passes through the screen

at K (Fig. 1), runs over the side of the aquarium and enters the lower compartment of the pot. Its course through the pot is shown in Fig. 2, C, as a dotted line in the form of a U-tube. On emerging from the pot the tube bends sharply up again over the further side of the aquarium and then leads away to waste (Fig. 1, L). The mouth of the lower chamber is closed by a large bung, which supports the heating tube. All joints in the

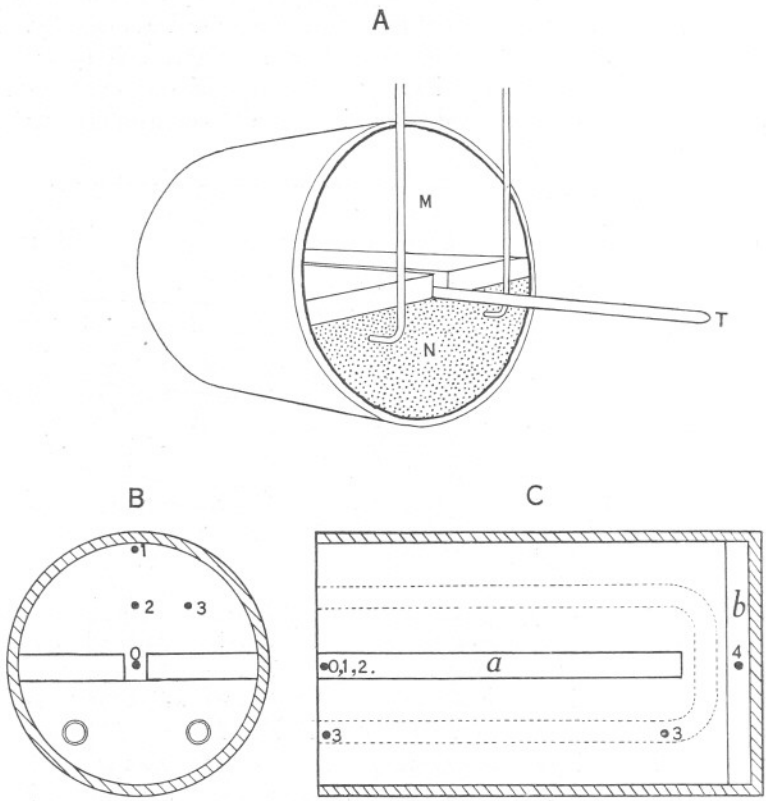


FIG. 2. Diagrams showing details of the apparatus used in the formation of conditioned responses in *Blennius gattorugine* towards *temperature* stimuli. Explanation in text.

pot, all crevices, and the surface of the bung, are well fixed and covered with marine glue, so that the lower part is completely closed except for the gaps leading to the upper chamber (Fig. 2 C, *a*, *b*). An accurate thermometer, graduated to 0·1° C. (Figs. 1 and 2 A, T) lies in the gap *a* (Fig. 2 C) in a horizontal position.

The aquarium was filled with sufficient sea-water to cover this pot, which, as will have been surmised already from the introductory note to this section, was to be the home of the blenny.

Now, on heating the water in the lower compartment of the pot by passing hot water from the vessel H (Fig. 1) through the tube G (Fig. 1), the *heated* water finds exit through the gaps *a* and *b* (Fig. 2, C), passes straight upwards to the top edge of the pot, then forwards to enter into the main water of the aquarium. A constant temperature of 70° C. for the *heating* water was used throughout. By passing this water through the tube GL (Fig. 1) for only a few seconds, a slight rapid rise in temperature is recorded on the thermometer in the middle gap, and by varying the time of flow this rise can be made as large or small as desired (cf. Table II). It must be clearly understood that this local heating is very rapid—not prolonged, and that the temperature required is attained in 2 or 3 seconds—the thermometer column rising suddenly. As soon as the passage of hot water through G is stopped, the thermometer quickly indicates only the normal temperature of the surrounding water. For the correct interpretation of the results it is necessary to know exactly what does happen with regard to temperature increments in the upper compartment. (It is hoped, after these preliminary experiments have been completed, to repeat them, using a thermo-couple, which will give more reliable measurements.) I therefore took a series of readings at various places in the upper compartment and compared them with the reading of the fixed experimental thermometer in the gap. They gave the following results for the positions indicated in Fig. 2, B and C.

TABLE I.

Position.	Rise in temp. per 1° C. rise on recording thermometer (T).
1	0·35° C.
2	0·75° C.
3	0·09° C.
4	0·35° C.

Observations thus made show that a convection current of warm water is created, which passes vertically upwards through the two communicating spaces to the top of the pot, and then forwards to the entrance. Slight conduction takes place and probably accounts for the very small rises at position 3. These results were further confirmed by the use of carmine in suspension.

Method of Experimentation.

It has been already mentioned that it is a natural habit of the blenny to live in suitable holes, etc., and the fish normally spent all its time in the upper half of the pot.

Several times daily for a period of three weeks, yet at irregular intervals during the day, the fish was subjected to a stimulus of 3·5° C., sometimes

to rises up to as much as 10° C. obtained in the manner described above. These stimuli, which were unassociated with food, caused no visible response in the fish upon any occasion. The blenny was fed at intervals during this period. The feeding times were far apart from the times when the fish was subjected to the temperature stimulus (at least 30 minutes either way). A record of these preliminary tests is unnecessary. The total number of stimuli given to the fish in this way was 42.

The experiments upon the formation of a conditioned response to a slight rise in temperature of the surrounding water as shown by the reading of the thermometer T were commenced on December 13th, 1926. They were carried out as follows :—Hot water at a temperature of 70° C. was allowed to flow through the tube GL (Fig. 1) until the thermometer T indicated the temperature desired ; this was attained in a few seconds, and the stop-cock closed, in accordance with the above description. The temperature started to fall at once. *Fifteen seconds* after the maximum temperature had been reached, a worm was dropped through E (Fig. 1). By this time the thermometer reading was back to within 0·2° C. of the original temperature. In most instances the blenny came out of its pot at once when its food, a Nereid worm, was given, snapped at it eagerly, gave a cautious glance round, and went back into the pot. This was the " unconditioned " motor response which was used in building up the *conditioned* response.

THE RESULTS.

Specimen No. 1.

The graphical record, Fig. 3, in which a dot in the lower (negative) position indicates a stimulus to which there was no response, and a dot in the upper (positive) position indicates that the fish responded by coming out of the pot before any food was given, shows at a glance certain distinctive features.* It shows an early period, lasting from the 13th December, 1926, to the first experiment on January 2nd, 1927, during which the fish showed no response to a temperature increment, no matter what its magnitude may have been. During this period the number of associations presented was 42,† although some allowance should be made for a period of eight days, December 21st to December 30th, 1926, when no experiments were made owing to my absence. What influence this may have had by retarding the progress of " learning " is not assessable. Very likely it was great, if a comparison can be made with some of the other fishes, or even the same fish, where the effect of an interval was noticed when learning had become more complete. From the 2nd January, 1927,

* The arrows indicate the occurrence of events, such as cleaning out the apparatus, or intervals when no experiments were made, which might cause an inhibition of the response. They are discussed more fully in their appropriate place in the text.

† It is a curious coincidence only that this number is the same as the number of preliminary unassociated stimuli.

until about the 26th the proportion of the number of definite positive responses to that of no apparent responses became progressively greater. After the 26th January and until the series was completed, the fully-formed conditioned response of coming out on perceiving the temperature stimulus remained perfectly stable, except when influenced by inhibitory stimuli. These are the broad features in the progression of learning in this fish. They can now be treated in more detail.

The record, firstly, gives no information upon the temperature rises used as the conditioning stimuli—limitations of space prevent it. These are accordingly given in a separate table (Table II). The correspondence between the graphic record and the tabulated temperatures is quite straightforward :—each dot on the record represents a stimulus given, whilst the temperature used is indicated in the table in similar sequence for each day.

TABLE II.

SHOWING THE AMOUNT OF THE TEMPERATURE RISES GIVEN AS CONDITIONING STIMULI TO SPECIMEN No. 1, CORRESPONDING TO THE RECORD OF THE RESULTS IN FIG. 3.

Date.	Temperature increments given. °C.
1926.	
Dec. 13.	3·0, 3·0, 2·0, 4·0, 3·0, 3·0, 3·0.
14.	3·0, 3·0, 2·9, 3·0.
15.	3·0, 3·0.
16.	4·0, 4·0.
17.	4·0, 4·0, 4·0.
18.	5·0, 5·0, 5·0.
19.	6·0, 5·0, 5·0.
20.	6·0, 5·0, 5·0, 5·0, 5·0.
21.	5·0, 5·0, 5·0, 5·0.
30.	5·0, 5·0.
31.	5·0, 5·0, 4·5.
1927.	
Jan. 1.	5·0, 5·0, 5·0.
2.	4·0, 3·0, 3·0.
3.	4·0, 3·8, 3·6, 4·0, 3·0, 4·4.
4.	4·5, 5·0, 4·1.
5	4·0, 4·0, 3·5.
6.	2·6, 3·3, 3·8, 3·6.
8.	2·0, 2·6.
10.	5·0, 5·5, 6·0.
11.	6·5, 7·0, 6·2, 5·0.
12.	5·1.
13.	4·8, 4·2, 5·2.
14.	4·2, 4·3.
15.	3·2, 6·0.
17.	5·0, 5·0, 6·5, 6·7.
18.	5·0, 5·5, 6·5.
19.	4·0, 6·0, 4·5.
20.	4·0, 3·3, 4·0, 3·0.
21.	6·4, 4·4, 4·5, 4·5, 2·5, 3·1.
24.	4·0.
25.	4·5, 4·4, 4·6.
Jan. 26.	3·5, 2·7, 2·5, 2·6.
27.	5·5, 4·7, 4·4.
28.	4·3, 1·0, 4·0, 1·8, 2·1.
29.	1·9, 3·0, 2·1.
Feb. 3.	5·0, 4·2, 3·8, 1·0, 3·3.
4.	3·5, 3·7, 3·1, 2·4.
5.	3·2, 2·0, 2·2.
8.	3·2, 2·0, 3·0, 2·8.
9.	3·0, 6·0, 2·0, 5·0.
14.	3·0, 3·0.
17.	1·0, 1·0, 0·9, 1·2.
18.	3·0, 2·0, 2·0.
19.	2·8, 3·2, 3·0.
21.	2·5, 2·3, 2·0.
22.	3·0, 4·5, 2·5, 1·6.
23.	1·3, 3·6, 3·0, 1·5.
26.	2·3, 2·4, 2·8.
28.	2·1, 1·5, 2·5, 0·7.
March 1.	1·0, 1·5, 1·0.
2.	3·0, 0·9, 3·5.
8.	1·5, 4·0, 1·5, 2·0, 3·4.
9.	2·1, 1·0, 3·5, 1·0.
11.	1·0, 1·2.
12.	1·3, 1·5, 3·5.
14.	0·6, 0·5, 2·4, 3·7.
15.	0·5, 0·7, 3·5.
16.	1·5, 0·7, 3·5.
17.	1·5, 0·4.
18.	3·2, 0·6, 0·5.
30.	4·0, 6·4.
April 1.	3·5.
2.	3·5, 1·5, 1·1.
3.	3·5, 1·2, 3·7.

During the period when the response was becoming established, the average temperature rise given as a stimulus was 4·1° C., with a minimum of 2·5° C. and a maximum of 7·0° C. After that time the stimulus was made as generalised as possible, in order to find the lowest temperature increment to which the blenny would respond if continually reinforced by food. On January 28th, test No. 2, no response is recorded to a rise of 1·0° C., the first time such a low rise had been used ; the worm was given after the 15-second interval. Later on the same day (tests 4 and 5) a positive response is recorded to a rise of 1·8° C. and 2·1° C. respectively. Increases of 1·9° C. and 2·1° C. evoked a positive response on the 29th, but again on February 3rd (test 4) a rise of 1·0° C. failed to produce a response. As it so happened, the last of these tests occurred at a time (arrow C, Fig. 3) when there was probably slight inhibition owing to disturbing external influences. The water in the apparatus had been changed and the fish had been removed to another tank for 4 days. Yet the previous stimuli of 4·2° C. and 3·8° C., being the second and third after the fish had been replaced in the apparatus, evoked a positive response, as also did the succeeding stimuli of 3·3° C., 3·5° C., etc., although the first test after its return, as invariably occurred, gave no response. Moreover, no such extraneous influence appears to have been present when 1·0° C. rise was first tried on January 28th. So that these two occasions when no response was shown towards the earliest rises of 1·0° C. may perhaps be interpreted as showing that the fish could discriminate between an increase of 1·0° C. and an increase of 2·0° C. or more, without differential training.

Some days later, after another 18 associations at which temperature stimuli had ranged from 2·0° C. to 6·0° C., with an average of 3·2° C., all of which with two exceptions had given strong positive responses, an increase of 1·0° C. was again tried (Feb. 17th, tests 1–4). Now, very strong responses were given. The stimulus had become more generalised and further evidence obtained upon the lowest temperature increase to which the fish was sensitive. A very interesting observation was recorded at this time.

Not only did the fish perform the motor response of coming out of its " home " very rapidly and eagerly, but it made very noticeable jaw movements (as though in anticipation). This has subsequently been seen in other blennies which have formed conditioned responses of a similar nature towards other conditioned stimuli, or I should consider that I have read more into this than the facts justify. It must be regarded as an additional feature of the conditioned response and seems to appear when the fishes are more hungry than usual.

Positive conditioned responses were given invariably towards stimuli of increments varying from 0·4° C. to 6·4° C. from February 17th until

April 3rd, when the experiment was stopped. The apparatus was not sufficiently delicate to give a rapid rise of less than 0·4° C. This was the lowest temperature increment given, and generalisation had become sufficiently wide to cause it to evoke a positive response when the fish was stimulated by it.

It can therefore be stated, *that this specimen of* Blennius gattorugine *was capable of perceiving, and of profiting by, a convection current giving a momentary rise of as little as* 0·4° *C. in the temperature of the water at a point on the ventral surface of the fish.**

It cannot be regarded as absolutely *proved* that the fish has formed a

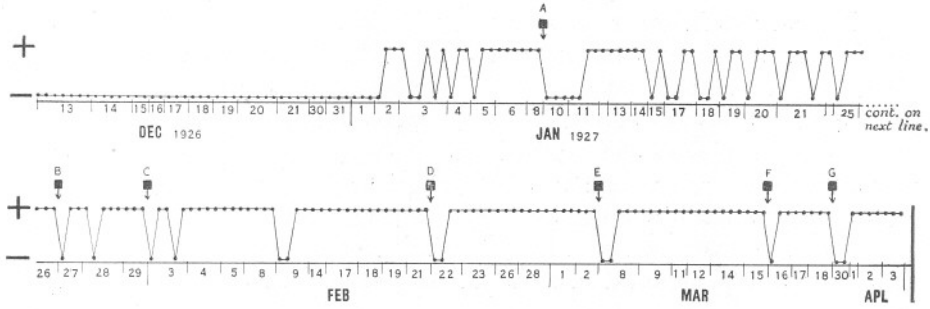


FIG. 3. Specimen No. 1.

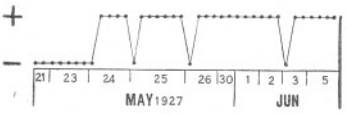


FIG. 4. Specimen No. 3.

FIGS. 3 and 4. Records of the process of formation of conditioned responses in *Blennius gattorugine* towards *temperature* stimuli. Explanations in text.

conditioned response towards the increase in temperature as an isolated force, for its necessary complement, the convection current, may also have been acting as the stimulus or a part of it. But it is legitimate to *infer* that the temperature was the sole stimulus, or differentiation would not have taken place in the early stages of the experiment.

The effect of changes in the external environment are very marked, especially when the conditioned response shows a long series of definite +s (positives). After the removal of the fish from the apparatus for

* As the apparatus was not provided with any form of thermostat, the temperature of the water in the aquarium was always that of the room temperature at the time of the experiments. All rises are not, therefore, of equivalent meaning. The initial temperature varied from 6·5° C. to 13·0° C. in Specimen 1 ; but well over 75% of the experiments had an initial temperature of between 8° C. and 11° C.

cleaning purposes, whether the interval was of short (a few hours) or of long (12 days) duration, the first one or two stimuli succeeding its replacement invariably gave no response whatever. The arrows A (Jan. 10th), B (Jan. 27th), and D (Feb. 22nd) are placed against the dates when the apparatus was cleaned. An interval of 4 days without experiments occurred at C (Jan. 30th to Feb. 2nd), one of 5 days at E (March 3rd to 7th), and one of 12 days at G (March 18th to 30th). The effect is clearly obvious in the diagram. Even slight adjustments in the apparatus inhibited the response, as at F (March 16th). This seems to be clearly comparable to the phenomenon regarded by Pavlov as indirect or external inhibition.

Frequently, in order to ascertain the nature of the time-relations between the stimulus and the conditioned response, it was not followed by the unconditioned at the correct interval of fifteen seconds. When a positive response was given during the transitional, " learning," period, the time interval was longer than this—it fluctuated around 30 seconds ; as " learning " progressed this became gradually reduced, until, at the last 80 presentations of the stimulus, it averaged only 10 seconds, with a range of 4 to 20 seconds. The " learning " curve is of the same general shape as those obtained in trial and error experiments of the " maze " type.

Specimen No. 2.

All conditions and methods were the same as for Specimen No. 1. The experiments lasted from April 30th, 1927, until 20th May, 1927, when the fish died. The conditioning stimulus was given in a similar manner to that described for Specimen No. 1. Fifty stimuli in all were given, but an entirely negative result was obtained. Not wishing to set up any disturbances, I had not interfered with the fish or the apparatus during this time. The fish regularly took the worms when given in reinforcement of the conditioned temperature stimulus, but on the 17th, 18th, and 19th May it never came out of the pot for food. On the 20th of May, to my regret, it was found dead with a tumourous outgrowth on the dorsal fin.

This pathological disturbance probably influenced the capacity of this fish to form the conditioned response, either by inhibiting it altogether, or delaying it for such a time that fifty stimuli were not enough to establish the response or to overcome the inhibition. Again, there is a striking parallel with Pavlov's observations on pathological disturbances in dogs, which is still further strengthened by other instances taken from my own work.

Specimen No. 3.

This specimen, for example, had been placed in the apparatus before commencing experiments with No. 2. For five days it showed great restlessness and would not remain in the pot even for a few moments when placed inside. It was hopeless trying to carry out experiments with her. This blenny was a large female very distended with eggs, large numbers of which were deposited during those five days in the tank. The day upon which she was removed, another large female very distended with eggs also, was introduced into the aquarium, and placed inside the pot. She also was given five days' trial, but behaved in the same way as No. 2. Pregnancy in dogs entirely inhibits the experimental formation of conditioned reflexes, says Pavlov. These blennies certainly appear to exhibit a similar phenomenon, for Specimen No. 3, which was kept in a main aquarium tank, laid all her eggs by the end of March, resumed normal behaviour during April, and when again placed in the apparatus on May 20th settled down at once in the pot and showed no further restlessness. Experiments upon this fish, to confirm the results on No. 1, were then started at once.

The record for this Specimen No. 3 is given in Fig. 4.

This fish formed the conditioned response remarkably quickly—after 3 days, and only 8 conditioning stimuli of an average temperature rise of 2·6° C., all of which were reinforced with food after the 15-seconds interval. It seems, as will be noticed in the record, to have become fully established suddenly. The nature of the temperature increments given is shown in Table III in exactly the same manner as that given for Specimen

TABLE III.

SHOWING THE AMOUNT OF THE TEMPERATURE RISES GIVEN AS CONDITIONING STIMULI TO SPECIMEN No. 3, CORRESPONDING TO THE RECORD OF THE RESULTS IN FIG. 4.

Date.	Temperature increments given. °C.
1927.	
May 21.	3·5, 3·5.
23.	2·5, 3·0, 3·0, 2·0, 3·1.
24.	3·2, 2·3, 2·0, 2·5, 2·5.
25.	3·5, 3·5, 2·5, 2·3, 0·6, 0·5, 1·4.
26.	2·5, 2·4, 3·0, 1·0.
30.	3·0, 3·0.
June 1.	2·5, 1·0, 0·5.
2.	2·5, 1·7, 1·7.
3.	2·6, 0·8, 0·8.
5.	1·0, 0·5, 0·7, 0·6.

No. 1 in Table II. The conditioned response was given by this fish on the first applications of temperature stimuli as low as 0·5° C. and 0·6° C. (May 25th). This fish jumped out of the tank before it had been used for long (June 5th, 1927), and so it hardly gave me an opportunity to carry out the programme I had intended. Possibly the rapidity with which the response became established was due to the high initial temperature of most of the experiments. It was hot weather, and the water temperature averaged 15·4° C., considerably higher than that of the water in experiments on No. 1.

The capacity of *Blennius gattorugine* to form conditioned responses to this type of stimulus is however substantially confirmed.

(B) The Formation of a Conditioned Response in *Blennius gattorugine* Bloch, towards Salinity Changes in the Surrounding Water.

Considerable care was required in dealing with this stimulus in order to be certain that we were observing its isolated effect. It will appear obvious that any great artificial changes in the salinity of sea-water will also involve appreciable changes in the alkali reserve, hydrogen-ion concentration, and tension of dissolved gases, unless suitable precautions be taken. Moreover, as may be perceived from my study of the temperature response, the temperature of the water used as stimulus must be absolutely equal to that of the water normally flowing over the fish. Further, in giving this stimulus, changes in rate of current-flow must be guarded against. Any one of these separate altering conditions might reasonably be acting as a conditioning stimulus unless controlled and eliminated.

The Apparatus.

This was placed against the north wall of a small room adjoining the main tank-room of the Plymouth Aquarium. The amount of foot traffic four or five yards away was considerable, but the immediate vicinity of the apparatus was quite free from unusual disturbances; the constant noise of the water circulating through the main tanks was always present.

Fig. 5 shows diagrammatically the arrangement used in giving this stimulus. A and B are two 3-litre glass aspirator bottles, with outlet tubes F and E (of glass) leading by a T-piece to a single tube G which passes downwards in the manner indicated, to discharge into the end of a black, opaque, circular, plain-glass bottle (J), open at the further end. This bottle formed the permanent home of our *Blennius gattorugine*. (Cf. introductory account to temperature response.) It rested on the bottom of a small glass aquarium, 30 cm.×45 cm.×15 cm., which was

entirely surrounded, save for the north side facing the window, by a wooden screen resting on the bench.

Normal sea-water entered the aspirator A through the tube C, which siphoned out water from one of the large tanks supplied with the circulating water of the Laboratory. The amount of water flowing through the bottle J over the fish into the aquarium K (provided with an overflow, not shown) was regulated by the tap G, so that its rate of flow was slightly less than that entering at C. It is obvious that water flows through F solely by virtue of the head of water in the aspirator A. A constant flow

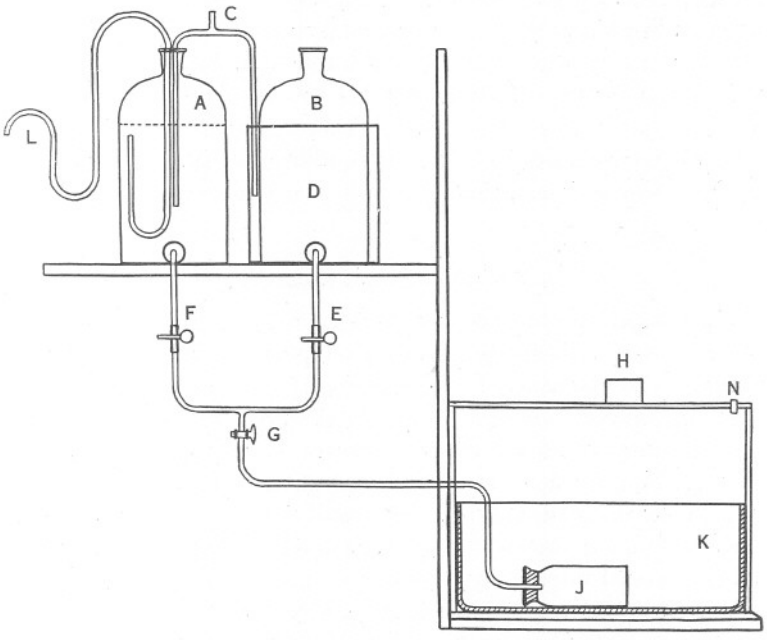


FIG. 5. Apparatus used in the experiments upon conditioned responses in *Blennius gattorugine* towards *changes in salinity*. Description in text.

was assured by fitting a constant level overflow tube, L. This flow of Laboratory sea-water formed the normal environmental medium of the fish. The water to be used as a conditioning stimulus was run from a larger supply into aspirator B in the same way. B was surrounded completely by a jacket D, fed through the tube C with the same water as continually flowed through C into A. This kept the two solutions at identically the same temperature. The water-level in B was maintained exactly on a level with that in A. Hence, by opening stop-cock E and closing F the merest fraction of a second later, the stimulating water was caused to flow through G into J without cessation or alteration of the rate of flow.

A small hole 5 cm. × 3 cm. was cut out of the screen above the opening of the bottle J. Over this was placed a modified periscope arrangement (H), through which the reaction of the fish was observed. N is the opening through which food (Nereid worms, usually *Nereis diversicolor*, an estuarine form) was introduced.

The first solution to be used as a conditioning stimulus was Plymouth tap-water, as it was considered preferable to distilled water on account of the possible toxicity of the latter due to traces of copper, etc. It is practically free from all dissolved solids, except for a trace of organic matter, and has a pH of about 6·8. Fishes are probably sensitive to large differences in pH, so that after preliminary titration of the Laboratory circulating water, the experimental water was brought to the same alkali reserve by the addition of 0·421 gr. of sodium bicarbonate per 1000 c.c. of water. The water was then thoroughly mixed and agitated for 24 hours to secure a similar degree of equilibrium ; its pH, alkali reserve, and CO_2 tension now being identical with that of the circulating water.

Method of Experimentation.

The fish used in the first of these experiments had been previously used for the series of experiments with temperature changes as conditioning stimuli (Temperature, Specimen No. 1). Its normal behaviour remained unchanged—and the reactions observed were similar ones. It lived continuously and naturally in the pot J. When food was dropped in through N, the fish at once came out of the pot, swam to below the point N, took the food, and returned hastily to the pot. This action was used as the " unconditioned " motor response. The conditioning stimulus was given several times daily for a month, unaccompanied by food.

This may, in reality, be called a strong noxious stimulus, since blennies, although frequently left stranded for long periods by the tide, will not long withstand immersion in fresh water. It should perhaps be mentioned that *Blennius gattorugine*, when given any noxious or disturbing stimulus, will retreat to the most remote corner of the pot rather than leave its shelter. At no time during this period, when the preliminary effects of this stimulus were being investigated, did the fish give any sign of coming out of the pot. This strong, positive reaction towards corners (stereotropism in Loeb's sense, thigmotaxis in Doflein's wording) is exhibited by many species of blennies, and is an additional point in favour of using the " coming out " response as a measure of the conditioned response.

The routine of the tests was similar in the main to that followed in the temperature response :—The change in salinity was allowed to act for 15 seconds ; then followed an interval of 15 seconds, at the conclusion of which the worm was given. The experiments were started on April 8th,

1927. The temperature and pH of the normal Laboratory water and of the " stimulating " water were taken daily and always kept identical with each other. The extent of the change in salinity presented as a stimulus varied slightly from time to time owing to changes in the initial salinity of the circulating water which fluctuated around 36 to 37 parts per thousand.

THE RESULTS.

Specimen No. 1.

Fortunately it is here possible to represent almost all the important points in the diagrammatic record, Fig. 6. It should be remembered that the fish had been thoroughly accustomed to aquarium conditions for several months, which, one would have thought, would have made it easier to build up further responses. Three main periods are to be noted during the time when the change in salinity was as much as 37 parts per thousand. Firstly, April 8th to May 8th, covering 30 presentations of the conditioning stimulus, during which no response is recorded throughout. However, there was a long period, April 10th to 25th, when I was absent from the Laboratory and no associated trials were made, although the fish remained undisturbed in the apparatus and was regularly fed. Some allowance should undoubtedly be made for this. Frequently during this period when no responses were given the fish did not come out at once to take food when given, there being a delay sometimes of one or two minutes.

Following this, there is the transitional period during which the response became gradually established (May 8th to 16th). The conditioned response was not fully integrated at the time of its appearance, and a gradual increase in its strength took place. At the early stages, this fish came out only a short way, so far that its head and pectorals alone were visible in the periscope. Later, when the response was fully formed, the fish came right to below the food-hole and remained there till food was given, before returning. Mouth movements similar to those recorded in the temperature response, Specimen No. 1, were in the later stages frequently observed.

Then, from May 17th onwards, the presentation of the stimulus never failed to evoke a response towards the change from $37°/_{\infty}$ to $0°/_{\infty}$ (approx.)

Causing the stimulus to become as generalised as possible again seemed the best way of finding out the smallest salinity change capable of eliciting the conditioned response. Accordingly, I decided gradually to decrease the magnitude of the change without attempting to bring about any differentiation by training.

Alterations in the salinity of the " stimulating " solution were made by mixing the Laboratory circulating water from A (Fig. 5) with Plymouth drinking water in the necessary proportions. The first alteration in the magnitude of the change in salinity used as a stimulus was made on

May 26th (arrow A in the diagram Fig. 6). The diagram shows the alterations in the strength of the stimulus as having been made suddenly; actually during the first day whilst the "stimulating" or "signalling" solution was altered, the change over was made gradually, the two solutions becoming slowly mixed. Increasing the salinity of the "stimulating" solution from $0‰$ to $7‰$, and thus reducing the difference between the normal water and the "signalling" solution, appears to have had no effect upon the conditioned response, which was given as before. A salinity change from $37‰$ to $7‰$ was thus used during the period A to C (Fig. 6), and constantly evoked a positive response. No experiments were made from the 10th to 16th June, indicated by arrow B, the

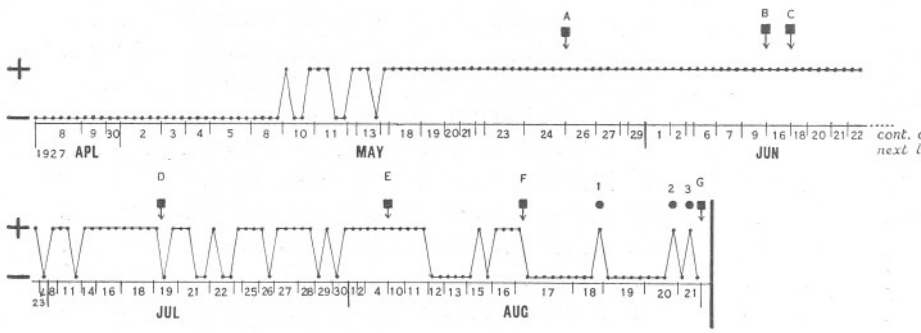


FIG. 6. Specimen No. 1.

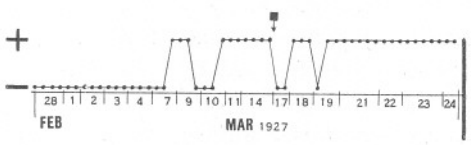


FIG. 7. Specimen No. 2.

FIGS. 6 and 7. Records of the process of formation of conditioned responses in *Blennius gattorugine* towards *changes in salinity*. Explanations in text.

fish being fed occasionally without previous "stimulation." This had no effect whatever upon the strength of the "conditioned response." From arrows C to D, June 17th to July 18th, the salinity of the solution in aspirator B was still further increased to $17‰$, thus giving as a conditioning stimulus a change from $37‰$ to $17‰$, a difference of $20‰$. On June 23rd and July 11th no response at all was given on one occasion upon each day, for which no reason was apparent, but an interval of 14 days (June 23rd to July 8th) with no experiments had no weakening influence so far as could be seen. At D, July 19th, another change was made in the salinity of the "signalling" solution—the salinity being increased to 30·2 parts per thousand. Before making this alteration, how-

ever, and in order to keep a check upon the true nature of the stimulus, I allowed the normal circulating water to flow into aspirator B (Fig. 5) and made the conditioned stimulus change from aspirator A to B in the usual way for 15 seconds, of course, without following it up with food. This was a precautionary measure to see whether movement of the stop-cocks or other manipulations were acting as stimuli. Four successive tests produced no response, and afforded a fairly definite proof that the salinity change was acting as sole stimulus. Conditioning tests were then resumed. Two days later, on July 21st (Test 3), we obtained signs of a falling off in the strength of the conditioned response. Absence of a response again occurred on the 22nd, 26th, 29th, and 30th. Upon each of these occasions the food however, when presented after the necessary interval, was itself ignored and the fish was apparently not hungry. The failure to respond does not appear to have been due to failure to discriminate the change.

The internal condition of the fish is one of the main forces of the experiment and it is a serious drawback to all discussions upon conditioned responses, that it cannot be considered in its logical relations with the situation as a whole, for we have no insight into it.

The salinity of the solution B was brought still nearer to that of the normal water on August 10th (arrow E) by being increased to 33·7°/$_{\infty}$. All stimuli given by this solution on the 10th and 11th evoked a positive response, but this was followed on the 12th by signs of failure to discriminate which, on continuing, seems to have been overcome on the 16th. This may, of course, have been due to other causes.

Finally, the limits of discrimination were reached with a salinity of 34·3 parts per thousand used as the " signalling " solution, which was first used on the 17th August (arrow F). No positive response was evoked by this solution at any time during the next 4 days, 20 trials in all, although solutions of 33·7°/$_{\infty}$ (arrows 1 and 2) and 17°/$_{\infty}$ (arrow 3), as used before, both evoked well-marked positive responses.

This specimen of a common shore fish is therefore shown to be able to discriminate a change in the salinity of the water around it of 3 parts per thousand, and, moreover, to be able to associate such a change or one of greater magnitude, with the acquisition of its food.

Specimen No. 2.

(Record in Fig. 7.)

This fish jumped out of the apparatus for some unknown reason, and eventually died before I had progressed very far with the experiments. Nevertheless, it substantiated the earlier portion of the results from specimen No. 1 and deserves mention. The fish was installed on February 7th, 1927, and left to accustom itself to its surroundings until February 28th,

Repeated introductions of the " strongest " conditioned stimulus without reinforcement (the change from $37^{\circ}/_{\infty}$ to $0^{\circ}/_{\infty}$) gave no response during this time. Conditioning to this stimulus commenced on February 28th, and within 7 days (18 trials) a positive response was obtained. The transitional period lasted until the 19th March. Dismantling of the apparatus may have been responsible for the failure to evoke a response on the 17th March. It was not necessary to do this at any time with Specimen No. 1, and we cannot therefore compare the effect with anything in the other fish. From the 19th until the untimely accident to the fish on the 24th March, presentation of the conditioned stimulus gave a fully-formed conditioned response on each occasion, seventeen associations in all.

(c) The Formation of a Conditioned Response in the Wrasse, *Crenilabrus melops* (L.), towards Vibratory (Auditory ?) Stimuli.

The Apparatus.

A wooden tank 100 cm. × 20 cm. × 20 cm. with sides 3 cm. thick contained the fish and was supplied direct with the Laboratory circulating water. The general arrangement is shown in the diagram, Fig. 8.

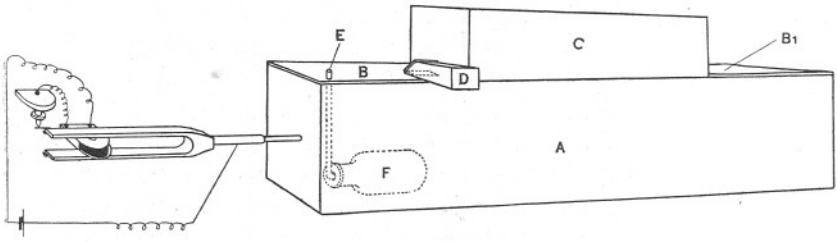


Fig. 8. Diagram of apparatus used in the formation of a conditioned response in *Crenilabrus melops* towards *vibratory* stimuli. Description in text.

A is the wooden tank ; it is covered at both ends for a distance of 25 cm. from each end (B, B1) ; C is a wooden screen which hides the uncovered portion of the tank from the observer, although leaving it open to the air on the other side, facing a blank wall, and a window. A small hole (5 cm. square) is cut in the covering piece B, and a small mirror placed over it at an angle of 45° ; this is fitted in an elongated box D, forming a modified periscope arrangement. Food (which consisted of an estuarine worm, *Nereis diversicolor*) may be introduced through the tube E and washed down into an opaque bottle F, the opening of which lies immediately below the periscope mirror. Vibratory stimuli were transmitted to the water by means of the large electrically-maintained tuning-fork, the prong

of which impinged on one end of the tank. A frequency of 128 D.V.'s per second was given by this instrument.

The Experiments.

The wrasses, unlike the blennies, are active swimming fish and not sedentary forms, so that in this case the fish normally swam about more or less continually, and only entered the bottle when food was sent down into it. The experiments were carried out in the same general manner, except that the sound was allowed to act right up to the time when the fish took the food from the bottle.

The tuning-fork was sounded for 15 seconds ; a worm was then sent down into the food-bottle ; the fish at once entered and took the worm. It was desired to condition the fish to enter the food-bottle on hearing the

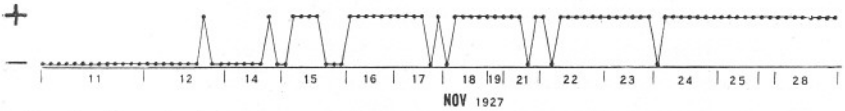


FIG. 9. Record of the process of formation of a conditioned response in *Crenilabrus melops* towards *vibratory* stimuli. Explanation in text.

sound, before food was given, and to wait there until it received the food. The results were, perhaps, the clearest of all that were obtained with any specimen and the record, Fig. 9, requires little comment.

A fairly large specimen of a wrasse, *Crenilabrus melops* (length 23 cm.), was used ; it was installed on November 10th, 1927, and at once became accustomed to its surroundings. Conditioning began on the 11th. After 20 associations with food, the first positive response was recorded in which the fish entered the bottle and waited until food was given. The response became speedily established, and on the 22nd November was quite complete. The same general phenomena observed in the previous fishes were thus also obtained here, but learning was relatively quicker than with most of the other fishes recorded in this paper.

At the time of writing up these results, further experiments are in progress with this fish, from which it is hoped to obtain evidence upon its capacity to discriminate between the vibrations from the tuning-fork and those from a submerged buzzer. The latter is associated with a food-bottle at the other end of the tank (B1), and an endeavour is being made to establish the correct associations between the respective sound and bottle. These results will be given in a later paper.

Other Experiments Involving the use of Vibratory Stimuli as Conditioning Stimuli, with Negative Results.

These were carried out on the same general principle as the last and previous experiments. But instead of the strong vibrations of the

tuning-fork being transmitted direct to the walls of the aquarium, a submerged telephone was used. A low-resistance ex-army, field headphone was completely encased in a thin metal box, one side of which was closely applied to the diaphragm of the 'phone. This was arranged to transmit the vibrations from the same tuning-fork introduced into an electric circuit. I could myself, with the head entirely submerged, hear the " telephone " clearly at a distance of five yards under water.

The first experiment was performed on a specimen of the wrasse, *Crenilabrus melops*, in exactly the same way as that which gave a successful result with the tuning-fork impinging on one of the walls of the tank. From November 20th to December 16th, 1926, there were no indications of a positive response whatever. There were secondary complications at this time, and the result cannot be regarded as definitive. For some unknown reason this fish, as well as other species subsequently tried about the same time in the same tank, refused to take food.

In another experiment, started on January 4th, 1927, the " telephone " was introduced so as to form the closed end of a jar in which a specimen of *Blennius gattorugine* (cf. temperature and salinity responses) lived. The reverse response was here aimed at, that of conditioning the blenny to come out of the jar for food on hearing the telephone. There seemed much more likelihood of this being achieved, since the distance of the blenny from the sound was very small and more or less constant. Nevertheless, from January 4th till February 14th, 1927, during which time 109 associations were given, no positive conditioned response was recorded on any occasion.

I am fairly convinced that with the wrasse faulty technique may have accounted for the failure to obtain a positive result. No certainty can be attached to either result until more information has been obtained, but the results should be compared with those given in Section B of this paper, where those obtained with the use of an electric shock as the unconditioned stimulus are recorded.

(D) The Formation of Conditioned Responses in the Wrasses *Labrus bergylta* Asc. and *Crenilabrus melops* (L.) towards visual Stimuli.

The Differentiation of Source, Intensity, and Wave-length of Light.

Specimen No. 1.

The first experiment of this series was of a very preliminary nature when begun, and improvements in apparatus and mode of treatment were being constantly made.

This, and all other investigations upon responses towards light, were

carried out in a small dark room where vibrations from traffic were negligible, and where the usual noises of the Laboratory were almost absent.

The experimental fish, *Labrus bergylta*, length 12·0 cm., taken from the Laboratory tanks, was placed in a small bell-jar aquarium, 45 cm. in diameter, which was provided with ample aeration from the compressed-air supply, but not with circulating water.

Although the fish was fed very well, it was found that under these conditions the hydrogen-ion concentration of the water hardly varied over a period of at least three weeks. The temperature ranged from 10° C. to 13·5° C.

The fish was completely screened by solid wooden partitions from the observer, except for a small hole 5 cm. square, through which its movements were watched. This was easily possible, as the room was kept in total darkness during the whole period of the investigations, and it should be remembered that the fish was therefore " dark-adapted."

The food given as the unconditioned stimulus was standardised both in nature and quantity, in the same way as food given to dogs when they are used for undergoing experiments on " natural " conditioned reflexes. Small pieces of Nereis, 2 or 3 cm. in length, were found most suitable. They were introduced from the exterior through a covered glass tube, by means of a small current of water.

Method of Experimentation.

An unshielded 60-watt Fullolite gas-filled electric lamp was suspended at a height of 16 inches from the surface of the water. The turning on of this light constituted the first stimulus to which the fish was trained to react.

From October 21st to November 3rd, 1926, the food on being introduced was simply allowed to fall on to the floor of the aquarium, but invariably in the same position.

Our first experiments were directed towards seeing whether the fish would swim to this particular spot of the aquarium when the light appeared —a very simple motor response associated with feeding. For two days the sudden appearance of the light caused the fish much uneasiness, and it swam violently round and round. Nevertheless the worm was taken immediately when given. For five days there was no noticeable reaction towards the feeding-place when the light was switched on, but on the sixth day the fish showed signs of swimming to the feeding-place when the light appeared. On the seventh day, after twenty such associations, a very definite reaction was noticed. A few seconds after the light appeared, the fish, which was at first motionless, swam to the feeding-place, and

remained there looking upwards at the spot where the worm was introduced. This reaction was given twenty successive times, spread over the next three days, and is in itself illustrative of the general phenomenon of learning in these fish.

After these preliminary experiments, the elicitation of a more complex form of response was commenced. The plain glass feeding-tube was removed, and a bottle, arranged as shown in the diagram, Fig. 10, was

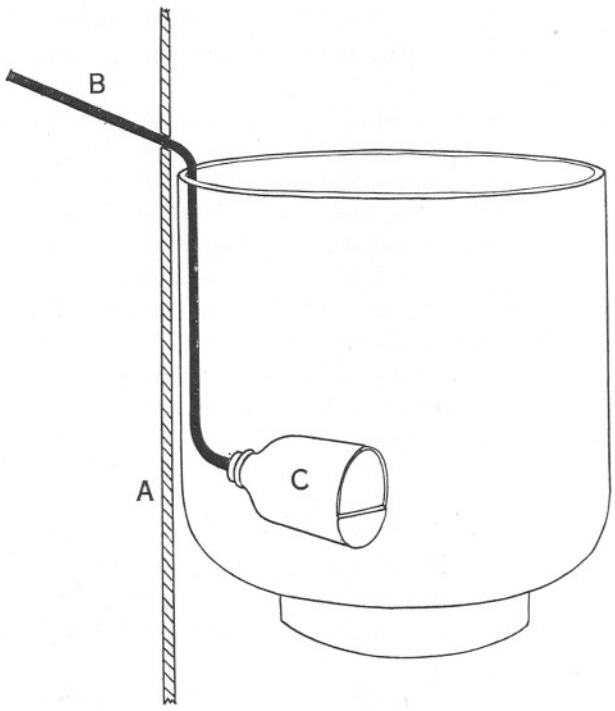


FIG. 10. Arrangement of the food-bottle in experiments on conditioned responses in wrasses towards *visual* stimuli. Explanation in text.

substituted in its place. A is the partition screening the fish from the observer : B is a covered tube through which the worm was introduced from without by a little water from a pipette : C is a plain glass reagent bottle, with the bottom partly cut out, leaving an opening in the shape of a segment ; the lower uncut portion served as a ledge to prevent the worm from falling into the main body of water.

Next day, when the worm was introduced into the bottle 15 seconds after the light was switched on, the fish made violent efforts to seize the worm through the glass, in typical " wrasse " manner. These violent attacks alternated with slow " feeling " round the bottle, which was

apparently invisible to him. After 5 hours 30 minutes, whilst " feeling " round the glass, the fish seemed suddenly to discover there was no resistance at the opening, went sharply in, and snapped the worm. The light was then switched off.

The time taken to gain entrance into the bottle became gradually reduced during the next six days, from several hours to a few seconds. But the fish gave up the useless efforts of trying to seize food through the glass bottle after five trials only. This is really only incidental to the main theme, yet it is interesting when compared with Möbius' account (**24**) of pike trying to seize minnows through glass.

On November 12th, at which date the diagrammatic record begins, the partition was taken down, and the bottle removed in semi-darkness. It was now thought desirable to eliminate all possibility that the sight of the worm was responsible for the fish's behaviour. Accordingly, the bottle was covered with plain white paper, and the whole thoroughly waxed. This rendered the bottle opaque, but left the interior sufficiently illuminated for the fish to see the worm inside when the light was switched on.

On November 15th the bottle was lowered so that it rested on the bottom of the tank. This was the last alteration in the feeding apparatus, and we may now re-state the problem attacked :—Could the fish be trained so that, when the light appeared, it would enter the bottle for food before food was introduced ? The sight of the worm under these conditions is the " unconditioned " stimulus, and the response of entering the bottle to fetch the worm is the " unconditioned " response involved in seizure of worm at sight. The appearance of the light is the " conditioning stimulus " with which we endeavour to build up a " conditioned response," involving entry into bottle when light appears, even when no food is given.

The light was left on for 15–20 seconds, and the worm then sent into the bottle. The response thus belongs to the class of " delayed responses."

THE RESULTS.

Over 500 associations with some form of light as a stimulus were made with this fish, and the diagrammatic record, Fig. 11, is thus very lengthy. It is a record of interesting successes and of interesting failures, and does not lend itself readily to a comprehensive survey.

The record has two distinct portions. The earliest, from November 12th, 1926, until January 22nd, 1927, being concerned with the results obtained upon the capacity of the fish to differentiate by training between the light from one 60-watt electric light bulb and that from two separate such bulbs. In other words, it gives information upon its *visual acuity*,

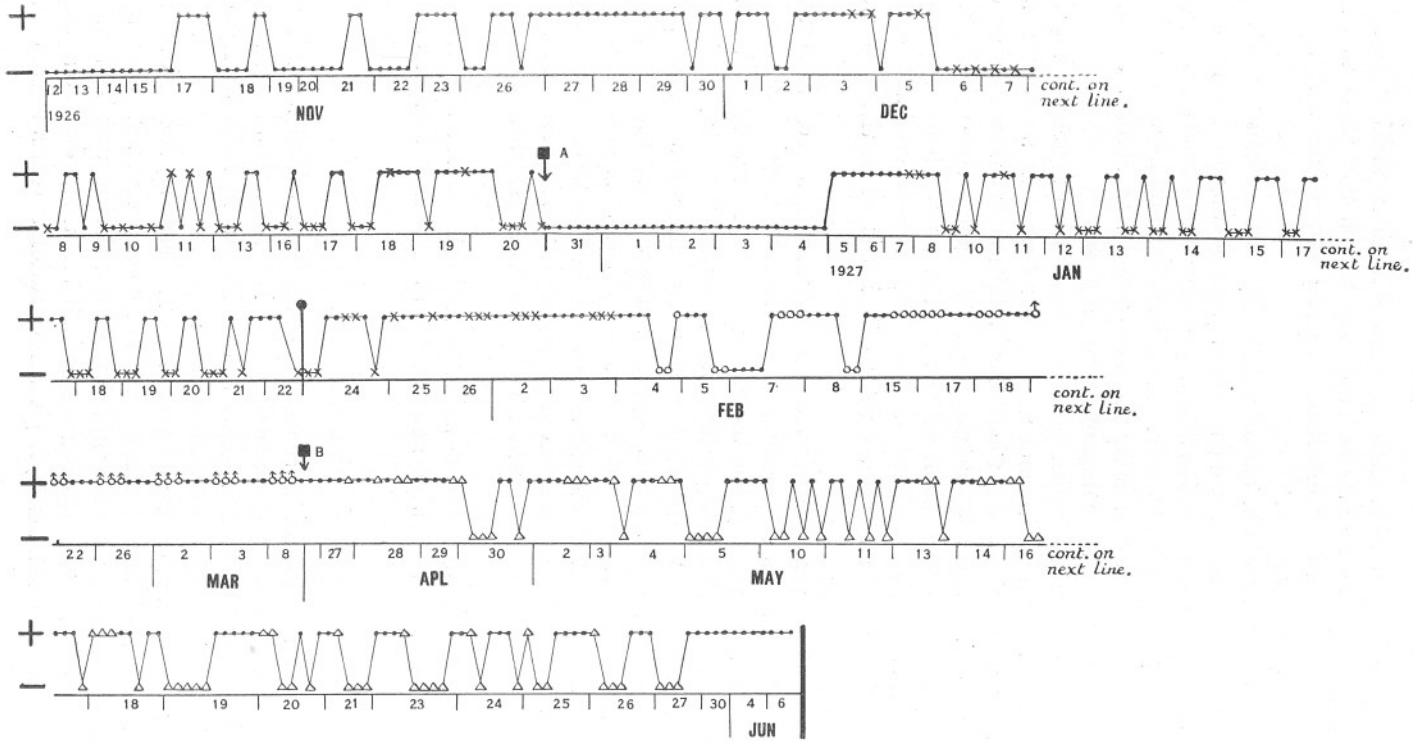


FIG. 11. Record of the process of formation of a conditioned response in *Labrus bergylta* towads *visual* stimuli. Specimen No. 1. Explanation in text.

as distinct from its *visual sensitivity;* that is, upon its capacity to discriminate the size, form, location, a number, etc., of such lights. Its capacity to differentiate between varying degrees of intensity in the light used as a conditioning stimulus is revealed in the second portion of the record, following January 22nd, 1927.

It has been necessary to use the same type of dot and cross for both portions, but they are not analogous. In the first portion a dot indicates that one unshaded lamp was used as a stimulus, a cross, that two lamps were used. In the second portion a dot represents one unit of *intensity*, the details of which will be given later, and the other signs indicate different multiples of this.

From the 12th to the 17th November, 1926, there were no signs of the building up of the response (which was here of the type described in the section on vibratory stimuli where a wrasse was used), and the fish showed a good deal of restlessness when the light was switched on. Four successive times on the 17th the fish entered the bottle before food was given. Entry into the bottle involved a somewhat sidewards inclination of the body of the fish on account of the narrowness of the opening. A gradual increase in the proportion of positive responses to those in which no conditioned response occurred is shown from the 17th to 26th November, by which time the conditioning appears to have become complete and to have remained so until December 3rd.

Additional features of the response soon became pronounced—much more so than those recorded for *Blennius gattorugine* in the temperature and salinity experiments. They seemed to be of the nature of anticipatory movements, and included waving of the tail and a peculiar side to side motion of the fish whilst in the bottle. So marked were they that during the later stages in differentiation they were of much help in determining the effect of a stimulus—the primary stimulus (of one lamp, or unit intensity) always evoking such movements whilst other stimuli being used frequently failed to do so, even though the fish performed the response of entry into bottle.

The only trials which failed to evoke a response during the period 26th November to 3rd December appear to have been influenced by internal conditions, for in my notes I recorded the fish as very sluggish at these times, and as ignoring the food also. As the response was now well established, I started discrimination tests. Another electric light similar to the first was placed alongside the latter on December 3rd; the two were so arranged that they could be switched on simultaneously or separately. The method of denoting this in the record has been mentioned above. The stimulus of two lights (represented by a cross in Fig. 11) was never followed by food, whilst the individual light (represented in the record by a dot) was invariably reinforced as before. No

differentiation was shown at first (Dec. 3rd and 5th). Indeed, for some days (6th to 16th) the original response to the primary stimulus became considerably weakened, and some features peculiar in the response to the two lights became also temporarily present in that shown towards one light. Such features included hiding reactions—the fish tried to hide beneath the bottle, these movements alternating with periods of restless swimming. Possibly, as the fish was *dark-adapted* (a point to be remembered), the two lights were sufficiently bright to cause discomfort.

From the 16th December onwards, the original positive response to the one light became re-established and remained stable until experiments were temporarily suspended on December 20th, 1926.

Here followed an interval of importance, up till December 29th (marked by arrow A in the record), during which the fish was removed from the tank in the dark room and placed in one of the main aquarium tanks, an absence from experimental conditions of 10 days. On my return, the fish was replaced in the experimental room, and left undisturbed in total darkness for 48 hours. Upon resumption of the tests, the primary conditioned response towards one light was found to have become completely lost, and it required 30 stimuli, constantly reinforced, to establish it once more (Jan. 5th, 1927). Further, it was not before January 19th that the additional features of the primary response described above as " anticipatory " movements, were again observed.

From January 7th to the 22nd a systematic attempt was again made to establish the differentiation which had begun before the vacation, and this time with entire success. Only 3 times in all, once on the 7th, 8th, and 11th, respectively, did the wrasse give a positive response towards " two lights," whilst at the remaining 32 trials, with this stimulus, complete absence of a response was recorded. During the earlier stages (7th to 11th Jan.) hiding reactions were shown towards the " two lights." These afterwards gave way to slow swimming movements only, accompanied by no attempt to enter the bottle, although the stimulus of " two lights " was allowed to act for 2 minutes.

The evidence shown in portion (1) of the record, November 12th, 1926, to January 22nd, 1927, together with that given in the text, is sufficiently definite to justify the statement that *this specimen could, by the method of differential inhibition as defined by Pavlov* (cf. Introductory (b)), *discriminate between one light and two lights* (*used together*) *when used as reinforced and non-reinforced stimuli respectively.*

When the evidence given in the second portion is considered, it appears likely that the fish was *not* discriminating between the different degrees of illumination, but between one and two points of light.

Here followed the change over to the " intensity " experiments.

An elongated wooden box (30 cm. $\times$ 30 cm. $\times$ 75 cm.) painted dull black

inside, was fitted up over the bell-jar. Across the lower opening of the box was fitted a translucent screen consisting of a piece of parchment paper between two pieces of glass. A 100-watt lamp fixed inside the box at a distance of 8 cm. from the screen gave an illumination at the screen approximately equal to that given by the original 60-watt lamp at the same distance from the bell-jar. When light of this intensity was used as a conditioning stimulus it is denoted in the record (Fig. 11) by the same type of dot used to denote the one lamp originally used. Another similar 100-watt lamp fastened to a piece of wire which could be moved up and down within the box, from outside the compartment, was used to provide any other intensity desired. Both lamps used simultaneously and at equal heights from the screen thus gave "2 × the original intensity." Very small intensities were obtained by pulling up the movable light away from the screen to the distance necessary.

It would have been quite rational to suppose that as the fish could differentiate between the light from one and that from two lamps used simultaneously, on being presented with a stimulus differing so widely in form as did the square illuminated screen from the unshaded lamp, the fish would have given no response. Initial generalisation of stimuli seems to be very wide, however, and except for three isolated occasions (on the day of commencement) when no responses were given the fish responded in a manner quite unchanged. It will be remembered that the "two lights" when first tried evoked a positive response, and that it was only after some time that the differentiation was obtained. Non-reinforcement of the stimulus undergoing differentiation actually inhibited the primary response upon that occasion. Now, although "2×unit intensity" was never reinforced, as it was desired to obtain evidence upon discrimination, "unit intensity" itself was constantly reinforced from the commencement. The initial generalisation was thus never broken down when "unit intensity" was used as stimulus and a constant positive conditioned response invariably resulted from its use up to the end of the experiments. It became, in fact, the new primary response.

Upon the 3rd February, as no signs of discrimination had been shown by the fish between "unit" and "2×unit intensity," I started an attempt to bring about discrimination between "unit" and "half-unit intensity" (denoted by a small circle in the record, Fig. 11), the latter, of course, not being reinforced by food. Distinct evidence for discrimination was shown at first. The "half-unit intensity" gave no response when first tried (Feb. 4th, tests 5 and 6); also upon the 5th (tests 4 and 5) and 8th (tests 5 and 6). For a short time (Feb. 7th) the fish was rather "sickly," and only gave very slow responses to the primary stimulus. It was put under circulating water for a short time and soon recovered. From the 8th to the 14th there were no experiments performed, but, contrary to

the experience in December, 1926, this interval had no inhibitive effect. The initial discrimination between the " unit " and " half-unit intensity " then seems to have become lost, and a positive response was given invariably to both stimuli. Another factor was brought in upon the 22nd to see if the discrimination could be re-established when some inhibitive or disturbing influence was associated with the " half-unit intensity." When this combined stimulus was presented at the tests denoted in the record (Fig. 11) by the sign ♂, the food-bottle was given a violent jerk, which, under normal circumstances, would certainly have startled the fish. Although the fish actually was startled on each occasion, in a few seconds it entered, and would try to do so even whilst the bottle was being agitated. The conditioned response was obviously very powerful.

No evidence for discrimination between these stimuli could be obtained, and the use of this stimulus was concluded on March 8th, 1927. A very long gap then occurred in the experiments—up till April 26th (indicated by the arrow B). During part of this time the fish was again placed in one of the main aquarium tanks in normal daylight. On replacing it in the experimental tank it was left undisturbed, as before, for 48 hours. In spite of this prolonged absence from experimental conditions (8 weeks), no reduction was observable in the strength of the conditioned response. " Unit intensity," when given as stimulus and not even reinforced, gave the typical response unchanged.

We may state now, therefore, *that when the response has not been long established* (as at Christmas, 1926), *an interval of several days without tests causes an extinction of, or a great weakening of, the conditioned response in fishes ; whilst when it is firmly established* (as on March 8th) *even a lengthy absence from experimental conditions brings about no perceptible influence.*

A very low intensity was now brought into use with the object of making the difference between the two intensities used in discrimination as great as possible. If discrimination could then be established, we could work backwards and find the limits. A small triangle (△) is used to denote trials where this intensity was used as stimulus. A full statement of the various degrees of illumination will be given later. No signs of discrimination were obtained until April 30th ; positive conditioned responses entirely similar to those given towards " unit intensity " as stimulus having been given. The record then shows a preponderance of negatives with this stimulus, denoting that no responses were obtained, but the positive responses shown can hardly be called true positive responses. Thus, from the 30th April onwards, when the wrasse was given △ as stimulus, even when it entered the bottle (denoted as positive), the anticipatory movements were quite absent. The entry into the bottle was very slow and very distinct from the quick entry given towards the primary stimulus. Later (from the 16th May onwards) it is seen that

this semi-positive response was given when △ was first tried each day, but subsequent trials on the same days evoked discrimination and no response. It appears that the comparison between the two had to be offered within a fairly limited period. The fish died on June 6th, 1927, and cut short any further discrimination, but the evidence is clear *that it only differentiates with difficulty between even very great differences in intensity of illumination.*

Whether these experiments should be regarded as throwing light upon discrimination of intensity of *illumination* of a surface, or upon *brightness* of a surface, is not certain ; with the type of screen used the terms have almost the same meaning.

The illuminations used in these tests were as follows :—By the term " unit intensity " as used in this paper is meant the *illumination* at the under surface of the illuminated screen when using one 100-watt Mazda lamp, on a 210-volt lighting circuit, at a distance of 8 cm. from that screen.

This equals approximately 7500 metre-candles, the others (2×) and (half-unit) being derived directly from this. Intensity △ (the lowest tried) was approximately 80 metre-candles.

The time-relations observed in this fish are interesting. The interval between presentation of stimulus and performance of response, which before conditioning had really begun averaged several minutes, became reduced in the earlier stages when the conditioned response had been formed to about 20 seconds. This time (20 secs.) was the latent period fixed by me as the time-interval between stimulus and food. Later, however, when the conditioned response was thoroughly established, the interval became reduced to a few seconds (about 5) ; indeed, the fish went into the bottle with great rapidity immediately the light appeared, and remained there during the remaining 10 or 15 seconds until food was given, before coming out. On May 6th and 7th no organised experiments were made, but the primary stimulus (unit intensity) was repeatedly given to demonstrate the nature of the conditioned response to representatives present at a Challenger Society meeting. None of these tests was followed by food, yet on each occasion the response was typical. The time-interval, however, between stimulus and response gradually lengthened to 50 seconds and indicated that, if this had been continued, the conditioned response would have undergone considerable weakening by " extinction." When reinforced with food, the response at once regained its normal time-relationship.

Specimens No. 2, 3, 4, and 5.

Introductory. These fishes were all very small, immature specimens of *Crenilabrus melops* or *Labrus bergylta* (about 6·5 cm. long), and were used in the formation of conditioned responses towards light of varying *wave-lengths*. I was particularly unfortunate with all of them, for they died before I had time to get absolutely conclusive evidence upon their sense of colour-discrimination as revealed by this method. Valuable information was however obtained, and they all serve to illustrate general phenomena relating to learning in fishes. The same method was followed as in Specimen No. 1, but the apparatus was on a smaller scale and there were minor

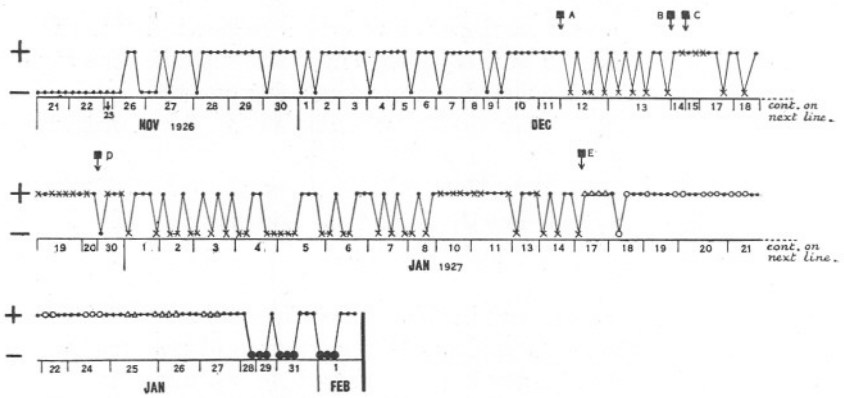


FIG. 12. Record of the process of formation of a conditioned response in *Crenilabrus melops* towards *visual* stimuli. Specimen No. 2. Explanation in text.

differences connected with the method of illumination, in order to allow of the ready interposition of a Wratten light filter between the source of light and the vessel containing the fish.

The time-interval and the nature of the response evoked were also the same.

Specimen No. 2 (Record in Fig. 12). This fish, *Crenilabrus melops*, was first conditioned to the unshielded light from a small 2-volt lamp worked by battery. As will be seen from the record, learning was relatively quick, the response having become well established in 7 days; it first appeared after 14 associated trials. There were occasions when no response was given. Such was the result when the first test was made on December 1st, 2nd, etc. On December 12th (arrow A, Fig. 12) tests were started with a Wratten's K3 light filter (yellow) interposed between the light from a similar 2-volt lamp of the same intensity placed alongside the first. This was used as a differential stimulus and never reinforced by food. If I had known then what I have since learnt from Specimen No. 1, that this left a loophole for misinter-

pretation of the results, I should not have used two separate sources of light, although contiguous with each other. This objection was afterwards removed, and is absent from other experiments in this series. There are periods, such as from the 12th to 13th December, 1926, and the 1st to 8th January, 1927, during the time when two separate sources of light were used, which show unmistakable signs of discrimination, either between source or between the actual colours, white and yellow. But there are other periods, 14th to 17th December ; 19th to 20th December ; and again from the 10th to 13th January, 1927, when no discrimination was shown. Why ? Upon the 14th December (arrow B) the position of the yellow and white lights was reversed, and on the 15th (arrow C) changed back again. This gave rise to the first confused period, which, except for two instances on the 17th and 18th December, remained confused at several trials up to the 20th. Whether it be considered that the fish had been discriminating between yellow and white, or between the relative positions of the sources of illumination, the confusion was to be expected, for a hitherto unreinforced stimulus became, on these occasions, reinforced by food. The fish would thus speedily react to either white or yellow—or to either light—as they were now apparently positive stimuli. Then followed an interval of 10 days, December 20th to 29th (arrow D), during which no experiments were carried out. This caused a slight weakening of the conditioned response, and moreover, on resuming, there was again no discrimination (cf. also with Specimen No. 1). By continuing to reinforce the white light and not reinforcing the yellow, in their original positions, discrimination was later established and remained stable for a considerable time. The lack of discrimination on the 10th and 11th January is unaccounted for.

Arrow E (Fig. 12) indicates the date when a 60-watt Fullolite gas-filled lamp, worked from the main 210-volt lighting circuit, was fitted up in the illumination compartment which had contained the white light in its original position. Wratten light filter No. 70 (red*) was interposed on the occasions denoted by a △, whilst this light unshielded was given as a stimulus at the trials shown with an open circle o. The original stimulus was placed in the other illumination compartment, previously occupied by the yellow filter. Continuing differentiation as shown, no discrimination between these new stimuli was obtained between 17th and 28th January, a positive conditioned response being evoked by all three.

Insertion of Wratten light filter No. 76 (violet) in the path of the light from the 60-watt lamp, gave, however, no signs of a positive response whenever it was given as a stimulus (denoted by a large black dot •, on Jan. 28, 29, 31, and Feb. 1st, 1927).

* Full details of these filters, showing their selectivity, maximum transmission, wavelength, etc., may be obtained from Kodak Ltd., Wratten Division, Kingsway, London, W.C. 2.

Specimen No. 3 (Record in Fig. 13). This was a wrasse of the same species and of the same size as No. 2.

The conditioned response was evoked towards the monochromatic green light obtained by interposing Wratten light filter No. 74,* in the path of the light from a 60-watt lamp, arranged as shown in Diagram 16 (T and H, light and filter respectively).

An exceedingly long time was required to make this fish " at home " in the tank. From March 27th, 1927, until April 11th the fish would not eat or move unless strongly disturbed. I was absent then for two weeks and

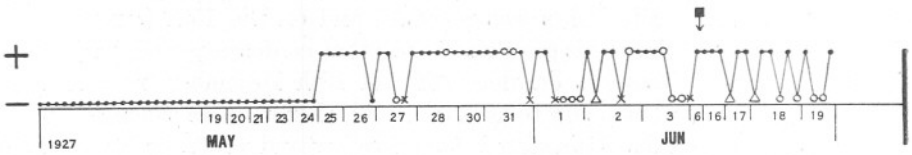


FIG. 13. Specimen No. 3.

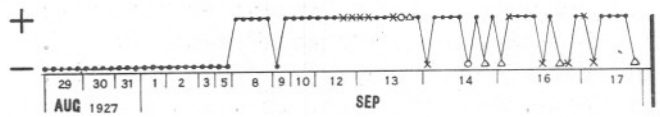


FIG. 14. Specimen No. 4.

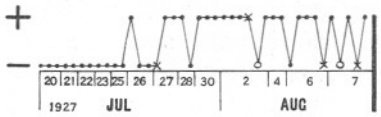


FIG. 15. Specimen No. 5.

FIGS. 13, 14, 15. Records of the process of formation of conditioned responses in wrasses towards *visual* stimuli. Explanation in text.

the fish was removed for this period to one of the main tanks, where I have no record of its behaviour. On being returned to the experimental tank the same difficulty was again experienced, but by May 1st the fish had become more accustomed to its surroundings and took food readily when given. It proved the most difficult of all the specimens investigated to " condition." Between April 26th and May 24th 134 associations of stimulus+food were given without evoking a positive response, but it then became called out very rapidly and completely (May 25th *et seq.*). The record after that is quite a straightforward one. Differential training was started early (May 27th). It will be seen that, as in Specimen No. 2,

* Full details of these filters, showing their selectivity, maximum transmission, wavelength, etc., may be obtained from Kodak Ltd., Wratten Division, Kingsway, London, W.C. 2.

no signs of a conditioned response were given at any time towards the violet light obtained with Wratten filter No. 76 (denoted by a × in the record). The evidence that the fish could discriminate by the method of differential inhibition between the original green (Wratten filter No. 74) and a monochromatic red light (Wratten filter No. 70), not reinforced by food (denoted by a small circle o in Fig. 13), is not very powerful, but definitely suggests that it probably could. When presented at three separate trials (June 2nd, 17th, and 18th) with the non-reinforced stimulus of unfiltered white light from the 60-watt lamp (△ in the record), a complete absence of a response resulted. An interval of nine days, when no experiments were performed (June 6th to 16th), had no effect upon the strength of the conditioned response.

Specimen No. 4 (Record in Fig. 14). A small example of *Labrus bergylta* (length 6·5 cm.). The conditioned response was here evoked by the same type of stimulus to which No. 3 was "conditioned," but using monochromatic yellow light obtained by using Wratten light filter K3 and a 60-watt lamp as source. The record requires little amplification. Twenty-three trials were sufficient to bring about the formation of the conditioned response (Aug. 29th to Sept. 5th, 1927) which became established rapidly. The evidence obtained upon colour-discrimination is inconclusive, owing to the limited nature of the record. Red, violet, and green (shown on the record by the marks △, o, and × respectively) were all discriminated on several trials, but positive responses towards these colours were also given.

Specimen No. 5 (Record in Fig. 15). A specimen of *Crenilabrus melops* (8·0 cm. long). The conditioned response was evoked by monochromatic red light, using Wratten light filter No. 70, with a 60-watt lamp as source.

No difficulty was experienced in forming the response, which, as will be seen in the record, became established fairly rapidly. A positive response first appeared after twelve trials (20th to 26th July, 1927). The fish died before sufficient evidence upon discrimination was obtained. Violet light from Wratten filter No. 76 (denoted in the record by a small circle, o), however, when tried on two occasions, produced a negative result as in the other specimens. A green filter (Wratten No. 74) was used at the trials shown in the record by a ×.

SECTION B. ELECTRIC SHOCK AS UNCONDITIONED STIMULUS.

(A) Introductory.

The method of carrying out these experiments was evolved with the intention of repeating Froloff's experiments (**10**) and (**22**) in a more natural manner. At the same time it eliminates other possible interpretations of

the reactions he recorded. A brief résumé of his method will make these points clearer. His experiments appear to have been carried out with great care and he lays stress upon the necessity for scrupulous standardisation of these experiments. Such standard conditions he maintained throughout. The fish was isolated in one room and the investigator remained in an adjoining room, all connections being carried through the separating wall and stimuli given cautiously and quietly. Of two wires from the secondary coil of an induction coil one was sunk to the bottom of the aquarium containing the fish being experimented upon. The other—a very light thin wire—was attached to a small wire clamp fastened into the dorsal fin of the fish. The same wire was further attached to the underside of a Marie capsule—thus suspending the fish. Any movements the fish then made were immediately registered on the Marie registration disc in the experimenter's compartment.

If left in the dark, and so long as there was no incidence of extraneous stimuli, the fishes used appear to have taken up a restful position in a few minutes from the time of suspension. When this restful condition had been maintained a few moments, one of the conditioning stimuli (light, sound, etc.) was presented, and after a definite interval the electric circuit closed. This at once brought about a registerable "flight-reaction." After a sufficient number of synchronous presentations (between five and thirty) of the conditioned and unconditioned stimuli, the fish reacted to the former alone, giving a "flight-reaction."

I tried in the first place to repeat these experiments exactly as described by Froloff, but without success or confirmation of his results. In my experiments the fish simply would not remain still when suspended in this manner.* A few moments' pause—then vigorous movement—pause again, perhaps for minutes—and so on for hours—was the invariable result. It was clearly impracticable to suspend them in this way without great disturbance of the results. As, however, I have substantially confirmed his conclusions, although in a different way, that fishes do form conditioned responses to light and vibratory (auditory ?) stimuli, it is possible that my duplication of his method was not exact. Under the circumstances, I concluded that it was desirable, both on humane as well as practical grounds, to eliminate the necessity for fastening the fish in any way whatever. This led to the construction of the present type of apparatus, which is essentially derived from Lillie's method (**23**) for sending non-polarised currents through Echinus eggs. Polarisation is better eliminated, as its effect, if present, would be an influence of uncertain character.

* The fishes tried included *Cottus bubalis*, *Gobius paganellus*, *Crenilabrus melops*, *Labrus bergylta*, *Blennius gattorugine*, *Motella* sp., *Pleuronectes flesus*, and *P. limanda*, *Leuciscus rutilis*, *Leuciscus leuciscus*, and *Cyprinus carpio*.

The Apparatus.

This is shown diagrammatically in Fig. 16. A is a shallow glass dish (30 cm. × 10 cm. × 5 cm.) placed inside a wooden box (C) (40 cm. × 17 cm. × 17 cm.) which has some 10 cm. of loose cotton-wool (B) on the bottom to lessen any vibrations from any external source. External to the box, at either end, are the two the non-polarisable electrodes. These consist of glass dishes (D) containing a saturated solution of zinc sulphate, in each of which is immersed a large plate of zinc (E), connected up with the

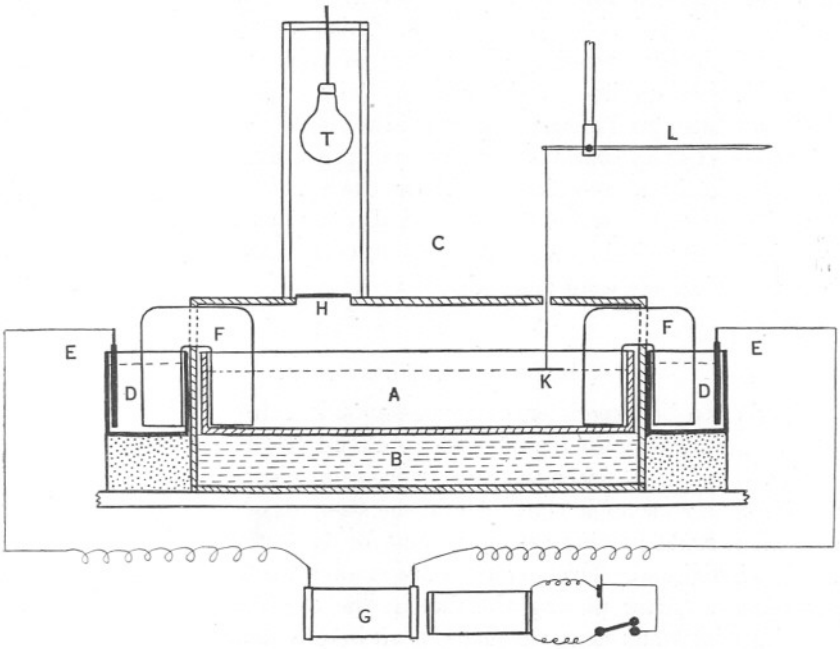


FIG. 16. Diagram of apparatus used in experiments upon conditioned responses in fishes in which an electric shock is used as an unconditioned stimulus. Explanation in text.

terminals of the secondary of an induction coil (G). The glass vessel A is filled with sea-water of the required amount and contains the experimental fish, which is allowed to remain quite free and not fastened or restrained in any way. A continuous aeration is maintained. Current is conveyed through the sea-water in A (and hence also through the fish) by means of bridges of agar-agar jelly (F), connecting with the electrodes D at either end. The current actually passed through the fish is extremely small, and the responsive movements are also small but decisive. Movements of the fish are recorded by the pointer of the pivoted reed (L). A piece of waxed silk thread is attached to this by one end ; the other end

is fastened to the centre of a microscopic cover-glass, $1\frac{3}{4}$ in.$\times$ $\frac{7}{8}$in. (K) which has been covered with a thin film of vaseline on both sides. This floats on top of the water. The vaselined cover-glass has a very high surface tension, and sufficient stress is maintained on the thread to keep the pointer horizontal. The slightest body movement of even very small fish contained in the water (such as *Gobius ruthensparri*) is registered by this means. The thread passes through a small hole in the box surrounding the dish A. Another small square opening in the top of the box, 5×5 cm., allows for the introduction of any required apparatus to be used as a conditioned stimulus. The diagram (Fig. 16) shows how this was adapted for introducing visual stimuli. T is a source of light, movable in a vertical plane, within a black box; H is a Wratten or other light filter. In the experiments with auditory (vibratory) conditioned stimuli the instrument producing sound was also placed through this opening. The whole of the apparatus, with the exception of the recording needle, was completely surrounded by black cloth before each experiment. Experiments were carried out in a small dark basement room, remote from Laboratory noises and interference, every care being exercised to keep conditions constant and quiet.

Method of Experimentation.

The fish to be experimented upon was taken from one of the main tanks and placed in the dish A with approximately 800 c.c. of sea-water. It was found that fishes vary in their behaviour towards an induced shock, but a reasonable constancy in the strength of the response in any individual could be obtained by the use of a constant amount of water for that individual. This amount varied more with the species than with individuals. After placing the fish in the apparatus and completely covering with black cloth, the fish was left in total darkness for a period of at least fifteen minutes. Under these conditions the fish usually became quiescent almost at once and made no further movement. (It is not likely that very active fish would do this, but only sedentary forms were used for this reason.)

The conditioning stimulus was then presented at intervals varying from one minute to five minutes, with an average of three minutes, and immediately followed, upon each occasion, by the "unconditioned" electrical stimulus, consisting of a single make-and-break induction shock. The latter at once evoked a decisive movement, which was indicated by oscillations of the pointer.

The object of the experiment is to see whether the fish will form the "shock-reaction" when given a stimulus, visual, auditory, or any other, to which it had been previously indifferent and to which it had shown no

signs of a motor response until " conditioned " to do so. All signalling or conditioned stimuli used were tried at least twenty times with the fish before the process of conditioning began.

It should be noted that these responses belong to the type described by Pavlov as " simultaneous," and in this respect they differ from the previous experiments.

The strength of the shock used was the lowest that would give a measurable response. This could be adjusted to a nicety either with the coil or by varying the amount of water in A. There was a definite quantity of water in which the fish could be placed, so that, when the make-and-break were made, no shock-response was given. Decreasing the amount of water by a further 20–50 c.c. and so reducing the ratio of the resistance of the fish to the total resistance, was then sufficient to give the slight decisive response required. There is a certain minimal strength of stimulation which will evoke a decisive movement when the head of the fish points towards the kathode, but not if it is orientated towards the opposite pole, when reversed and placed in such a poisiton. The amount of current required to cause a movement in a fish appears to bear some relation to the nature of the epidermal coverings. Both these points deserve further investigation.

The number of associations made daily in the course of the experiments averaged 8, and varied from 6 to 14. Fifteen minutes or more after the last daily test had been made the fish was returned to the main tank from which it was taken.

This method of investigating conditioned responses in fishes is much more in line with Pavlov's method for dogs, though it is not necessarily a more convenient one for the present purpose. Neither is it likely to give such good results with fishes as with mammals on account of the difficulty of keeping them. A great desideratum for this work is a harmless unconditioned response which will evoke in fishes a registerable response of a quantitative nature.

The possibilities of this method have only been lightly explored as yet.

THE RESULTS.

(B) The Formation of a Conditioned Response in *Blennius gattorugine* towards Visual Stimuli.

Specimen No. 1.

The conditioning stimulus was the light from a 60-watt Fullolite gas-filled lamp on the main lighting circuit passed through Wratten light filter No. 74 (green) and allowed to act for 2 seconds. The record is given in Fig. 17.

The conditioned response became established after 20 associations (Sept. 13th, 1927, trial 6). Upon the 14th a completely negative result was obtained ; the reason for which was immediately apparent when the apparatus was uncovered at the conclusion of the day's experiments, and it was discovered that the air circulation had become stopped byaccident. This had completely inhibited the response, but the effect did not persist long on the morrow. Upon the 15th, 16th, 17th, and 19th September the earliest trials made during the day evoked no positive conditioned response, but later trials on the same days evoked a positive reaction, gradually increasing in magnitude. No diminution in the

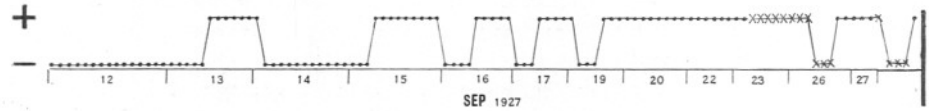
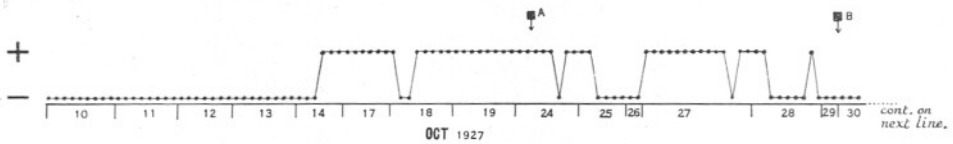


FIG. 17.



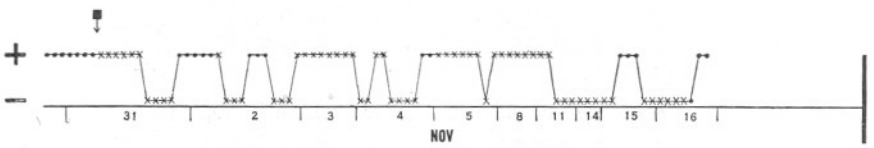


FIG. 17. Specimen No. 1. FIG. 18. Specimen No. 2.

FIGS. 17 and 18. Records of the process of formation of conditioned responses in *Blennius gattorugine* towards *visual* stimuli. Explanation in text.

strength or constancy of the response having occurred from the 19th to 23rd, experiments upon the capacity for colour discrimination were commenced. The × in the record denotes trials in which the same light source was used, but the green filter was removed and Wratten light filter No. 70 (red) was interposed. This stimulus was not reinforced. At first no discrimination was shown, the positive shock-reaction being given towards the red light just as to the green. After 9 trials, not reinforced, the red light failed to evoke a positive response (Sept. 26th, trials 4, 5, and 6). Tested immediately afterwards (Sept. 26th, trial 7) with the primary stimulus (green), a strong positive conditioned response was obtained. Experiments on September 27th began with the use of a green filter and a constant positive response was still given ; on being presented with the differential stimulus, red light

(trials 4 to 7), discrimination was at once shown. A trial with the green followed two minutes later and gave an unchanged positive response.

Specimen No. 2.

Conditioning stimulus, as No. 1, but using monochromatic red light obtained through Wratten light filter No. 70. Procedure also as in No. 1. Record in Fig. 18.

Thirty-five associations, spread over five days, were required to establish the conditioned response in this specimen, but once formed, it did not suffer diminution daily as in No. 1. It remained exceedingly stable and on October 24th (see arrow A) I decided to see if it could be "extinguished" or caused to disappear by simple non-reinforcement. The course of this phenomenon was erratic (see Oct. 24th to 29th), and there was no gradual diminution. It became a zero response on the 28th and remained so on the 29th, and at the first trials on the 30th. It was then decided to rebuild the response by again reinforcing it with the unconditioned electric stimulus (arrow B). Three trials only were necessary, though the response did not immediately regain its maximum. On the 31st October the conditioned response was very marked. An attempt was now made to obtain evidence upon the capacity of the fish to discriminate the primary stimulus of red from one or more allied shades of grey (shown by a $\times$ in the record). These were obtained by interposing photographic lantern slides in the path of the light. To obtain these tints, grey No. 1 was exposed for 5 seconds, grey No. 2 was exposed for 10 seconds at a distance of 30 cm. from a 30-watt lamp, and both developed simultaneously for 10 minutes. Grey No. 1 gave a brightness equal approximately to that of the red filter No. 70 as judged by my own eye, dark adapted; grey No. 2 was rather less bright. Very definite evidence for discrimination is shown on the record. The differentiation being complete from the 11th to 16th November, 1927. The greater part of these differential trials represents the result obtained with grey No. 1, but grey No. 2 (darker) was also presented at tests No. 8, 9, and 10 of October 31st and tests No. 6 and 7 of November 15th, with a negative result.

(c) The Formation of a Conditioned Response in the Eel, *Anguilla vulgaris* Turton, towards Vibratory Stimuli.

A large number of experiments were carried out by this method, using, in place of the visual stimulus, an electric buzzer enclosed in a small glass rectangular jar. This was placed in the vessel A (Fig. 16) and rested on the bottom at the end F. Procedure was the same as with visual stimuli, but a period of five seconds, during which time the buzzer was kept sounding, was allowed to elapse before giving the shock stimulus. The only fish

which gave indisputable evidence of forming the conditioned response to this sound was a small fresh-water eel, 16 cm. long. Fig. 19 shows the progress of the experiment.

There are three typical periods. A period of 30 trials (10th to 16th Aug., 1927), during which there were no signs of a response to the sound ; a second period (16th and 17th Aug.) in which the response became established ; and the final period (19th to 24th) when the conditioned response was firmly established. Owing to the shallowness of the dish, on the three occasions denoted by arrows in the record, the fish wriggled out after receiving the shock, and being so slimy it was rather difficult to recapture it. It will be noticed that these strong disturbances resulted in no responses being given at the trials immediately following the return of the eel to the apparatus.

Other fishes tried with this stimulus included *Gasterosteus aculeatus*, *Cottus bubalis*, *Pleuronectes platessa*, and *Gobius minutus*. The results

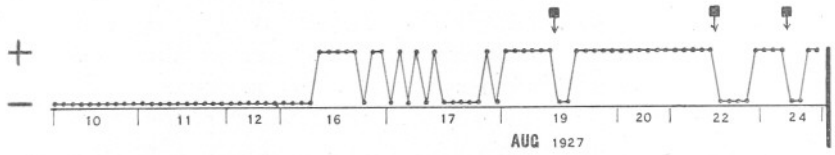


FIG. 19. Record of the formation of a conditioned response in *Anguilla vulgaris* towards *vibratory* stimuli. Explanation in text.

from these are of an indecisive nature, all of them having responded on occasions to the sound, but only in an erratic sequence which seemed to bear no relation to the progress of conditioning. It is most likely that the nature of the sound stimulus was not a suitable one for the purpose.

Experiments of a similar nature were also carried out in which a key D tin-whistle was used as a stimulus. *Blennius gattorugine* was the fish tried. All the holes in the whistle were closed and the bottom sealed with a very thin sheet of brass ; this end was immersed in the water. The whistle was connected with the compressed-air supply and a constant note was obtained by regulating the pressure ; it was sounded by removing a damper placed over the throttle. Eighty-three associations given between October 7th and 19th, 1927, were not sufficient to produce the slightest indications of a conditioned response to the sound of the whistle in the specimen tried. I had previously satisfied myself that this note could be heard plainly with the head completely submerged at a distance of four yards from the whistle when sounded in the same manner.

Considered in conjunction with the experiment upon this species of blenny recorded in Section A (cf.), in which a submerged telephone was used, it appears probable that this fish is incapable of forming conditioned

responses to sound produced in either of these two ways. It would be foolish to infer from these premisses alone that the fish cannot hear. It did not prove difficult to establish the response towards vibratory stimuli with the wrasse, and Dr. Allen states that only a relatively short time was required to produce such a response in pollack (*Gadus pollachius*) and rudd (*Scardinius erythropthalmus*). The possibility that the blenny really cannot hear this type of sound or vibration is thus increased.

ACKNOWLEDGMENTS.

This work was suggested to me in the first place by Dr. E. J. Allen, F.R.S., as a general problem to be attacked. I have especially to thank him for his interest and help throughout, and for the loan of the Wratten light filters used in the experiments on visual stimuli. The work was carried out during the holding of a Student Probationership in the Plymouth Laboratory of the Marine Biological Association during the years 1926 and 1927.

My wife has rendered me invaluable service.

SUMMARY.

It has been shown by experiments formulated upon the " conditioned response " principle that the blenny, *Blennius gattorugine*, is able to perceive and to profit by very small changes in its environment. This fish is able to form conditioned motor responses using food as unconditioned stimulus, towards a momentary increase of 0·4° C., or more, in the *temperature* of the surrounding water.

It is also able to form similar conditioned motor responses towards a momentary decrease in the *salinity* of the surrounding water, of as little as 3 parts per 1000, or towards a change of greater magnitude (up to 37 parts per 1000).

Conditioned responses have been established in the wrasses, *Crenilabrus melops* and *Labrus bergylta*, towards *visual* stimuli of varying kinds. It appears that these fishes can discriminate after differential training between one or two sources of light, and between monochromatic red, green, yellow, or violet light, but not readily between even comparatively large differences in intensity of a luminous source. These results are those obtained upon " dark-adapted " fishes. More extensive experiments will be necessary before a final statement is made upon their capacity for colour discrimination.

Using an electric shock as an unconditioned stimulus it has been shown that *Blennius gattorugine* can also form *visual* conditioned responses towards monochromatic red and towards monochromatic green light; and that it can, by the method of " differential inhibition," distinguish red from green, and red from closely allied shades of grey.

Conditioned responses have been formed in the wrasse, *Crenilabrus melops*, towards *vibratory* stimuli, using a tuning-fork of 128 D.V's. per second, and food as unconditioned stimulus. A conditioned response towards the vibrations from an electric buzzer has been formed in the common eel, *Anguilla vulgarius*, using an electric shock as unconditioned stimulus. Up to the present time it has not proved possible to establish conditioned responses in *Blennius gattorugine* towards the vibrations produced by the tuning-fork, a submerged telephone transmitting the same note, or towards the basic note of a key D tin-whistle, arranged as a closed pipe.

Many of the phenomena relating to conditioned reflex formations in mammals are shown to occur during the formation of similar responses in fishes.

Froloff's observations have been confirmed in most respects.

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Physical Factors on the Sandy Beach. Part I. Tidal, Climatic, and Edaphic.

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With 3 Figures in the Text.

CONTENTS.

INTRODUCTORY.

IN no other region of the biosphere does it appear that the purely physical factors of the environment exercise so profound an influence upon living forms as on the seashore, for not only the animals and plants which live upon it to-day, but the various groups of organisms which have passed through it in their evolutionary history, reveal, in their structure, rhythms

and reactions, the indelible impress of the littoral discipline. The intertidal zone, in which these special conditions are operative, is very extensive —amounting in the British Isles alone to 620,000 acres—and the investigation of so large and important a region must necessarily be of considerable scientific and economic interest.

While much attention has been given, in recent years, to the physical ecology of the open sea (*vide* Atkins, 1926, for bibliography), and even to the special conditions obtaining in limited or almost land-locked sea-areas (Marshall & Orr, 1927), the study of the seashore itself has progressed on different lines. Much detailed ecological work has been carried out (*vide* Flattely & Walton, 1922, for bibliography), leading to the recognition of definite "zones," both algal and animal, corresponding to the successive levels of the intertidal and subtidal regions, but in no direction has it been found possible to establish those general principles of interdependence which have done so much to clarify our knowledge of the open sea and its inhabitants. This failure is due, partly to the complexity and fluctuating character of the factors involved, but even more to the lack of adequate data, and the failure to utilise existing data, bearing upon the magnitude and incidence of the physical, rather than the biological, agencies which are so evident in the area. In this paper an attempt is made to survey some of the physical conditions obtaining upon the seashore, with special reference to that distinctive region known as the sandy beach.

The outstanding factor, of course, is the tidal ebb and flow, which not only modifies and determines the incidence of all other factors, but is the characteristic and dominant influence of the littoral region. The effect of currents and of wave-impact, also, as other types of water movement, have been considered along with the tide. The climatic factors of temperature, light and wind are of special significance in so exposed an area, though only the first is here given special consideration, since the effects of sunlight upon the shore will form the subject of a separate communication, and wind, so far as it operates upon the intertidal region, does so indirectly, through the action of the water-waves which it induces. The relation of the wind to dune formation does not fall within the scope of the present survey.

Salinity as a factor in the life of beach organisms is as potent an influence as in the sea, and calls for special consideration, in relation to drainage, sand-grade, and tidal movement. Finally, the sand itself, as the permanent factor in the beach environment, enters into those other variables of porosity, evaporation, and capillarity, which stand in such intimate relation to the life-processes of the littoral biota.

The Tide.

While the mean tidal range is, of course, the prime factor in determining the extent and development of the fauna and flora of the portion of shore lying between the tide-marks, it is obvious that with any given vertical range, the width of the intertidal zone may vary from a few feet, on a rocky or steeply shelving coast, to hundreds of yards, or in extreme cases miles, on a flat sandy beach. Under the latter conditions there is afforded an opportunity for studying, in their fullest development, those features which depend most intimately upon the tidal ebb and flow.

Ebb and Flow.

For the sake of simplicity and brevity, consider the ideal case—that of a symmetrical tide, of twelve-hour period, rising over a smooth and evenly sloping beach. The course of such a tide can be represented by a simple harmonic expression :—

$$h = \cos 30^\circ t$$

where h is the relative height of the tide, above or below mean sea-level, and t is the time-interval after high water. The curve given by this expression (Fig. 1) is similar, in its essentials, to that produced by any

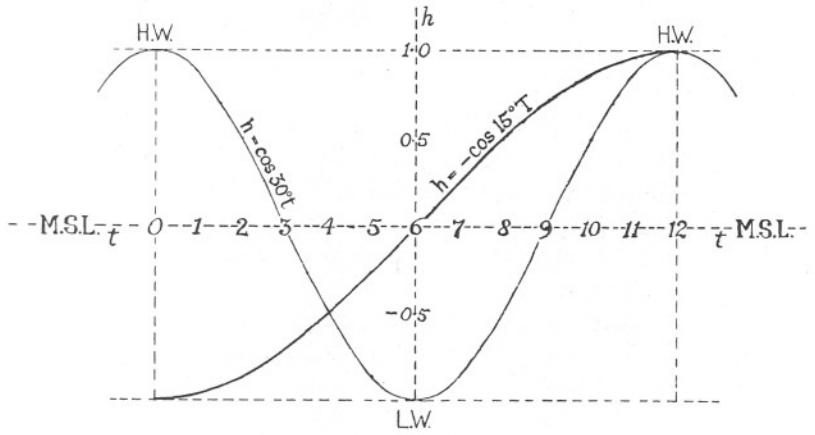


Fig. 1.—Diagram to illustrate the periodic exposure and submersion of the beach.
h, Relative height above or below Mean Sea-Level;
t, Time Interval after High Water; T, Total time of exposure during one tidal oscillation.

recording tide-gauge. It is clear that the period of submergence or exposure experienced by any point between the tide-marks is determined by its position relative to the mean levels of high and low water, a point at high-water mark being only touched by the sea once in twelve hours,

and another at low-water mark having an equally brief exposure to the air. The expression

$$h = -\cos 15^\circ T$$

(h being the height of the point above or below mean sea-level) affords a measure of T, the total time of exposure during one tidal oscillation. The results are relative only, but they may be fixed for any station by the insertion of the appropriate numerical values. This relation is of fundamental importance in the study of the shore, since its periodicity is superimposed upon every other factor operating in the intertidal area, such as temperature and insolation, or chemical and biological changes, whether of themselves periodic or aperiodic.

The relations of tide and temperature are discussed in a subsequent section (p. 540). Among the important biological and chemical factors depending upon the tidal movement, are those associated with the metabolic products and residues of the plankton and larger algæ of the coastal area. These chemical influences, varying from season to season, are borne into shallow water by each returning tide (Atkins, 1922 ; Bruce, 1924 ; Moberg & Allen, 1927) profoundly affecting the onset of successive stages in animal and plant development (Knight, 1923). It is probable, too, that the periodic removal of the products of metabolism of the microflora and -fauna of the beach is a no less important result of the tidal movement. These, however, are chemical problems, with which it is proposed to deal in the second part of this paper.

Currents and Wave-action.

The major problem of coastal erosion and accretion is one that has called for detailed treatment at the hands of the civil engineer and the economic botanist (Royal Commission on Coast Erosion, etc., 1907–11 ; Carey & Oliver, 1918), but it is rather to the local effects of wave-action and water-movements upon beach deposits that attention is now directed.

The mechanical forces which operate upon the sea-beach, leading to the attrition, transport, and segregation of its various materials, are essentially the same as those at work on the sea-bed in shallow seas. On the beach, however, the water-movements are of much greater violence, and, in consequence, erosion and attrition proceed more rapidly, and where separation of the different grades of material occurs, it is on a steeper scale. As Cornish (1910) has pointed out, the breaking waves on the sandy beach, and especially those of the flood-tide, are responsible for a selective transport of the coarser grades in a shoreward direction. This is usually accompanied by a further drift, in a direction parallel to the shore-line, occasioned by the resultant set of the inshore current, whether of wind or tide. Such influences, however, are only of relative permanence, and the

construction of sea-walls, revetments, and harbour works, even at considerable distances, may lead to a complete redistribution of inshore and littoral deposits, while the effect of long-continued winds, whether inshore or offshore, in modifying the character of sandy beaches, is well known.

Permanent or temporary, the movements of winds, tide, and currents ultimately determine the contour of the beach, and the grade-distribution of its materials. These, in turn, modify such biologically significant features as the height above the water-table, drainage, exposure, and porosity. At this stage, however, the effects are no longer tidal, but edaphic, and under that heading they are more appropriately considered (p. 543).

Temperature.

The Annual Cycle.

The temperature of the coastal waters passes through an annual cycle which, like the tidal oscillation, is capable of harmonic expression. Numerous observations are available, of both sea and air temperature, made at various offshore stations, lightships, etc., around the British coasts, and these are summarised in the Monthly Weather Reports of the Meteorological Office. A series of observations of greater relevance to the purpose in view, however, are those from Port Erin Bay, made daily at a point close inshore, in one or two fathoms of water. The monthly means of daily readings, at 9 a.m., G.M.T., over a period of 25 years, together with the mean difference between the temperatures of air and sea, are shown in the following table, and graphically in Fig. 2.

Temperature of Sea and Air, at Port Erin, at 9 a.m. (25-year Means, 1903–27).

Month.	Sea-Temp. °C.	Air-Temp. °C.	Excess of Sea- over Air-Temp. °C.
January	7·78	5·77	2·01
February	7·08	5·28	1·80
March	6·78	5·44	1·34
April	7·43	7·22	0·21
May	8·97	10·71	−1·74
June	10·94	13·14	−2·20
July	12·77	14·77	−2·00
August	13·76	14·43	−0·67
September	13·32	12·73	0·59
October	12·29	10·49	1·80
November	10·44	7·62	2·82
December	8·74	6·44	2·30

Temperature and the Tide.

The periodic inundation of the beach by the incoming tide results in a sudden change of temperature—a change which, while of less extent than the mean diurnal range in summer, introduces, by the abruptness of its incidence, a new and significant factor into the shore environment. From the above table, or from a comparison of the curves in Fig. 2, it will be

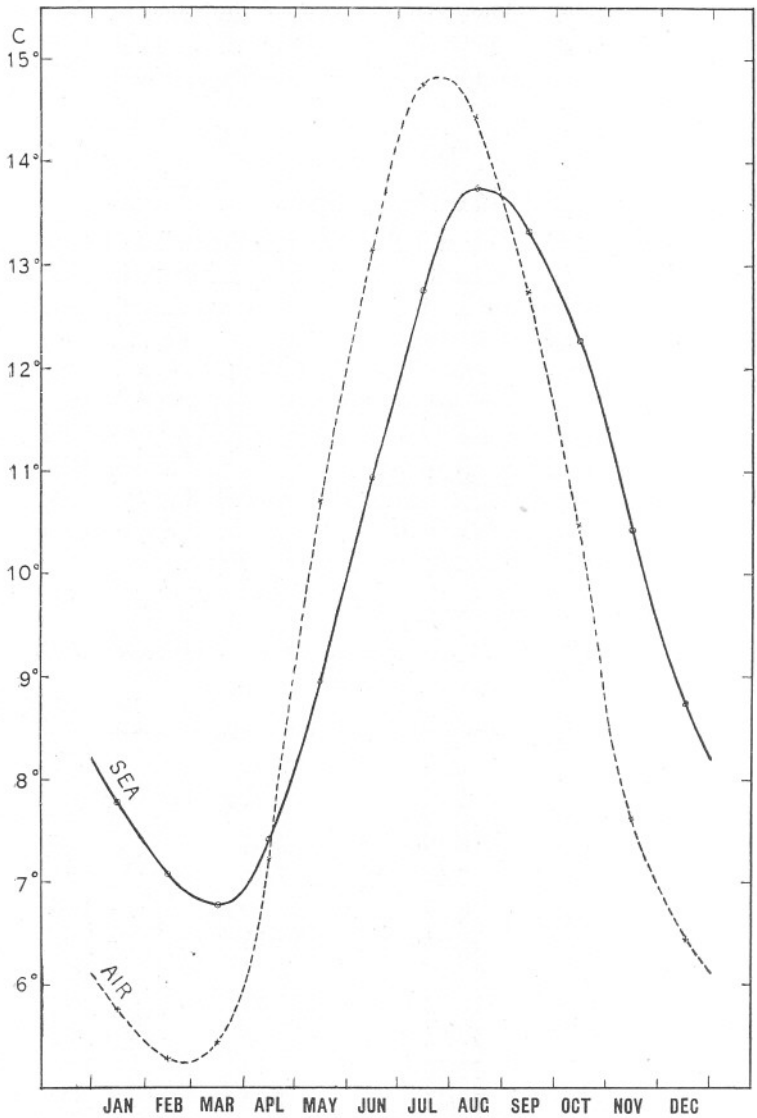


FIG. 2.—Mean Monthly Temperature of Sea and Air at Port Erin, at 9 a.m. G.M.T. during the 25 years, 1903–27.

noted that the disparity is at a maximum at the end of June, and in November, when the temperature of the sea is, in the one case, 2°·4 C. below that of the air, and in the other, 2°·8 above it. These differences are those obtaining at 9 a.m., G.M.T., when the air and the beach-sands are approximately isothermal. At a later hour, when insolation has raised the surface-temperature of the beach, the inequality is greater, but evaporation from the moist surface usually prevents any excessive rise of temperature. The specific heat of the sand *in situ*, itself a function of grade, air- and moisture-content, enters also into the thermal relations.

Surface Temperature of the Beach.

Numerous observations, extending over several years, gave the following mean values for the temperature of the upper 1 cm. of moist sand, between tide-marks, on Port Erin beach :—

June, 16°·5 ; August, 18°·8 ; October, 10°·7.

The highest surface-temperature recorded was 21°·0, in full sunshine, in June. It must be emphasised that these values refer to the intertidal region only, much higher temperatures being attained by the dry blown sand above the reach of the highest tides. No readings of the surface-minima are available, but during the winter months the sand is occasionally coated with snow or hoar-frost.

Subsurface Temperature of the Beach.

A considerable temperature gradient occurs, especially in summer, between the surface of the sand and the deeper layers which, at depths below 20 cm., approximate to the temperature of the sea. The following is a typical depth-range, observed on Port Erin beach, in August :—

Depth, cm.	0	5	10	15	20
Temperature, °C.	18°·8	17°·6	16°·5	15°·6	15°·3

The significance of the subsurface temperature will be apparent in connection with the numerous organisms—molluscs, annelids, echinoderms, etc.—which pass a considerable part of their existence below the surface of the sand, and also as a controlling factor in those chemical and bacteriological processes which take place in the deeper layers.

Salinity.

Equally with the inhabitants of rock-pools or the open sea, the animals and plants of the sandy beach require water for the essential acts of their physiology. During the ebb-tide period of exposure to the air, the supply

may be derived from the film held around the sand-grains by surface-forces, or else, by capillary rise in the interstices, from the permanent water-table at some depth below the surface. In either case, renewal of the source, usually with a change of salinity, will accompany every rising tide. The study of the salinity of the sandy beach and its changes is thus of great importance from a biological point of view.

Salinity of Beach Waters.

In the simplest possible case, the interstitial waters of the beach are isohaline with those of the adjacent sea, except for the purely surface concentration resulting from evaporation, or the dilution resulting from local rainfall. Numerous factors, however, notably the presence of superficial or subterranean streams of fresh water, lead to a departure from the ideal conditions. Such streams, carrying away the sea-salts, give rise to regions of greatly diminished salinity. In the case of subsurface waters, the salinity of the uppermost layers of the beach is determined by the capillary lift of the pore-spaces between the grains, and this, in turn, as shown in the following section, is a function of grade. Thus it comes about that isolated areas of low salinity may occur upon a level beach, at some distance from any visible source of fresh water, and this fact has been associated with the remarkable distribution of certain sand-living dino-flagellates, which require a definite range of salinity for their optimum metabolism (Bruce, 1925).

Under these circumstances the actual rate at which the salinity falls, at any given point on the beach, under the influence of fresh-water streams, will depend more upon the washing effect of such streams, than upon any mutual exclusion of the fresh and salt waters. The rate and completeness of washing is limited by the volume of fresh water poured upon the beach, the porosity and retentive capacity of the sand, and the rapidity of escape of the surface-water. Such factors are difficult to evaluate, and it is generally necessary to determine the rate of change of salinity by actual trial, in any given case. The following example, from a point at about three-quarter flood level, on the smoothly-sloping surface of Port Erin beach, may be typical :—

Time.	State of Tide.	Salinity. Sea. ‰	Salinity. Beach. ‰	Remarks.
5.30 a.m.	H.W.	–	–	Observation station submerged.
9.0 a.m.	Half-ebb	32·9	–	——
11.0 a.m.	Nearly L.W.	–	23·0	Sand-surface damp, but not streaming. Sunny. E. wind. 10° C.
12.45 p.m.	Rising	–	19·4	,, 11° C.
2.30 p.m.	Half-flood	–	18·2	,, 12° C.
3.45 p.m.	⅔-flood	–	15·1	,, 11°5 C.
4.30 p.m.	¾-flood	33·0	20·3	Edge of advancing tide 1 foot from station. 11° C.
6.0 p.m.	H.W.	–	–	Observation station submerged.

It is evident, from the above figures, that there is a progressive fall in salinity, from the time the beach is uncovered, until the advancing tide has nearly reached the point of observation, when the salinity rapidly rises to the full sea-value. Under these conditions, the diminution of salinity occurring at any point on the shore, between successive tides, is proportional to the distance of the point above low-water mark.

The Beach Sands.

Under this heading, it is proposed to include those factors which, in an ecological study of a land-area, would be termed "edaphic." Such factors are associated with the solid medium of the "ground," as distinct from the fluctuating conditions of tide, temperature, and salinity.

Chemically and lithologically, the shore-sands from various points around our coasts are not greatly dissimilar; they consist, for the most part, of more or less rounded grains of quartz, with a coating of iron oxide, and a greater or less admixture of calcareous matter, in the form of fragments of chalk, limestone, or comminuted shells. Important differences between beach sands become apparent, however, when they are subjected to mechanical analysis, either by sieving, or elutriation.

Distribution of Grade on the Beach.

It is a matter of common observation that differences of "grade," or grain-size, occur at different points on the sandy beach. The distribution of grade upon the beach, as indicated in a previous section (p. 538), seems largely to be due to local currents, and to the deflection or obstruction of the tidal flow by rocks, groynes, or harbour-works, while winds may also exert a selective influence, especially on beaches which quickly become dry. The sorting effected by these agencies is naturally far from perfect, on account of turbulence, and fluctuating velocities. Nevertheless, the long-continued incidence of currents and wave-action on the shore has led to the elimination of both the finest and coarsest grades, with the result that most beach-sands contain a high proportion of medium-sized grains, and under special local conditions may be almost perfectly graded (Boswell, 1918).

On a small scale, the varying distribution of grades can be seen in the bed of the numerous runnels which traverse the flat surface of any sandy beach, while on a more extended scale it is found that samples of sand, taken from different parts of the beach, reveal, on elutriation or sifting, a marked difference of grade-composition.

Effect of Local Conditions.

On the sandy beach at Port Erin, where the onset of the flood tide, the prevailing run of the sea, and the protection of a pier and breakwater on the south side of the bay, all combine to bring about a surface-drift in a southerly direction, a series of surface-samples were taken, at low water mark. The samples were separated into their constituent grades by sieving. The sieves used were of woven brass wire, square mesh, and as the sand was perfectly "free-running," they were used dry. While the best modern practice requires the use of round-meshed sieves for coarse material (down to 0·5 mm.), and elutriation for the finer grades (Borley, 1923), neither of which methods were at the time available, the sieves used were carefully measured, and in view of the fact that the sand-grains were not very angular, and were free from flaky material, it is felt that the results are comparable with other and more standardised work.

Calibration of Square-meshed Sieves.

Meshes per linear inch.	Measured width of square holes. mm.	Standard I.M.M. square-mesh sie mm.
30	0·54	0·421
60	0·28	0·211
90	0·16	0·139
120	0·12	0·107
150	0·09	0·084

The sieves used differed considerably in mesh, as will be seen, from the standard I.M.M. sieves of corresponding number. Sample A was taken at the south end of the beach, and the successive stations were about 200 feet apart, E being close to the rocks at the north. The sequence showed the following grade-composition :—

	Percentage by Weight retained by Sieves.					Representative
Sample.	Mesh *60*	*90*	*120*	*150*	(Passing *150*)	Number.
A	1·7	53·7	42·0	0·7	1·8	0·14
B	30·3	52·2	15·3	0·8	1·4	0·19
C	15·6	62·0	19·8	0·8	2·0	0·17
D	26·5	62·7	8·6	0·8	1·5	0·19
E	21·7	48·4	27·7	0·6	1·6	0·17

The individual values vary irregularly, but the "representative numbers" (Borley, *loc. cit.*)—obtained by multiplying the minimum diameter of each selected grade by the weight percentage of that grade in the sample, and dividing the sum of the products by 100—indicate a

tendency for the finer grades to segregate at the southern extremity of the beach, a complementary residuum of coarser material remaining at the north. Not the least important aspect of such surface-drift is the indication it affords that the organic detritus of the beach, lighter than the finest grades, will tend to advance in the same direction.

Grade, Pore-space, and Surface.

The most important quantities associated with grade, so far as that quality affects the sandy beach, are—

(i) the volume of the " pores," or interstitial spaces, in relation to the volume occupied by the grains, and

(ii) the aggregate surface presented by the grains in unit volume of the sand.

These values are familiar to the agriculturist, in connection with the texture of the soil, and they are no less significant to the marine biologist, if in a slightly different direction. The importance of the interstitial space, whether occupied by water or air, lies in the fact that the animals and plants inhabiting the sandy beach are practically limited to that volume for their life-processes during the periods when the beach is uncovered by the tide. It is also a measure of the resistance of the beach to overheating and desiccation during prolonged periods of sunshine, since the specific heat of the damp sand varies from one-tenth to one-third that of pure water, according to the relative volumes occupied by sand, air, and water (p. 541). The width of the capillary interspaces is also one of the factors which determine the availability of the subsurface water, and, where such is fresh, the salinity of the surface-layers of the beach.

The aggregate surface-area presented by the grains determines the capacity of a sand for retaining moisture in the form of a liquid film around its particles, and it is in this film, confluent from grain to grain, and more or less filling the interstitial space, that dinoflagellates and other minute but teeming organisms of the sandy beach find their habitat. The extent of the surface is also to be associated with solubility and several chemical reactions which take place at the interfaces in this complex system of sand, air, and water (*vide* Part II of this paper, *Journ. Mar. Biol. Assoc.*, Vol. XV, No. 2, p. 553). Finally, it has been shown by Stowell (1927) that positive adsorption of the ions of sea-water takes place on the surface of the sand-grains, giving rise to a film of higher salinity. At the same time, calcium ions are liberated from the sand, in exchange for those of magnesium and sodium.

Pore-space and its Influence.

It has been calculated that in a system of equal spheres, in the closest possible contact—a condition attained when each sphere touches twelve others—the aggregate volume of the spheres is 74·04% of the total space occupied, the pores therefore accounting for 25·96%. It will be evident, upon consideration, that these values are quite independent of the absolute size of the spheres. In nature, however, these ideal conditions are never realised, since the sand grains depart from the spherical shape, and in most cases large and small grains are present side by side, the smaller filling the interstices between the larger. Under these conditions, it becomes necessary to make empirical determinations of the relative volumes of sand and pore-space.

Determination of Pore-space.

Sand from Port Erin beach was separated by sieving (p. 544) into a number of grades. Samples of the different grades were dried at 100°, and after cooling, 50 g. of each grade were placed in a wide, dry, measuring cylinder. Sea-water, at 10°, was then added, from a second cylinder, which originally contained 100 c.c. After thoroughly incorporating the sand and water, " excess " of the latter being present, the cylinder was allowed to stand until, after slight tapping, the sand was level and well-packed. The supernatant water was poured back into the original cylinder, allowing one minute for draining of the final drops. The volume of the wet sand was read off, and, by difference from the other cylinder, the volume of sea-water it had absorbed. The results are expressed in volumes of water per 100 volumes of wet sand, this being the most significant relation from the biological standpoint.

Water Content, at Saturation, of Different Grades of Sand.

Grade. Meshes per inch.	Mm.	Vols. of water present in 100 vols. of wet sand.
Greater than 30	> 0·54	35·8
30– 60	0·53–0·28	39·0
60– 90	0·27–0·16	42·0
90–120	0·15–0·12	42·2
120–150	0·11–0·09	44·7
Passing 150	< 0·09	43·4
Ungraded, natural sample		20·0

It is at once observed that the volume of the pore-space, in all the graded samples, is strikingly higher than the theoretically deduced value of 26%. This is in part to be accounted for by the fact that the sand-grains, very light in weight, and somewhat irregular in outline, do not readily fall into the position of closest contact, but rather into stable arcades, a condition enhanced by the imperfection of grading. It is noticeable that the departure from the ideal value becomes greater in the case of the smaller and lighter grains, while the ungraded, natural sample, containing a fair proportion of fine material, shows a very low pore-space, for reasons already indicated.

Grade and Rate of Evaporation.

The rate of evaporation from the surface of the sandy beach is obviously a factor of some importance, since it affects not only the temperature of the surface, but its availability as a habitat for those organisms which live in the water-film around the sand-grains, at or near that level. To determine the effect of grade upon the rate of evaporation from a surface of wet sand, a number of dishes were exposed, containing graded samples of sand, saturated with sea-water, but in a fully drained condition. The dishes (11·5 cm. petri dishes) contained their quota of wet sand (approx. 120 g.) in a layer 5 mm. thick, and each exposed to evaporation a surface-area of 100 sq. cm., this factor being regarded as of greater importance than the absolute weight of sand taken. The dishes were placed in the open air, under identical conditions, and the loss in weight ascertained periodically. The results obtained, expressed as the absolute loss of water, in grammes, per 100 sq. cm. of surface, at successive stages of drying, are given below :—

EFFECT OF GRADE UPON RATE OF EVAPORATION FROM THE SURFACE OF WET SAND.

Grade (meshes per inch).	Loss of Water, in grammes per 100 sq. cm., at 11°·5–14°·5 C. (Progressive Totals.)					
	1 hr.	*4 hrs.*	*15½ hrs.*	*21 hrs.*	*29½ hrs.*	*"Air-dried."*
30– 60	5·2	12·4	15·6	20·7	25·1	(25·3)
60– 90	5·6	14·3	17·5	23·0	25·9	(26·1)
90–120	5·3	13·8	15·7	20·5	22·2	(22·4)
Ungraded	5·5	12·0	17·5	20·0	–	–

It is evident from these figures that grade has but little influence in determining the rate of evaporation under the conditions described. It is somewhat remarkable that the initial rate of loss from a saturated sandy surface is not appreciably different from that of an equal area of sea-water. It would appear that the internal surface, as it may be called, of the damp

sand, contributes but little to the total evaporation loss, the actual escape of water molecules being limited by the rate of diffusion through the narrow interstices. Another factor tending to reduce the rate of evaporation, especially in the case of the finer grades, is the diminished vapour pressure exerted by the concave liquid menisci at the ends of the capillary channels.

Rate of Capillary Rise.

On the beach, as upon the land, evaporation from the surface is usually compensated for, in whole or in part, by accessions of water from neighbouring sources. These may be either pools upon the surface or, more usually, the subsurface layers in which the pores are fully occupied by water, and which correspond to the " water-table " of cultivated lands. These subsurface reserves may consist of sea-water, infiltrated from the margin of the tide, or, as at Port Erin and elsewhere, of fresh water derived from streamlets which, sinking through the sand where they reach the shore at high-water mark, are arrested by an impervious layer at some little depth below the surface. In either case, the availability of these supplies for surface requirements depends upon (*a*) their depth and amount and (*b*) the rate of capillary rise through the overlying sandy layers. As to the slight depth of the water-table, and the abundance of its reserves, no one who has dug between tide marks on the sandy beach can be in doubt, and it would seem that the rate at which the water is able to rise through the capillary channels is the more significant factor.

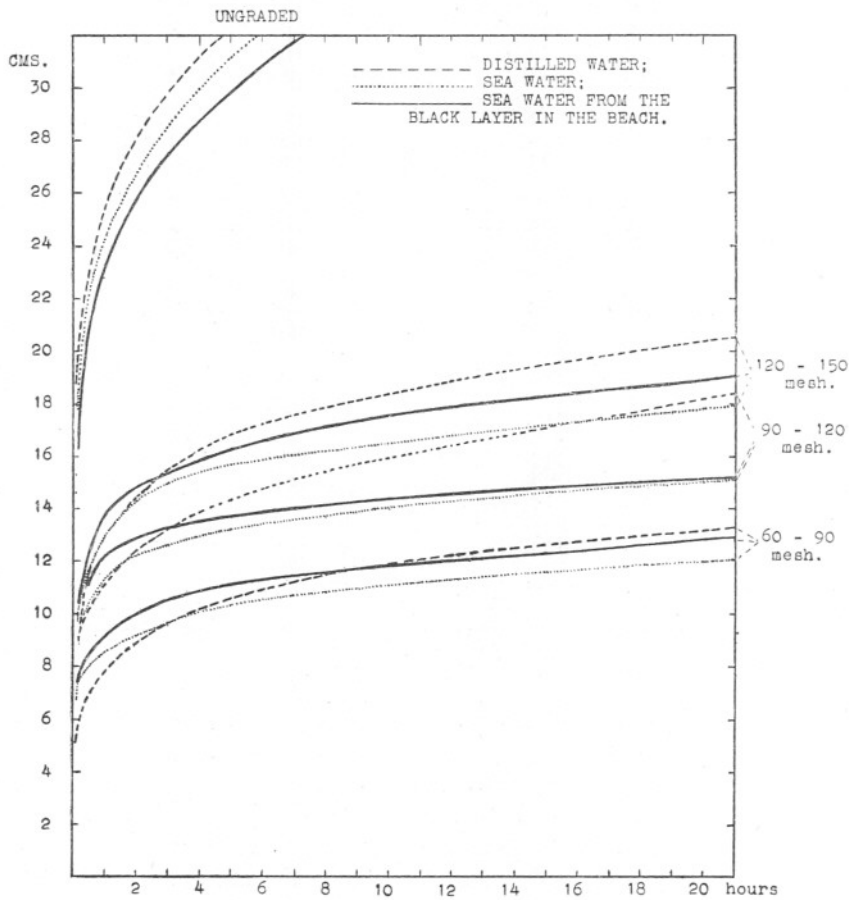
Determination of Capillary Rise.

The rate of rise, through sands of different grade, was determined in the following way. A series of glass tubes, 13 mm. in internal diameter, were fixed in a frame, their lower ends resting in a shallow dish, their upper ends open, and a centimetre scale affixed at the back. The tubes were filled, each with a particular grade of sand, and water was poured to form a shallow layer in the dish. The water was absorbed by the sand, and the height of the saturated column was read from time to time. Fresh water, sea-water, and sea-water drained from the black layer in the beach, were used. The temperature throughout was between 17° and 19° C. ; results obtained at other temperatures would be different, owing to the changing viscosity, but the effect should be calculable. The values given are the means of several determinations in each case, with a view to minimising errors due to differences of packing.

Time-Interval.		Height of Capillary Rise (cm.). 60–90 mesh.	90–120 mesh.	120–150 mesh.	Ungraded.
10 mins.	A.	5·0	9·2	9·5	18·5
	B.	7·5	8·9	10·0	18·2
	C.	7·7	10·0	10·5	17·0
30 mins.	A.	7·0	10·2	11·6	23·0
	B.	8·1	10·4	11·7	22·3
	C.	8·6	11·4	12·5	20·5
1 hr.	A.	7·8	11·1	13·0	25·5
	B.	8·6	11·3	13·0	23·5
	C.	9·2	12·2	13·8	22·8
2 hrs.	A.	8·9	12·4	14·5	28·0
	B.	9·2	12·2	14·3	26·8
	C.	10·0	12·9	14·8	26·0
3 hrs.	A.	9·6	13·3	15·5	–
	B.	9·7	12·6	15·0	–
	C.	10·5	13·2	15·4	–
5 hrs.	A.	10·6	14·3	16·9	–
	B.	10·3	13·3	15·7	–
	C.	11·1	13·7	16·3	–
8 hrs.	A.	11·5	15·4	17·9	–
	B.	10·8	15·4	17·9	–
	C.	11·5	14·1	17·2	–
20 hrs.	A.	13·2	18·2	20·4	–
	B.	12·0	15·1	17·9	–
	C.	12·8	15·2	18·9	–

(A. Fresh water; B. Sea-water; C. Sea-water from the black layer in the beach.)

From Fig. 3, in which the results are represented graphically, it will be observed that the height to which the liquid column rises in a given time is a function of grade or, more strictly, of the width of the capillary channels between the grains, since this, irrespective of the total volume of the pore-space, becomes less as the grains decrease in size. The mean height attained after 12 hours, in the case of 60 mesh material, is 11·8 cm.; with 90 mesh, 15·1 cm.; with 120 mesh, 17·9; and in an ungraded sample, 35·0 cm., this being an extrapolated value. It is not apparent that the differences of surface-tension between fresh water and sea-water, or between the two samples of the latter, from different sources, result in any constant or significant difference of capillary rise, under the conditions of the experiment.



EFFECT OF GRADE AND SOURCE UPON RATE OF CAPILLARY RISE OF WATER THROUGH SANDS.

FIG. 3.

SUMMARY.

1. The distribution and activities of animals and plants upon the sandy beach are largely influenced by the special physical factors operating in that environment. The paper is a contribution to the knowledge of these factors.

2. The tidal ebb and flow, and the resulting alternations of exposure, are the outstanding factors. The extent to which other factors may be operative upon the beach, during the period of ebb-tide, depends upon the vertical distance of the point in question above or below mean sea-level.

3. Tidal and other currents, and wave-action, lead, on the larger scale, to coastal erosion and accretion, but their biological significance lies rather in their local translocation of beach material, with partial separation into its constituent grades.

4. The surface temperature of the beach varies with insolation, grade, and moisture-content, and, under the influence of the recurring tide, alternates twice daily between that of the air and the sea. The temperature of air and sea, in turn, passes through an annual cycle. There is a marked temperature gradient throughout the upper 20 cm. of the beach.

5. The salinity of the interstitial waters of the beach depends upon the volume of fresh water flowing from the land, the effectiveness of the washing being determined by its duration, the grade of the sand, and the local conditions of contour and drainage.

6. The differences between beach sands are largely those of grade, since, chemically and lithologically, sands from various points on the coast are not greatly dissimilar. Grade determines the water-retentive and absorptive capacity of a sand, as well as its capillary lifting power and its porosity to water and gases.

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Physical Factors on the Sandy Beach. Part II. Chemical Changes—Carbon Dioxide Concentration and Sulphides.

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With 3 Figures in the Text.

CONTENTS.

INTRODUCTORY.

THE sandy beach, considered as the environment of living organisms, affords a range of physical factors of unusual type and complexity (Bruce, 1928). A vast assemblage of animal and plant forms, more or less consonant in physiology and distribution with the demands of that environment, introduces the biological factor into the physical nexus. The gases evolved in respiration and carbon-assimilation, the ultimate residues of digestive processes, and the products of bacterial degradation of dead organic matter, become, in their turn, factors in the life-processes from which they arose. Factors of this kind, biochemical and biophysical, arise rather from the products than from the direct activities of life, and are among the outstanding influences on the sandy beach. In common with the more purely physical factors, however, their exact measurement is a matter of some difficulty.

Carbon dioxide—that elusive constituent of sea-water—becomes associated with the limy matter of the sand, and hydrogen-ion concentration ceases to be an effective index of its changes. Metabolic processes may be, and often are, confined to certain narrow zones in the sand, and the measurement of their products is rendered correspondingly difficult and uncertain. Salts and ions are adsorbed on to the relatively enormous aggregate surface of the sand-grains, and their apparent bulk-concentration is thereby vitiated. Organic matter is so greatly diluted with incombustible material that its accurate determination is very difficult, and in any case no distinction is made, in analysis, between the living and dead organic materials which are so intimately associated in beach sands. Finally, the great barrier to ready diffusion presented by the sand itself leads to oxygen-deficiency and many special reactions in its depths, including the formation of hydrogen sulphide through bacterial agencies, and the appearance of the well-known black layer.

The paper is a contribution to the knowledge of some of these factors, chemical in nature, but biological in origin.

Carbon Dioxide Concentration and Excess Base.

The Gaseous Exchanges of Marine Organisms.

The gaseous metabolic exchanges of aquatic organisms, whether output or intake of carbon dioxide, involve an alteration in the hydrogen-ion concentration of the medium, the extent of such alteration, for a given difference of CO_2-concentration varying with the buffer-effect of the medium. The "excess-base," the pH, and the CO_2-concentration form a triple group of values, of which any two serve to define the third, and this fact has been made the basis of a method for estimating the carbon dioxide exchanges of marine, brackish-water, and freshwater organisms (Bruce, 1924).

Regulation of pH in the Sea and on the Shore.

In the open sea, where extended surface and continual agitation ensure the maintenance of equilibrium with the air, the concentration of carbon dioxide can never become a limiting factor in the life of plants or animals. In rock-pools, on the other hand, whatever their salinity and excess-base content, the accumulation of the gaseous products of metabolism will ultimately set a limit to their production, which cannot take place beyond certain limits of hydrion and hydroxyl-ion tolerance. It follows, therefore, that dilution, quite apart from any effects of lowered salinity *per se*, must lead to a narrowing of the potential range of metabolic activity corresponding to the reduction of excess base or buffer content. A few organisms have become adapted to extremes of pH, but even in the case

of certain highly resistant algæ, a final barrier to the progress of carbon-assimilation is reached when, in the neighbourhood of pH 10, the entire bicarbonate reserve is exhausted.

The inhabitants of the sandy beach, however, are in this respect more favourably situated, since in the intimate presence of sand, with its admixture of calcareous particles, a local increase in the concentration of hydrogen ions leads to solution of calcium carbonate, and a restoration of the acid-base equilibrium.

Experiment. A sample of sea-water, pH 8·2, and excess base 23·7, was treated, at room temperature, with carbon dioxide until the pH was reduced to 6·4, and then stirred in a closed vessel, with a considerable quantity of sand, and out of contact with the air. The reaction is slow, but after $5\frac{1}{4}$ hours' stirring, it was found that the pH was 7·5, and that the excess base had risen to 39·0.

In a state of nature, this greatly increased concentration of the bicarbonate ion, after diffusion to the photosynthetic zone on the surface of the beach, occupied by diatoms and holophytic dinoflagellates, would add to their potential reserves of available carbon dioxide. High concentrations of carbon dioxide, such as that employed in the above experiment, are not, of course, realised as a result of respiratory activity, but equal and even higher concentrations are found in those parts of the sandy beach where rapid decomposition of organic matter is in progress, and a sample of the interstitial sea-water from such a locality, with a salinity of $29{\cdot}6^{\circ}/_{\circ\circ}$ and a pH of 8·3, was found to contain the enormous excess base of 120·4. It is evident, therefore, that the calcareous matter in the sand functions in a manner precisely analogous to the limy reserves in the shells of certain bivalve molluscs (Collip, 1920), and by its regulatory influence upon hydrion concentration contributes an important chemical factor to the conditions of life on the beach.

Sulphides and the Black Layer.

The existence of a darker zone, at a slight but variable depth below the surface of the sandy beach, is familiar to observers on almost every part of the coast. It was early recognised that the phenomenon was closely connected with the formation of black deposits in the depths of certain seas, notably the Black Sea, the Caspian Sea, and certain inlets of the Baltic. The features exhibited in common by the littoral and deep-sea deposits include (*a*) their dark or black colour, discharged on exposure to the air ; (*b*) the evolution of a stench of, or resembling, hydrogen sulphide ; and (*c*) their occurrence under similar conditions of stagnation and oxygen deficiency (Andrussow, 1897 ; Johnstone, 1921).

Omelianski (1906) showed that, in the case of the Black Sea deposits,

the dark colour was in reality due to ferrous sulphide, and Johnstone (1921) established the same conclusion for the sands of the Lancashire coasts. The rapid oxidation of this substance to the brown or yellowish ferric oxide underlies the colour-change on exposure to the air. It is evident, then, that the level at which the black layer occurs—and its upper surface is usually quite sharply defined—represents a position of equilibrium between the sulphide-producing reactions in the depths, and the oxidising effects of the atmosphere from above. The factors entering into such a system are obviously of a complex kind, and must involve not only the temperature and concentration of the reactants, but the varying rate of their addition to the reacting system. On the one hand, the supply of sulphur is conditioned by the local intensity of metabolism, the access of decaying organic matter, and availability of inorganic sulphates ; on the other hand, the rate of diffusion of oxygen to the reaction-zone is influenced by the grade and porosity of the sand, and its solubility by the salinity of the interstitial water. When it is realised, further, that bacteria play an active part in the process, and that the ultimate reactions may be ' heterogeneous,' taking place at the interface between the sand-grains and water, it will be obvious that to measure the final products, and to define a few of the conditions, represents the only possible approach to a solution of the problem.

Examination of the Natural Conditions.

Locality. The black layer is well developed on the sandy beach at Port Erin, where the following observations were made (see Plan of Port Erin Bay, Fig. 1). At the south end of the beach, harbour-works and a solid masonry pier, 200 feet in length, afford protection from wave-action, and have led to considerable silting and accumulation of organic débris. Several streamlets discharge on to the beach after heavy rain, but only one, that debouching between stations 11 and 15 (see Plan), is at all permanent or of any considerable volume. There is no access of sewage, from any source, and every form of pollution is rigorously excluded from the beach.

Methods. Samples of the sand were collected by means of a simple borer, fashioned on the lines of a cork-borer. This consisted of a tube, 60 cm. long, and 10 cm. in diameter, made from heavy-gauge tinplate, and soldered at the joint. The upper end was reinforced by a collar of sheet iron, 6 cm. deep, and this was pierced with holes, permitting a length of iron tubing, 1·5 cm. in diameter, to be inserted from side to side, to form a handle. In use, the sampler was forced vertically into the sand, by rotation, the depth attained rarely exceeding 40 cm., owing to the resistance offered by the sand. Not infrequently, stones or gravel obstructed the passage of the sampler at a much less depth.

Samples of the sand, and wherever possible of the water draining into the bore-hole, were taken at 27 stations on the beach. The physical characters of the samples were noted immediately, and the chemical tests were made, in every case, within an hour of sampling. The survey was carried out, for the most part, in the months of November and December, but observations have extended, in all, over four years (1923–27), and in every month of the year there is a remarkable similarity of the subsurface conditions. The following values, and their schematic representation in Fig. 1, may be taken, therefore, as generally applicable.

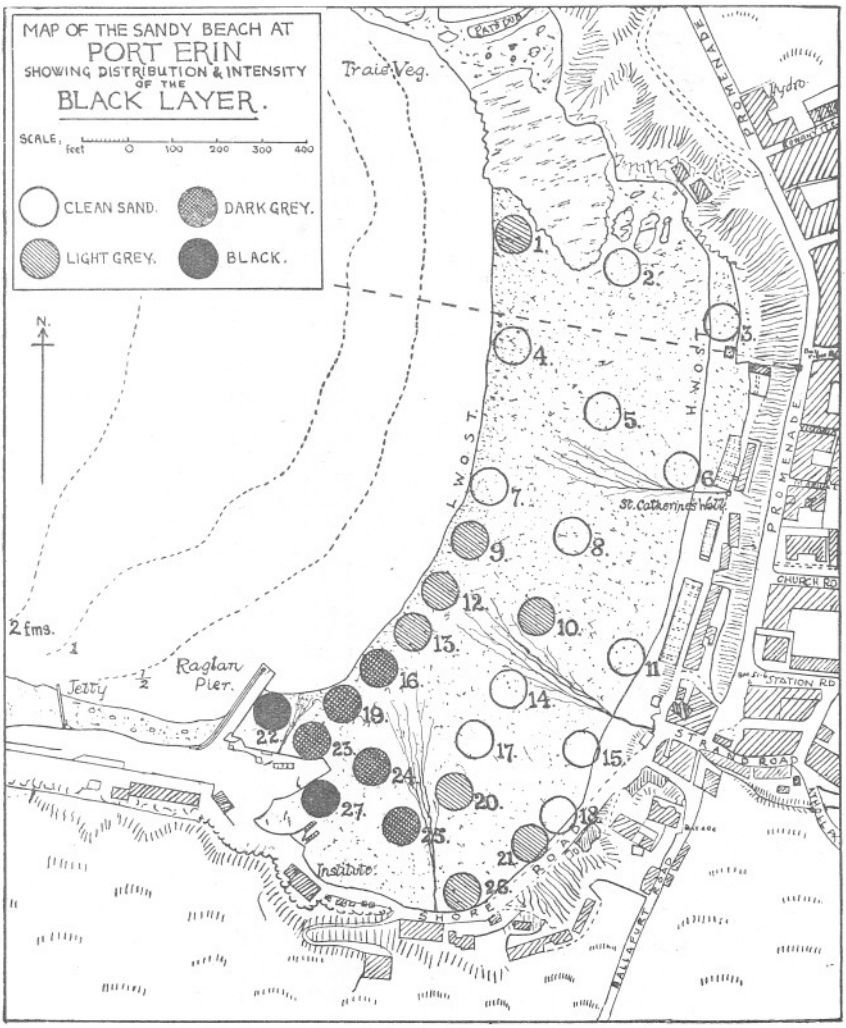

FIG. 1.—Map of Beach at Port Erin (based upon the Ordnance Survey Map with the sanction of the Controller of H.M. Stationery Office).

TABLE SHOWING THE DISTRIBUTION, IN DEPTH AND AREA, OF THE BLACK LAYER, AND OF THE SALINITY AND *p*H OF THE INTERSTITIAL WATER, ON PORT ERIN BEACH, ISLE OF MAN.

Station. (See Plan, Fig. 1.)	Water Sample. Salinity. ‰	pH (corr.).	Sand Sample. Depth-Range. *cm.	Description.
1.	32·75	7·9	0–15	Clean sand and gravel
			15–*36*	Less gravelly, light grey round rocks and stones
2.	–	–	0– 4	Clean sand
			4–16	Gravel
			16–*28*	Less gravelly
3.	–	–	0– 5	Clean sand
			5–*38*	Coarse gravel and pebbles
4.	29·55	8·1	0–*20*	Sand, clean, but gravelly below
5.	–	–	0– 5	Clean sand
			5–*25*	Pebbly gravel
6.	–	–	0– 5	Coarse clean sand
			5–*45*	Pebbles
7.	32·36	8·05	0–*27*	Sand, gravelly below
8.	–	–	0–*10*	Clean sand, gravelly below
9.	31·48	7·9	0–*24*	Grey sand, gravelly below
10.	–	–	0–10	Clean sand
			10–*27*	Grey sand, gravelly below
11.	–	–	0–12	Clean sand and gravel
			12–*40*	Very coarse gravel
12.	15·68	8·2	0–10	Clean sand
			10–*22*	Grey sand, gravelly below
13.	32·23	8·0	0–10	Clean sand
			10–*16*	Sand grey, gravelly below
14.	–	–	0–*13*	Clean sand, coarse gravel below
15.	–	–	0–*13*	Sand and gravel, coarse pebbles below
16.	32·11	7·9	0–12	Light grey sand
			12–*41*	Dark grey sand
17.	–	–	0– *7*	Clean sand, gravelly below
18.	–	–	0–*33*	Clean sand, gravelly below
19.	31·34	7·85	0–12	Grey sand
			12–*30*	Dark grey sand
20.	–	–	0–10	Clean sand
			10–*27*	Light grey sand
21.	–	–	0–*20*	Clean sand, grey below
22.	32·23	8·0	0– 3	Grey sand
			3–*36*	Black sand
23.	32·5	7·8	0–10	Clean sand
			10–*40*	Very dark grey sand
24.	–	–	0– 7	Clean sand
			7–17	Grey sand
			17–29	Dark grey sand
			29–*58*	Sand lighter than above
25.	–	–	0– 4	Clean sand
			4–19	Grey sand
			19–*55*	Dark grey sand
26.	–	–	0–20	Clean fine sand
			20–*41*	Light grey sand
27.	29·6	8·3	0– 4	Clean sand
			4–10	Dark grey sand
			10–*40*	Very black sand

* The final depth (*italics*) is that reached by the sampler, and is not necessarily the termination of a particular zone.

Conclusions based on Shore Observations.

Several general conclusions emerge from these figures. In the first place, the darker zone is practically confined to the south end of the beach (Fig. 1), where, as the present field-notes and previous mechanical analyses (Bruce, 1928) indicate, the finer sand-grades are predominant. The layer assumes its most marked development in the immediate vicinity of harbour-works, where the circulation of air and water in the sand must necessarily be impeded, and where organic débris, washed from other parts of the beach, naturally accumulates. The fact that a slight darkening occurs at Station 1, at the north end of the beach, where there are underlying rocks, supports this view. In general, the darkest layers occur near low-water mark, where the period of exposure to the air, with consequent oxidation, is naturally at a minimum, and here also the layer approaches to within 3 or 4 cm. from the surface ; at Stations 21 and 26, the only two points at high-water mark where a slight darkening is noted, the darker zone is at 20 cm. below the surface.

The pH of the Black Layer.

On several occasions during the course of the field work, a more detailed investigation has been made of the pH and other properties of the successive depth-zones. This has been done by separating the core of damp sand from the sampler, and slicing it into short cylinders, about 5 cm. in thickness. Each " sub-sample " was then filtered under slight suction, and tests made, without delay, upon the several filtrates. Two examples are given :—

Station. (Fig. 1.)	Depth-Range. cm.	Description.	pH of Filtrate. (corrected).
24 (June, 1923)	0– 2	Clean sand	8·0
	2– 7	Slightly grey	7·9
	7–12	Darker	7·95
	12–17	Dark grey	8·05
	17–22	Dark grey	8·1
23 (Nov., 1923)	0– 5	Clean sand	7·9
	5–10	Clean sand	7·9
	10–20	Grey sand	7·9
	20–40	Very dark and malodorous	8·1

In all cases, the filtrate from the dark layers, originally clear, became opalescent on exposure to the air, and the pH fell. In neither of the above cases did the lead acetate test reveal the presence of soluble sulphides or free hydrogen sulphide in the filtrates, although on addition of acid to the black sandy residue the gas was copiously evolved.

Determination of Sulphides in Sand.

Many previous workers have expressed the need for a method of determining the sulphide-content of sands or muds. The determination is one which presents several practical difficulties. It must be carried out on the moist sample, with the least possible delay, since oxidation proceeds with great rapidity, especially on the relatively large surface of a small sample. Evaporation leads to change of weight, while any attempt at previous drying leads to the complete disappearance of the sulphide. After many trials, an effective method was evolved, in which the *volume* of hydrogen sulphide, liberated from a known *volume* (10 c.c.) of the damp sand, is determined, the result being expressed in volumes of H_2S per cent. The use of volume, rather than weight of sand, is justified on the ground of its more immediate biological application (in connection with density of population, etc.), and in view of the fact that the weight of a sample of indefinite moisture-content has, in any case, no useful significance.*

Method. The sample is taken by thrusting into the compacted sand a $\frac{3}{4}''$ brass cork borer, fitted with a glass plunger bearing two marks, and so arranged that when pushed in from one mark to the other, a 10 c.c. cylinder of sand exudes at the other end, where it is cut off squarely, and allowed to fall into 25 c.c. N/50 Iodine solution, contained in a wide-mouthed Erlenmeyer flask, thus immediately " fixing " any free hydrogen sulphide. To the mixture of sand and iodine solution, 5 c.c. of 5N. HCl (specially pure and Chlorine-free) were added, setting free CO_2 and H_2S, the latter combining with the excess of iodine. After standing five minutes, the mixture is titrated with standard sodium thiosulphate solution, with starch as indicator. The end-point is perfectly easy to determine, in the presence of the sand and turbid solution. The N/50 iodine is, of course, periodically standardised against the thiosulphate, and its concentration is conveniently expressed in c.c. of H_2S, measured as at N.T.P., equivalent to 1 c.c. of iodine solution.

Employing the above method, numerous determinations have been made of the sulphide content of the black layer *in situ*. This is found to vary in samples taken at Port Erin from 10 or 12 volumes up to 78 volumes per cent. Only occasionally is free hydrogen sulphide present, and the total, both free and combined, has never been found to exceed 20% of the theoretical total, assuming that the whole of the available ferric oxide were converted into ferrous sulphide. It is of interest to note, however, that the actual iron-content of the black sand, determined in one case as 1·13% of Fe_2O_3, is considerably above the normal value for shore sands,

* The mean dry weight of sand in a 10 c.c. moist sample, collected and delivered by the borer-sampler, as indicated in the method, is 14·0 g.

and may indicate that *Crenothrix*, the iron-bacterium, is as active in this region as it appears to be, under similar conditions, in the beaches of the Clyde Sea Area (Ellis, 1925).

The Rate of Oxidation of Sulphides.

The oxidation of the sulphides in beach-sand takes place, as already indicated, mainly in the surface layers, to which the atmospheric oxygen has ready access. At the same time, oxidation is by no means confined to these layers, and the sharpness of the upper boundary of the black layer

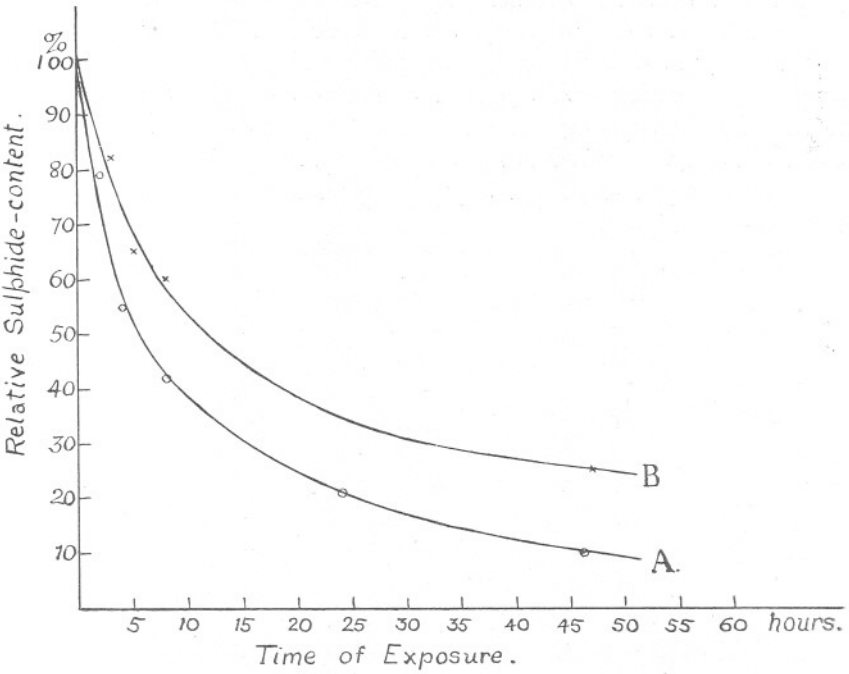

FIG. 2.—Rate of oxidation of Sulphides in sand. A. In air; B. In sea-water.

gives a fallacious impression of a sudden discontinuity of reaction. This zone of demarcation is to be regarded rather as the end-point of one stage of a serial process—a stage rendered evident by the colour change of one of the reactants, ferrous sulphide. The fact is, that free oxygen exists, in appreciable concentration, even in the blackest shore sands, and the occurrence in them of numerous organisms—annelids (especially cirratulids), small crustaceans, echinoderms, etc., none of which are known to be even facultatively anaerobic—has been recognised for many years (Lewy, 1846).

A sample of black sand from Station 23 on Port Erin beach (Fig. 1) was

found to contain 24 volumes per cent of hydrogen sulphide, while the interstitial water drained from the sample contained 1·81 c.c. of oxygen per litre, or roughly 25% of the saturation concentration. For certain precautions to be observed in the determination of oxygen by Winkler's method in the presence of sulphides reference should be made to Fox, 1905.

Experiment. The effective velocity of the oxidation reaction, under natural conditions on the beach, depends, as already indicated, upon several factors difficult to reproduce in the laboratory. The results obtained in a given experiment must, therefore, be accepted as relative only. Two series of equal samples of fine sand from the black layer were taken by means of the 10 c.c. borer-sampler, and exposed to oxidation in shallow evaporating dishes, special precautions being taken to ensure homogeneity of sampling and conditions. One series stood in the air, the other beneath a very thin film of sea-water, and both at 15° C. Samples were removed periodically for sulphide determination, with the following result :—

Time Interval. Hours.	Relative Sulphide Content. Series A (in air).	Series B (in water).
–	100	100
2	79	–
3	–	82
4	55	–
5	–	65
8	42	60
24	21	–
46	10	–
47	–	25

As might be expected (Fig. 2), the rate of oxidation is somewhat slower when the pores between the sand-grains are filled with water, but in either case, twelve hours (the maximum period of intertidal exposure of the beach) suffices, under the conditions stated, for a 50% reduction of the sulphide-content.

Conclusions as to the Source and Fate of Sulphides in the Beach.

From the preceding observations upon the occurrence and concentration of ferrous sulphide in shore sands, and the conditions of its oxidation, it may be permissible to draw certain conclusions as to the source and fate of sulphur in the beach, and as to the agencies at work at each stage of the process. Recent hydrological work in the Black Sea (Danilčenko and Čigirin, 1926) emphasises the conclusion that the reduction of sulphates

by bacterial agency, in the presence of organic matter, is a more important source of sulphide than the direct bacterial decomposition of the organic matter itself. The reduction takes place in two stages :—

$$\text{i. } CaSO_4 + 2\,C \xrightarrow{\text{Bacteria}} CaS + 2\,CO_2,$$
$$\text{ii. } CaS + 2\,H_2O + 2\,CO_2 \longrightarrow Ca(HCO_3)_2 + H_2S.$$

If the same reaction took place in the midst of a mass of sand, the hydrogen sulphide would at once combine with the hydrated iron oxide, itself possibly of bacterial origin, which forms a coating on the grains, giving rise to ferric and ferrous sulphides, while the calcium bicarbonate would add to the already high concentration of excess-base which has been found under such conditions (p. 555).

In the present state of knowledge, it is not possible to say whether the reduction of sulphates or the direct decomposition of organic detritus is the more important source of sulphur in the beach. The almost invariable association of putrefying algal débris with the black sand of littoral and shallow water deposits, and the known high content of ethereal sulphates in the marine algæ, suggest the hypothesis that these compounds, on hydrolysis, furnish both the sulphate ion and the organic residue demanded by the first-named process—the possibility, at any rate, is being further pursued.

On the access of air, the black iron sulphides, whatever their source, are oxidised :—

$$2\,Fe_2S_3 + 3\,O_2 \longrightarrow 2\,Fe_2O_3 + 6\,S,$$
$$4\,FeS + 3\,O_2 \longrightarrow 2\,Fe_2O_3 + 4\,S,$$

the nett result being the conversion of the hydrogen sulphide into free sulphur, and the reformation of ferric oxide, ready again to enter the reaction. It will be noted that, as a result of these processes, there should be a continuous increase in the amount of free sulphur in the sands. Buchanan (1891) was only able to find 0·003% of free sulphur in certain oceanic deposits, and while an analysis of the black sand at Port Erin has yielded over twenty times this amount (0·07%) the proportion is still very low. Since sulphur is practically insoluble in sea-water, its removal from the beach is probably effected by direct oxidation, through sulphites to sulphates, while under certain special conditions (which are apparently imitated in sealed vessels) ferrous sulphide may combine with free sulphur, giving rise to iron pyrites, FeS_2.

No reference has been made, so far, to the possible rôle of thiobacteria, since the investigations of Ellis (1924), still in progress, point to the conclusion that *Beggiatoa*, at any rate, does not flourish except in the higher concentration of organic matter afforded by actual sewage pollution. At the same time, it is not improbable that other members of the group

may flourish under less polluted conditions, and by the oxidation of hydrogen sulphide and secretion of sulphur, add to the chemical and biological significance of this element on the sandy beach.

The views as to the source, reactions and destination of sulphur, which

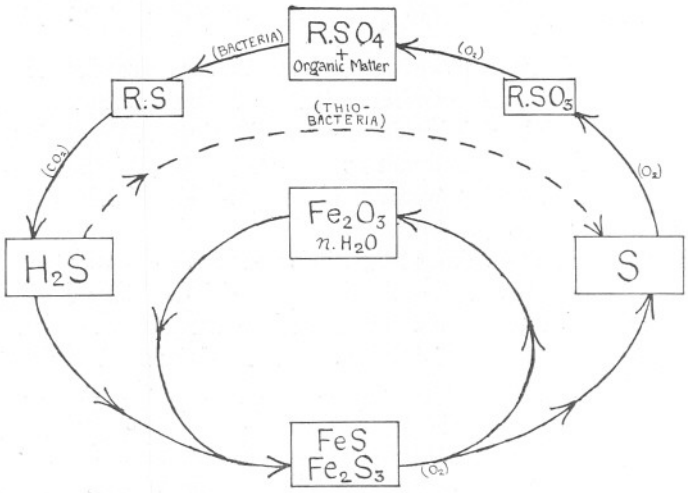

FIG. 3.—Scheme of circulation of Sulphur in the Sandy Beach.

the foregoing observations and experiments have suggested, are embodied in a diagram (Fig. 3), in which the reactions and compounds on the right side are oxidative, those on the left, reducing or anaerobic. It may be claimed that, while points of detail remain to be investigated, the general lines of the sulphur-cycle in the sea-bed and in the sandy beach are provisionally established.

SUMMARY.

1. The presence of living organisms and their metabolic products introduce a further series of biochemical factors into the physical conditions of life on the sandy beach.

2. The gaseous exchanges of animals and plants lead to changes in the pH of the interstitial waters of the beach, but the calcareous matter associated with the sand acts as an alkali-reserve, preventing undue rise of acidity, and incidentally widening the potential range of carbon-assimilation of the surface flora.

3. The conditions leading to the formation of the " black layer " are surveyed and discussed, with special reference to Port Erin beach. An iodimetric method for the determination of sulphides in sand is described,

and is used to demonstrate the rate of oxidation when the black sand is exposed to the air.

4. It is concluded that the formation of ferrous sulphide in the beach is associated with diminished circulation of air and water in the mass of the sand, due either to gross obstruction or to fineness of grade, or both. The presence of organic detritus, usually of an algal nature, appears to be essential to the reaction, and bacteria play an important rôle in the sequence of changes. Sulphur, in common with other elements, passes through a cycle of reactions on the sea-bottom and in the sandy beach.

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The Larvæ of *Polydora ciliata* Johnston and *Polydora hoplura* Claparède.

By

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With 7 Plates and 4 Figures in the Text.

CONTENTS.

1. Introduction.

There are numerous descriptions and figures of Polydora larvæ scattered through the literature dealing with Polychætes, but only in one instance, that of Leschke, has a series of reared larvæ from the egg to metamorphosis been illustrated and described. Most other workers have contented themselves with describing odd larvæ caught in the plankton, a procedure which involves grave doubts as to the species. Leschke's work on *P. ciliata*, though good on the whole, is not free from error on minor points, and his drawings are few in number and rather sketchy. It is hoped therefore that this new description of the larval development of *P. ciliata*, and that of *P. hoplura* which, so far as I am aware, is here described for

the first time, will prove of interest and value, although only the external characters are dealt with.

My best thanks are due to Dr. Allen for his helpful interest in this work, to Dr. Orton for several useful suggestions, and to the Staff generally for assistance in various matters.

2. Methods.

I am indebted to Dr. Orton for the original suggestion that I might obtain the larvæ of *Polydora ciliata* Johnston from the tubes of the parents which bore in large numbers into the shells of oysters. The oysters were obtained from the estuary of the River Yealm, the soft parts removed, and the shells broken up into bits, which were examined under a lens. The shell splits between its layers, and as the burrows of the worm generally run more or less in the plane of the layers they are easily exposed along their whole lengths. It was easy to see which worms had spawned and had eggs-sacs attached to the walls of their tubes, and these were then removed with the aid of a fine brush to dishes of fresh sea-water. In every case the adult was removed along with the egg-sacs and its species carefully checked. Egg-sacs obtained without the adult were rejected.

The larvæ were reared in dishes and in plunger-jars. It was found most satisfactory to use water which had been obtained from outside the Breakwater and passed through a Berkefeld filter. Nitzschia, from a culture kindly supplied by Dr. Allen, was added to this water and on this the larvæ fed. It was found important not to allow too vigorous a growth of diatoms as they then adhered to the spines of the larvæ, frequently causing the latter to stick to the glass, where they perished. Large numbers were lost in this way, and only after several trials was success obtained.

Polydora hoplura Clap. is also found in Yealm oyster shells, although in much fewer numbers, and its larvæ were obtained and dealt with in a similar way to those of *P. ciliata*.

Larvæ were examined alive in cavity slips and all the drawings (except those of the modified chætæ of the fifth segment) were made from living active specimens able to move about freely in the cavities. This was possible on account of their tendency to head-up against the edge of the cavity on the side nearest the light and so remain in approximately the same place and position for a short time before swimming away again. While doing this all the cilia beat actively and the whole body is in a tense state of vibration and every few seconds wriggles vigorously. During the periods of comparative quietude measurements were made with a squared-net micrometer in the eyepiece, and the form of the

larva gradually built up on squared paper. The outline was then transferred to smooth white paper or bristol-board, worked up in pencil, and subsequently inked in. The original larva of each drawing, as well as others, was fixed and mounted and the drawing, as far as was possible, checked from it.

3. The Development of *Polydora ciliata* Johnston.

(*a*) *Development within the Egg-sacs.*

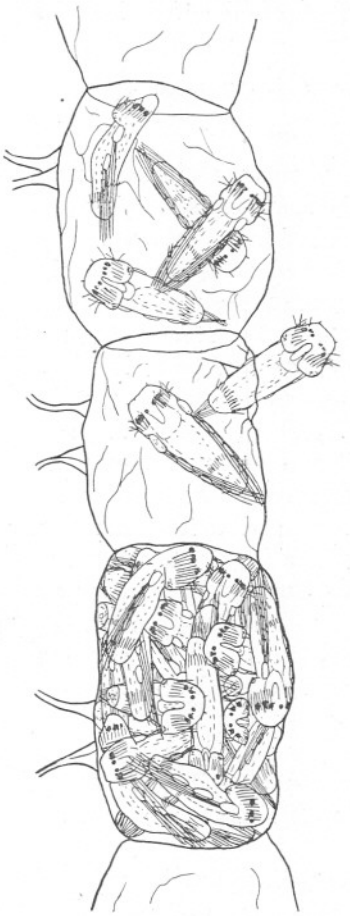
A few individuals spawn in January, and worms with larvæ can be found up to about the end of October, but the spawning season appears to be at its height about March. The eggs are laid in sacs of a very thin transparent membrane, and each sac is attached to the wall of the burrow by two filaments, and is fused with its neighbour at either end so that the series forms a long string (see Text-Fig. 1). The eggs are not spawned freely to drift about on the sea-bottom as described by Leschke. It is difficult to remove an entire string without damage, but the number of sacs present in any one string appears to be about 15–20. The sacs are flattened against the outer wall of the U-shaped burrow to allow room for the worm which lies internal to them, apparently with its back against them. This can clearly be seen when an infected shell is fixed in Bouin and the calcareous matter dissolved away with acid. It is difficult to estimate exactly the number of eggs in each sac, but usually there appear to be 15–20, sometimes more, sometimes a few less. Söderström (**16**, p. 185) gives 70–80 as the number in each sac, but I have not seen one which approached anywhere near that figure. The number of larvæ in a complete string of sacs will thus be about three or four hundred.

Exactly how these sacs are formed is unknown. They have been specially studied in this and other Spionids by Söderström (**16**), who thinks that they are secreted by the nephridia through which the eggs are probably discharged.

The eggs are opaque and densely granular with yolk; by reflected light they have a pale pinkish-yellow hue. They are said to develop rapidly (Leschke, **10**), but as I have been unsuccessful in keeping them alive in dishes I am unable to give times for the earliest stages. A very early stage is shown in Fig. 1, Plate I, in what is presumably lateral view. It is still very dense, and little structure can be made out. The posterior end is more transparent than the rest of the body, and there is here a broad tract of short cilia with a large dorsal gap. Anteriorly there is another broad tract of short cilia, very difficult to see, which seems to have two gaps, one dorsal and the other ventral. Possibly these are the first signs of the telotroch and prototroch respectively. It was drawn thirty-six hours after removal from the tube of the adult.

A later stage is shown in dorsal and ventral view (Plate I, Figs.

2 and 3), and several structures are now marked out. The central mass indicating the gut is still very dense and granular, but the surrounding tissues are more transparent. The larva is well rounded dorsally, less so ventrally, and the head region forms a sort of anterior ridge. The lateral eyes have appeared, the first signs of the future mouth and vestibule are seen, and the chætæ in the first pair of chæta-sacs are forming. The prototroch is formed by a single row of cilia on each side of the head. The telotroch is a single row of rather longer and stronger cilia forming a partial ring which does not extend on to the dorsal surface. Just posterior to the prototroch on the ventral surface there is on each side a finely ciliated swelling. The larva can bend its body slightly (as drawn), but it scarcely moves about yet.



TEXT-FIG. 1. Portion of a chain of egg-sacs of *Polydora ciliata* Johnston. Larvæ in process of liberation. Sketch from life. × 65.

About twenty-four hours later the appearance is as indicated in Fig. 4, Plate I. The three primary pairs of provisional bristles are projecting from well-marked chæta-sacs and the head has undergone a big transformation. The ventral surface of the head is almost flat. In the centre the vestibule* is forming and is well ciliated around its edges and on its roof. The gut is still very granular, and brownish by reflected light. The median pair of eyes has appeared and the eye-like chromatophore (see below) is forming. The prototroch and telotroch are as in the last stage, but stronger. The finely ciliated swellings form curious ciliated plates nearer to the middle line. The function of these remains problematical; they disappear immediately after this stage. In one specimen I was watching they suddenly came off and stuck to the cover glass, where they disintegrated, and their owner swam away without them.

A day later the typical Polydora larva shape is reached (Plate I, Fig. 5). The body and the bristles are longer, and the gut, although still very

* This could be called a mouth, but as its limits are later obscured by the development and ciliation of the cheeks Gravely's term "vestibule," given to the fully-formed structure, is probably better, the mouth being regarded as the anterior opening of the oesophagus.

granular, has now a lumen. In addition to the prototroch and telotroch, a nototroch has appeared on the third chætigerous segment. A ventral view of the head (Plate II, Fig. 1) shows the greatly increased size of the developing vestibule, the sides of which are strongly ciliated and the roof thickly covered with fine cilia. The lateral cheeks are becoming well rounded and pigmented at their corners. The curious sensory cilia (see p. 572) are growing out. The larva is very active, and swims and wriggles about among the other larvæ in the same egg-sac.

A day or so later the larvæ are liberated into the sea and their general appearance about that time is indicated in Fig. 6, Plate I. The gut is no longer granular and is ciliated internally. The whole larva is very transparent; there is yellowish tinting on head and body and brownish pigment around the anus. The gut is greenish yellow, and is the predominating colour of the larva. The eyes are jet-black. There are two pairs of eyes, a median pair of approximately circular ones and a lateral pair situated more ventrally. The latter are roughly kidney-shape, but the shape varies considerably. I have not been able to detect a lens in these eyes, as described by Leschke. Just above the inner border of each of the lateral eyes there lies the main body of a black chromatophore whose ramifications extend over the eye region. The shape of this chromatophore is exceedingly variable, and its main body has generally been regarded as a third eye by previous workers. The ventral view of the head is similar to that drawn for a slightly later stage (Plate III, Figs. 1 and 2), and is described below (see p. 572). There are three pairs of bristle bundles. The first pair are the longest, and there are about eighteen bristles in each bundle, about nine in each of the second pair, and about six in each of the last pair. Under a high power the bristles are seen to be very finely barbed along one side. There is a sensory cilium on each side of the anus.

In order to determine the stage at which the larvæ are liberated naturally, the shells from four well-infected oysters were placed in a large dish of sea-water. During the next three days larvæ were continually being given off, and as these always collected towards the surface in the corner of the dish nearest to the light they were easily removed, at intervals, with a pipette. All the larvæ so obtained were at approximately the stage just described (Plate I, Fig. 6), some being a little earlier, with the gut still slightly granular, others a little later, with the first dorsal black pigment band (see below) appearing. No earlier and no later stages than these were found. It must be noted in connection with this experiment that although I have broken up a large number of oyster shells from the Yealm estuary and examined hundreds of Polydora I have only found the two species, *P. ciliata* and *P. hoplura*, boring in them. At the time of the experiment (early March) the latter species had not begun

to spawn, and their larvæ in any case are easily distinguishable from those of *P. ciliata*. Text-Fig. 1 shows three egg-sacs, from two of which larvæ are escaping through ruptures in the wall, although the latter may have been caused during the removal of the sacs from the tube of the parent. One of these larvæ is drawn in Plate I, Fig. 6. It is interesting to note that once the egg-sacs have been removed to a dish enclosed larvæ do not appear able to escape, their spines stick through the membraneous wall and they perish.

(*b*) *Structures associated with the Head.*

Attention was first called to the complex vestibule associated with the mouth in these and other Spionid larvæ by Gravely (**7**), who described and figured that of an advanced larva of his Polydora A. He also discussed its probable development, basing his conclusions in part on a figure of a trochophore which had been supposed by Claparède to be that of Leucodora, but which was most probably that of Sabellaria (see p. 587).

The early development of the vestibule in *P. ciliata* has already been noted in this paper. Commencing as quite a small hollow or opening, it rapidly enlarged backwards and deepened upwards until the condition was reached which is indicated in Fig. 1, Plate II. The steep and deep side walls are thickly covered with cilia and the roof with finer cilia. The opening can be closed by the meeting of the side "cheeks" in the middle line. Shortly after liberation, and at a stage in which the dorsal black pigment spots on the third chætigerous segment have appeared, the partially open vestibule has reached the condition represented in Fig. 1, Plate III. It has deepened still further backwards, and has also extended more forwards, and the cheeks on either side form prominent swollen pads, which, meeting in the middle line, completely close it in. The prototroch extends as a paired row of cilia running downwards and backwards over these cheeks until it meets the outermost of the strong cilia which clothe the sides of the vestibule. The latter are much more numerous than it has been possible to indicate in the figure. Anteriorly the vestibule shallows until its ciliated roof meets the ventral surface of the anterior part of the head. This part of the ventral surface immediately anterior to the vestibule appears to be exceedingly finely ciliated. Posteriorly the vestibule deepens and leads, through what is probably the true mouth, into the gut. On the fold of skin which forms the posterior ventral border of the vestibule is a patch of fine cilia, supposed by Gravely to represent a neurotroch. Fig. 2, Plate III, shows the vestibule wide open, in which condition it forms a kind of funnel directed forwards and rather downwards, through which food particles are swept as the larva swims through the water.

The head is beset with several curious stiff, strong, apparently sensory

cilia. On each side there are two very conspicuous ones just anterior to the prototroch and one strong one about the level of the lateral eye. Smaller ones occur ventral to the lateral eye region, at the anterior corners of the head, and just by the anterior end of the vestibule. The latter project inwards towards one another. On the dorsal surface there is a sensory cilium a little anterior and lateral to each median eye. Just in front of this I have, in this species, detected another very much smaller cilium (not shown in the drawings), and there may possibly be one or two other small ones elsewhere on the head which have so far eluded observation owing to the difficulty of seeing them. At the anterior extremity of the head there is a tuft of very fine cilia.

The sensory cilia, especially the three largest pairs, are usually held projecting stiffly outwards, but every now and then they bend back and beat among the prototroch. Leschke (**10**) appears to have observed one or two of these cilia, but Gravely apparently overlooked them, probably because they are much smaller in proportion to the size of the head, and hence less conspicuous, in the later stages he examined.

The vestibule remains more or less in the condition just described throughout larval life, but during the later stages it is rather more funnel-shaped (see Plate III, Fig. 3, and p. 574).

(*c*) *Development in the Plankton.*

Shortly after liberation at the stage figured in Fig. 6, Plate I, black pigment in the form of two spots, often coalesced to form an irregular band, appears on the anterior part of the third chætigerous segment in front of the nototroch. About the same time a nototroch begins to appear on the developing fourth segment, and by the second day after liberation two spots of black pigment appear in front of it also. A few days later the fourth pair of chætæ are prominent, and the fifth segment is forming (Plate I, Fig. 7). As new segments appear, in front of the telotroch, each acquires in order a nototroch, black pigment and chætæ. Fig. 2, Plate II, shows the general appearance about ten days after liberation. The dorsal parapodial lobes are now forming and are most prominent on the third and fourth chætigerous segments. There is a good deal of brown pigment in the region of the anus. A week or so later the larva is much more massive than formerly (Plate II, Fig. 3), the dorsal parapodial lobes are well developed, except that those on the second segment are not quite as far advanced as those on the following segments. At the end of each lobe are a few fine sensory cilia and one much stouter cilium ; the latter are shown in the drawing of this and later stages. The black pigment now forms a double row of spots down the back. Gastrotrochs are present on the third, fifth, and seventh chætigerous segments ; their cilia are longer and stronger than those of the nototrochs.

Fig. 4, Plate III, is a lateral view of a larva about a month after liberation, and several important points are to be noted. The developing tentacles form prominent swellings posterior to the prototroch and to the outside of the anterior pair of chæta-sacs. The ventral lobes of the parapodia have appeared and chætæ of the ventral bundles are growing out. The modified chætæ of the fifth segment can now be seen, but this segment still carries dorsal bundles of provisional bristles. A black pigment spot, which was also present at somewhat earlier stages, is seen near the base of the second parapodium. At the corner of each cheek there is a very dark brown, almost black, pigment mass. This patch of pigment has been present all through the pelagic stages, but in many specimens it is light brown in colour, and in a few is absent altogether. Gastrotrochs are present on segments 7 and 10, and one is just appearing on segment 13. In some cases they are present also on segments 3 and 5. The œsophagus now reaches back to the hinder end of the third chætigerous segment before it passes into the stomach. It is strongly ciliated.

About two weeks later, nearly six weeks after liberation, the larvæ reach the stage drawn in dorsal and lateral views on Plate IV. The larva is now at the height of its larval development and is worth describing in some detail. Since the last stage a great increase in bulk has taken place. There are nineteen chætigerous segments with well-defined boundaries and a large anal segment bearing the telotroch. The head carries a pair of long wrinkled tentacles which have wide shallow, densely ciliated grooves down their anterior ventral borders. From behind the eyes, the lateral pair of which are in a more anterior position than formerly, a high mid-dorsal ridge arises and runs back as far as the anterior border of the second segment. A slight groove runs longitudinally along each side of this ridge at the base. From close to the base of each tentacle a slight backward fold of skin forms a posteriorly projecting ridge which, running transversely inwards, meets the longitudinal groove on the corresponding side of the mid-dorsal ridge at right angles. Along each of these transverse ridges there is a row of rather long, fine, rapidly beating cilia which give a flickering appearance to this region. Gravely's figure (**7**, Plate 14, Fig. 2) of this region of his Polydora A is thus incorrect, unless this species differs markedly from *P. ciliata*, a supposition which is very unlikely. Ventrally the vestibule (Plate III, Fig. 3), when widely open, is a well-marked forwardly directed funnel, densely ciliated internally with fine cilia on the roof and longer and stouter cilia on the lateral walls and rim. Gravely figures for his Polydora A (**7**, Plate 14, Fig. 1) a single row of these stout cilia along each margin. In *P. ciliata* they are certainly not arranged in a single row ; there are a great many of them on the lateral walls and rim ; but whether they are arranged in regular rows or not I have been unable to determine. The prototroch has a wide

dorsal gap and runs round on each side of the head until it is difficult to distinguish from the cilia at the posterior ventral margins of the vestibule. The sensory cilia are as before, but are smaller in proportion to the size of the head. The short neurotroch is present.

The parapodia are well developed, the ventral lobes are present, and there are several chætæ in the ventral bundles. The ventral bundles of the first six segments are composed of sabre-shaped bristles, those of the seventh and succeeding segments carry hooded crochets in addition to these. The actual numbers of these bristles in the ventral bundles are correctly illustrated for the specimen from which the drawing on Plate IV was made. With the exception of the fifth segment the dorsal bundles are well provided with long provisional bristles, but among these shorter dorsal bristles of the adult type (about six each in most bundles) have appeared, except on the first segment. The provisional dorsal bristles of the first segment are the longest and number about fifteen in each bundle, those of the following segments about half that number. The ventral lobes of the first pair of parapodia are turned upwards instead of downwards, as are those on the succeeding segments. Colourless branchiæ are present on segments 7 to 12.

The fifth segment is now much modified. The provisional bristles have been lost, while the strong specialised bristles, each, except the first pair, with a strong lateral tooth, are very conspicuous. Four pairs of these project outwards, their curved tips being directed rather upwards and backwards. They are moved about and thrust outwards as the larva wriggles. Behind two other pairs are developing. These strong bristles are accompanied by a few small winged chætæ and by a fairly thick bristle lying between the first and second specialised bristle on each side. Text Fig. 3 shows a group of the specialised bristles from one side of another larva of approximately the same age.

The third and all succeeding segments carry nototrochs. Gastrotrochs are present on segments 3, 5, 7, 10, 13, 15, and 17. Those on 3 and 5 have shorter cilia than the others. There is frequently great irregularity in the development of the gastrotrochs ; one larva of twenty chætigerous segments had them developed as follows : None on segments 3 and 5, one on segment 7, partial ones on segments 8 and 9, normal ones on segments 10, 13, and 15, a partial one on segment 16, and fully developed ones on segments 17 and 18. The nototrochs were normal.

The large anal segment carries the powerful telotroch, the cilia of which are longer and stronger than those of the prototroch. The dorsal gap is relatively smaller than before. The presence of this gap was remarked by Gravely (**7**) to be a characteristic feature of the larvæ of Spionidæ and Polydoridæ.

The pigmentation is of special interest. The eyes, and the pair of

eye-like chromatophores which ramify around them, are black. The spot at the corner of each cheek is usually very dark brown or black, sometimes it is much paler or absent altogether. There is a patch of irregular black pigment at the anterior base of most of the parapodia (see side view, Plate IV). This is especially well marked anteriorly, where it often appears to coalesce with the dorsal pigment bands. In dorsal view black pigment appears as a series of irregular bars on the anterior borders of segments 3–8, the posterior bars being longest. On segment 9 in place of bars there is a much ramified stellate spot on each side of the middle line, and similar spots occur on all the posterior segments, gradually becoming smaller as they are situated farther back. The ramifications of the spots may extend on to the segment in front. There are a few spots of black pigment on the anal segment.

The irregular anterior bars and the stellate spots are each a single chromatophore. These chromatophores undergo expansion and contraction; they may expand so that almost the whole of the dorsal surface appears to be covered by a very finely ramified net of black pigment, or they may contract to irregular black bars or spots without ramifications. The drawing shows an intermediate condition. The chromatophores of the earlier larvæ also possessed this faculty. It is thus important to note that the shape and degree of ramification of the pigment spots in Polydora larvæ form no basis for the discussion of specific differences, although some writers have tended to use them for that purpose. Moreover, the change from bars to stellate spots may not be as sudden as is here illustrated, or it may take place on the segment in front or the segment behind, or the pigmentation may be otherwise irregular, some spots may be missing, or supernumerary ones present.

The general body colour is brownish and the larva is fairly transparent. There are two rings of stippled dark brown pigment on the anal segment, one in front of the telotroch, the other behind. The œsophagus is slightly sinuous and now extends back to about the posterior border of the sixth segment before enlarging to form the "stomach." The gut then gradually narrows to the anus; it is faintly indicated in the dorsal view on Plate IV. The anal segment is notched on the dorsal surface; this is the first indication of the dorsal notch of the future anal cup. On each side of the notch there is a sensory cilium; these cilia have been present throughout the pelagic existence. The ventral surface of the larva is slightly hollowed to form a wide shallow trough.

I have unfortunately been unable to induce my larvæ to metamorphose. Pieces of broken oyster shell were supplied, but none of the larvæ settled down, but died off after growing one or two more segments. Probably metamorphosis is almost identical with that in *P. hoplura*, which is described on page 583.

(*d*) *Swimming Movements and the Grasping-cilia.*

So far little mention has been made of the movements of the larvæ. They are strongly positively phototropic, and the early stages especially will swim across a dish towards a source of light in an almost straight line. The body is stretched out, the spines closely laid along the sides, and the vestibule usually opened widely. They swim forwards, often on their backs, frequently slowly rotating on their longitudinal axes. Sometimes they swim in circles about one place. When irritated, as when they bump up against some object, the body is rapidly curled round ventrally, bringing the anal segment against the now closed vestibule, the spines at the same time being erected so as to point in all directions. The later stages sometimes swim by lateral wriggles, but they also still swim by means of their cilia with the body stretched out and the spines laid along the sides.

Close inspection of the living larva reveals a most interesting series of cilia in connection with the method of swimming. At each end of every nototroch there is a short longitudinal row of cilia that project outwards. These cilia do not beat regularly along with the other cilia, but have a sort of trembling movement, and always remain more or less curled. Their function is to curl round and take hold of the bristles when the latter are laid along the sides of the body in swimming. So far as I am aware cilia with this function have not been described before, and I therefore propose to call them "grasping-cilia." I first noticed cilia of this kind on the telotroch of Sabellaria larvæ (a paper on which will subsequently be published), where they are large and strong, and during swimming are used to grasp the ends of the long provisional chætæ which arise from a pair of large chæta-sacs situated in the head region. They do not occur on the telotroch of Polydora, nor in Sabellaria on the nototrochs that develop just before metamorphosis.

The presence of these cilia raises anew the old question concerning the function of the long provisional bristles. These bristles have usually had two functions assigned to them, that of suspension organs and that of protection. It is possible that they fulfil both those functions, but in addition another possibility suggests itself. Owing to the manner in which the bristles are laid along the sides of the body, the bundles in front overlapping the bundles behind, and then all these held in by the grasping-cilia curling round them, apparently fairly tightly, an increased rigidity of the whole body must result. This increased rigidity will increase the driving efficiency of the cilia, and of the swimming as a whole. The bristles are also held in to the stream-line with less exertion than would be entailed if the grasping-cilia were absent.

Some, at least, of the bristles always project dorsally beyond the

telotroch, and the tips of those of opposite sides meet or are crossed behind. These bristles pass through the dorsal gap in the telotroch and thus possibly explain the presence of that gap, for even if the telotroch were a complete ring the beating of the most dorsally situated cilia would be hindered or prevented altogether by the presence of the bristles close above them. Gravely (**7**) has suggested that the dorsal gap in the prototroch is correlated with the ventral gap caused by the presence of the vestibule.

The nototrochs are formed (as they are in the adults) by short rows of cilia placed end to end with slight gaps between them. These gaps are faintly indicated in the drawings, they are rather more conspicuous in *P. hoplura*. The first nototroch in the larvæ just liberated from the egg-sac has two such rows, the latest larva drawn has six in each nototroch. The cilia of each row are longest in the middle and shortest at the ends. The gastrotrochs are formed in a similar manner, and the prototroch and telotroch can also be seen to be formed of rows of cilia placed end to end without gaps between them.

4. The Development of *Polydora hoplura* Claparède.

(*a*) *Development within the Egg-sacs.*

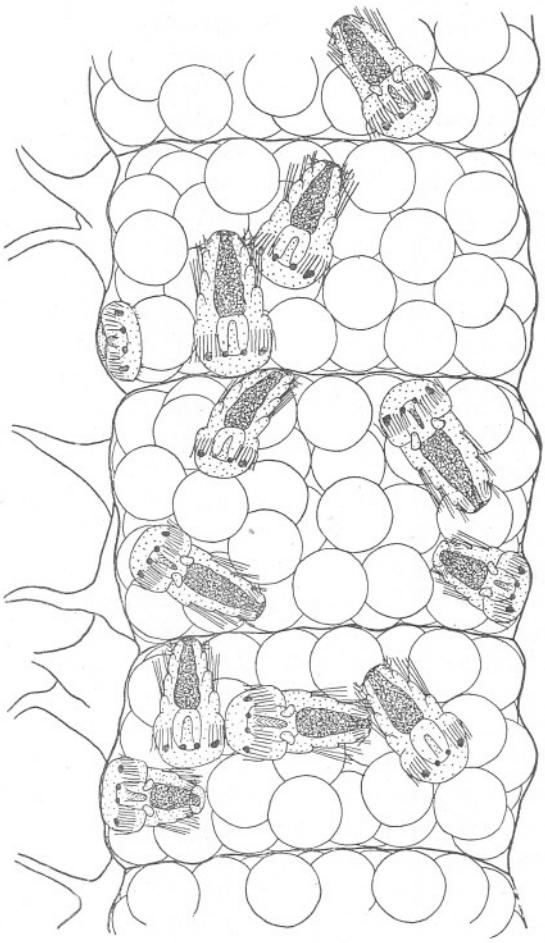
Polydora hoplura is a much larger species than the foregoing, and there are never more than a few individuals in any one oyster shell. The breeding season commences much later than in *P. ciliata*, and does not last as long. In oysters from the River Yealm they started to spawn in 1927 about the end of June, and all had finished by the end of October.

The egg-sacs (Text-Fig. 2) are much larger than in *P. ciliata*, and when freshly spawned the contents have a deep bright yellow colour by reflected light. The sacs are similar in structure to those of *P. ciliata*. I have been unable to obtain a complete undamaged string and count the sacs, but they are several times more numerous than in the smaller species ; there appear to be about fifty to each individual worm.

The general appearance of the sacs is shown in Text-Fig. 2. In each there are a few larvæ, and what appear at first sight to be a large number of segmenting ova. The latter (Plate V, Fig. 1) are roughly spherical, and are surrounded by a definite membrane, and are very opaque on account of the dense yolk they contain. They are, in fact, yolk masses. When crushed under a cover glass they break up into a great number of oily globules of all sizes. The tight packing of these globules inside the membrane causes them to assume hexagonal and other shapes and to appear at first sight like the cells of a segmenting ovum. Sections have failed to reveal the presence of nuclei in these yolk masses, nor can nuclei be seen in the living ones. The yolk masses always present the same

appearance whatever the stage of the larvæ may be. The larvæ in any one string are always at the same stage.

By carefully slitting open with fine needles and emptying twelve sacs counts varying from thirty-four to ninety-four yolk masses and from one



TEXT-FIG. 2. Portion of a chain of egg-sacs of *Polydora hoplura* Claparède, showing early larvæ and yolk-masses. Sketch from life. × 65.

to six larvæ per sac were obtained. These gave an average of sixty yolk masses and three larvæ per sac. All these sacs were from the same portion of a long string.

The yolk masses form the food of the larvæ. Instead of becoming planktonic at a stage with three pairs of bristle-bundles, as in *P. ciliata*,

the larvæ remain within the protecting burrow of the parent amid a plentiful supply of food until a very late stage, thus shortening pelagic life to a few days, possibly to a few hours in some cases.

That the larvæ actually feed on these yolk masses there is no reasonable doubt. Their guts are seen to be full of yolky globules which have exactly the same appearance as those of a crushed yolk mass. The yolk masses, too, are fewer in number the older the larvæ found in a sac, until finally large well-developed larvæ, such as that drawn on Plate VII, are found along with only one or two yolk masses or with none at all.

A similar condition of things has been described by Söderström (**16**) for *Pygospio elegans*, and he has also found very late larvæ of *Polydora natrix* Söder. in egg-sacs which contained also a mushy mass that he supposed to be their food. Mesnil (**12**, p. 225) many years ago observed what appears to have been a very similar state of affairs for *Polydora polybranchia*. Mesnil and Caullery (**13**) have also described an analagous case in *Spio filicornis* O. F. Müller, in which they distinguish two kinds of spawn. One which they call A gives rise to larvæ that become pelagic at a stage with three pairs of bristle-bundles; in the other, which they call B, some of the larvæ feed on undeveloped ova and larvæ arrested in their development.

Although the larvæ of *Polydora hoplura* thus feed on special food material provided for them by their parents they are quite able to lead a pelagic existence, and if removed at the stage with three chætigerous segments can be reared in plunger jars on Nitzschia. Larvæ so reared appear to be identical with those developing in the egg-sacs in the normal way. In the plunger jar they took about six weeks to reach the stage at which they metamorphose. How long they take to develop under normal conditions it has been impossible to determine. Egg-sacs, once they have been removed from the burrows, soon putrify.

In spite of the striking difference in the mode of life the larvæ of *P. hoplura* are similar in all important respects to those of *P. ciliata* and the development follows the same general course. The early larvæ are, however, considerably larger. Fig. 2, Plate V, shows in ventral view an early larva in which the vestibule is forming and in which the pair of problematical ciliated ventral plates are prominent. The sensory cilia and the nototroch on the third chætigerous segment are just appearing, but the prototroch and telotroch with their usual dorsal gaps are well developed. Both pairs of eyes are present. The gut is still very full of granular yolk material. The sensory cilia on each side of the anus are rather long. The larva is quite active, and swims and wriggles among the surrounding yolk masses.

The stage with three chætigerous segments is shown in Fig. 3, Plate V. In all important respects it closely resembles the corresponding stage in

P. ciliata, but it is larger, the sensory cilia are more prominent and there is a spot of black pigment on each side between the first and second pair of bristle bundles that did not occur in the smaller species, and the pigment around the anus is also much blacker.

A ventral view of the head of a little older larva is shown in Fig. 1, Plate VI. The vestibule is partially open and its structure is essentially the same as that already described for *P. ciliata*. There is, however, no pigment on the corners of the cheeks and no fine cilia on the ventral surface of the head in front of the vestibule. The sensory cilia are almost the same as in *P. ciliata*, but there are some minor differences in the region ventral to the lateral eyes. These differences are clearly seen when the corresponding drawings are compared.

Development proceeds in all essentials as in the former species. Fig. 4, Plate V, shows a larva with several segments in which the dorsal lobes of the parapodia with their apical sensory cilia are quite distinct. In this species at this stage the lobes of the first and second pair are as distinct as those immediately following. Just behind the eyes, in the dorsal gap of the prototroch, the first signs of the future dorsal ridge and the long fine cilia on each side can be seen. These could also be seen from very early stages in *P. ciliata*, but they were very indistinct and difficult to detect and have not been indicated in the drawings of that species. Gastrotrochs are present on segments 3 and 5. The body is slightly trough-shaped ventrally. Another black spot has appeared on each side of the second chætigerous segment; it is situated below and behind the one present in the last stage and cannot be seen in dorsal view.

A lateral view of the stage in which the tentacles are budding out as small swellings is shown in Fig. 3, Plate VI. This stage is very similar to the corresponding stage in *P. ciliata*, and is about the same size. Some individuals, as is the one drawn, are now actually smaller than corresponding *P. ciliata* larvæ. The ventral lobes and chætæ are appearing on most of the parapodia, but not on the first pair. The two black spots on the side just in front of the second pair distinguish the larva from that of *P. ciliata*, where there is only one. There is also a very dark, almost black, patch of pigment above the anus. An important difference is that there are still no signs of the modified chætæ of the fifth segment, these do not appear until a little later in development, later than they do in *P. ciliata*.

The larva drawn on Plate VII was one of a number found quite free in the tube of the parent, not enclosed in sacs, and no yolk masses were seen with them. Most probably they were just about to be liberated into the plankton. This larva is so similar in its structure to the corresponding stage in *P. ciliata* that a separate description is unnecessary. There is a slight difference in the general appearance, and this is sufficiently indicated in the figure. The fifth segment is not yet much modified, due

to the later appearance of the strong specialised chætæ in this species. Three of these chætæ here project on each side, and a fourth is developing behind them. The first has no lateral spur, the others have two spurs each, a strong one on one side and a smaller one on the other side. Lying between the first and second chætæ there is a fairly thick bristle, and a few winged bristles accompany them. The specialised chætæ of one side of a specimen at a rather earlier stage are shown in Text-Fig. 4. The long provisional dorsal chætæ of the other segments appear to have already started to fall out as there are now only two or three of them in most bundles. Dorsal bristles of the adult type are fairly long and numerous. The ventral bundles are all provided with sabre-shaped chætæ, and the seventh and succeeding segments with hooded crotchets as well. Six pairs of colourless branchiæ, ciliated on their inner surfaces, are present on segments seven to twelve. Pigmentation is very similar to that of *P. ciliata* with the addition of a pair of small lateral spots on the sides of each segment above the parapodia. These spots commence on about the eighth segment. In a side view black pigment on the anterior part of the base of the parapodia, arranged in a similar manner to that in *P. ciliata*, can be seen. Gastrotrochs are present on segments 3, 5, 7, 10, 13, 15, and 17, those on 3 and 5 having the shortest cilia.

The vestibule of this specimen is illustrated in Fig. 2, Plate VI. Its structure is mainly the same as in the other species, but the opening is directed rather more downwards.

In order to determine the stage at which the larvæ are liberated in the normal way, a similar experiment to that performed for *P. ciliata* was carried out for the present species. The shells of two dozen oysters were placed in large glass dishes of sea-water, and in a few hours a good number of larvæ had been given off and had gathered against the glass on the side nearest to the light. While the majority of these were rather earlier than the stage just described, and a few had not yet even started to grow their tentacles, a good proportion of them were quite as advanced. This big variation in the stage at which the larvæ were liberated may have been due to the disturbance involved in the removal of the oysters from their native estuary, or because some broods are possibly not as plentifully supplied with yolk masses as others, and are released as soon as the food-yolk has been all used up. We have seen that the larvæ are quite capable of leading a pelagic existence from very early stages (see p. 580).

(*b*) *Development in the Plankton.*

If the above-mentioned experiment gives a true picture of the normal release of the larvæ, it will be seen that the length of time a larva spends in the plankton will depend on the stage of development at which it is

liberated. In some cases possibly only a few hours elapses before the larvæ settle down and metamorphose, in others probably as long as two weeks is passed in the plankton before the larvæ are ready to infect fresh oysters. Larvæ placed in a plunger-jar and in finger-bowls, and supplied with broken pieces of oyster shell sterilised by boiling, took from a few days to two or three weeks to settle down. But in any case the pelagic life is much shorter than in *P. ciliata*, and the larvæ are protected during the greater part of their development.

(*c*) *Settling-down and Metamorphosis.*

A few larvæ from the same brood as that drawn on Plate VII were, four days after removal from the burrow of the parent, placed in a shallow dish containing sterilised broken pieces of oyster shell and their movements followed with low powers of the microscope. The larvæ often still swam by means of their cilia and with the body stretched out straight, the spines being laid along the sides and held by the grasping-cilia. On alighting on a piece of shell larvæ would start to crawl about over its surface in the usual Polychæte manner. While thus crawling they adhere very tenaciously, apparently by a secretion of mucus, and are very difficult to dislodge by squirting water at them. They can also cling very firmly to the sides of a pipette. As they wander about, often for comparatively long distances and for a long time, they carry the tentacles stretched obliquely forwards and outwards. They now appear to be no longer affected by light, but should they, as often happens, suddenly take to swimming again, they usually move towards the light. As they crawl about they explore any small hole or cavity they come across, and do not hesitate to crawl in between the overlapping layers of periostracum. Holes and pits do not seem to be explored so much with the tentacles as with the head and lips. If not satisfied they move away again, often crawling backwards for a time.

Only in one case was I able to observe a larva actually settle down. This one came across a small concavity in the chalky layer which was overhung by a projecting shelf of hard shell. After exploring it for several minutes, and once or twice almost crawling away again, it wedged the middle part of its body under the projecting shelf which was too small to cover it completely, and then moved restlessly about, turning round to face the opposite direction several times. Soon it had secreted a quantity of transparent mucus, which more or less covered it up, and in this mucus a number of its longer bristles were lost. At times it appeared to be exerting the region of the fifth segment below the shelf in a position which was out of sight. Occasionally, when it crawled forwards so that this segment could be seen, it pressed the points of the strong modified

bristles against the chalk and jerked them sharply backwards and upwards. It did not however do very much of this, and after about an hour of restless wriggling quieted down. By the next day the mucous coat was a little thicker, and entangled in it were particles of the chalky layer of the shell and other debris. The tentacles had lengthened and become slenderer, and were waved about after the manner of the adult. The fore-part of the body was often stretched well out of one end of the mucous-tube which was still shorter than the body. Four days later the tentacles were still longer, about as long as the worm itself, and the snout had a pronounced forward prolongation. The lateral eyes had been carried forwards and brought closer together, and were much anterior to the median pair. The anal cup was well formed. Eight days after it had first settled down this specimen was removed and carefully examined. In general appearance it resembled the adult except for coloration and in only having 22 segments. It was, however, unmistakably a *P. hoplura*. The forward elongation of the snout, the lengthening of the tentacles, and formation of the anal cup have already been mentioned. The dorsal ridge extended back almost to the posterior border of the second chætigerous segment. The sensory cilia had gone, so had the prototroch, telotroch, gastrotrochs, and the nototrochs anterior to the seventh segment as well as those on the most posterior segments. Nototrochs were present only on the middle segments of the body, and were most pronounced on those bearing branchiæ. There were no signs of grasping cilia. The sensory cilia at the ends of the dorsal and ventral parapodial lobes had gone. The long provisional bristles had been lost. The last four segments had in each dorsal bundle one strong curved bristle of the kind characteristic of this species. The ventral bundles of the seventh and succeeding segments carried only hooded crotchets, the sabre-shaped bristles found among them in the larva had gone. The fifth segment had become more prominent. There were still only six pairs of branchiæ, but these had grown much longer and more strap-like, the fourth and fifth pairs being the longest, the sixth pair the shortest. Each had a row of strong and fairly long cilia on the inner or dorsal surface. Nearly all the black pigment had disappeared, there being only a few specks here and there. The eye-like chromatophores had gone. The body-wall was very transparent and almost colourless. The œsophagus extended back to about the ninth segment before passing into the stomach, which was brown owing to its contents.

Larvæ liberated in a natural manner, from infected oyster shells placed in dishes, were put into a plunger-jar together with broken pieces of oyster shell which had been boiled. Within about a fortnight all the larvæ had either died off or settled down on these pieces and there metamorphosed. Most of those that settled chose the cracks along freshly broken edges,

but others had got in between the overlapping layers of periostracum that are found round the edge of an oyster shell. Each young Polydora had collected debris and formed a tube. In some cases these tubes were almost straight and ran along the length of the crack in which the larva had settled ; in others the ends projected and from first one and then the other the tentacles were waved about in the usual manner. Three months later the pieces were examined and some of the worms removed. They had penetrated very little if any further into the shell, and the largest one seen had only 30 chætigerous segments. Most of them had six pairs of branchiæ, the second to the fifth pair being the longest, the sixth pair the smallest, but a few had only five pairs, in which case the fifth pair was the shortest. The specialised bristles of the fifth segment all had lateral teeth, the first pair without lateral teeth, the rather thick bristle found in the larva having disappeared. Three months later still, when the pieces of shell were split open, a few of the young worms were lying in distinct grooves in the brown horny layers, but on the whole they did not appear to have penetrated very far. The seventh pair of branchiæ was appearing in most cases, and the sixth pair was now as long as the first, but in others the sixth pair was only just putting in an appearance. The largest individual seen had 35 chætigerous segments, and the ninth pair of branchiæ was developing. Probably in the sea growth is much faster than this.

(*d*) *Comparison with* P. ciliata.

Although there still remain several species of British Polydora whose larval developments have yet to be worked out, it may nevertheless be of value to plankton workers to state briefly those characters by which *P. hoplura* larvæ can most easily be distinguished from those of *P. ciliata*. They can be tabulated as follows :—

P. CILIATA.	P. HOPLURA.
1. Released at a stage with three pairs of bristle-bundles.	1. Usually not released until after the appearance of the tentacles.
2. Majority of larvae of all stages after formation of vestibule have a mass of pigment, often dark brown, at the corners of the cheeks.	2. Never have any dark pigment at the corners of the cheeks.
3. No lateral black spots between first and second pair of bristle bundles in early stages. Later a pair of spots, corresponding to the later ones of *P. hoplura*, appears.	3. From 3 chætigerous segments stage onwards there is a pair of lateral black spots between first and second pair of bristle bundles. Later another pair of spots appears below and rather behind this pair.
4. A little brown pigment in the anal region in early stages. Later a few black spots may appear.	4. Considerable quantity of black pigment in the region of the anus at all stages.
5. In latest stages two rows of black chromatophores down the back.	5. In latest stages four rows of black chromatophores down the posterior half of the back. Spots of outer rows small.

These are the best characters by which to distinguish the two species, especially as the pigment is preserved fairly well in alcohol and in formalin. It must be emphasised, however, that the pigment is liable to great variation, thus the cheek spots in *P. ciliata* may be absent altogether, and the rows of spots on the back may, in both species, become irregular owing to the absence of some spots or the presence of supernumerary ones. But by taking account of all the characters mentioned, it is almost always possible to separate these two species one from the other.

TEXT-FIG. 3.
Modified chætæ of the fifth segment of a late *Polydora ciliata* larva. Traced with a drawing eyepiece. × 264.

TEXT-FIG. 4.
Modified chætæ of the fifth segment of a late *Polydora hoplura* larva. Viewed somewhat from the convex sides of the curved tips. Traced with a drawing eyepiece. × 264.

The latest stages can also be distinguished by the difference in the shape of the specialised chætæ of the fifth segment. In *P. hoplura* there is a small secondary spur on the second and succeeding chætæ which is absent in *P. ciliata*. (Compare Text-Figs. 3 and 4.)

5. PREVIOUS RECORDS OF POLYDORA LARVÆ.

The first writer to figure a Polydora larva was Örsted (**14**), who in his "Conspectus" of 1843 gives a sketch (Plate VI, Fig. 96) of one he found along with adult examples of *Leucodorum ciliatum* Johns. He shows three pairs of bristle-bundles and four eye-spots, and I have little doubt that this was actually a *Polydora ciliata* larva. Twenty years later Claparède (**4**) published a beautifully illustrated account of the development of *Leucodora ciliata*, but, as has been pointed out first by Agassiz (**1**) and then by later writers, and by Claparède himself in conjunction with Mecznikow (**5**), this is probably not Polydora. Gravely, however, thinks that it may be (**6**, p. 51). Claparède and Mecznikow (**5**) figured a larva they then supposed was that of Polydora, but this also has been shown by various writers to belong not to that genus but most probably to Pectinaria. Agassiz (**1**) figures and describes, from specimens obtained from the plankton and kept in confinement, the development of an undoubted Polydora larva from a stage in which the tentacles were just appearing to a late stage after metamorphosis. Whitelegge (**17**) found the ova and larvæ of a species of Polydora attached alongside the adults to the walls of their burrows in oyster shells at Newcastle, in New South

Wales. He believed the species to be *Polydora ciliata* Johns, but his figure of the egg-sacs resembles more closely that given by Söderström (**16**) for *Polydora ligni* Webster. His original figures of the larvæ are too poor to discuss. Andrews (**2**) figured and described the egg-sacs and early larvæ of his *Polydora commensalis*. Leschke (**10**) appears to have been the first to rear the larvæ of *P. ciliata* from the egg to metamorphosis. Apart from minor errors and some slight differences from my account, the chief of which have already been pointed out, his account is good as far as it goes, but his figures are few and poor. Gravely (**6**) described and figured different stages of Polydora larvæ picked out from the plankton at Port Erin; he considered they belonged to two species that he called A and B, neither of which appear to correspond with either of the two species described in this paper. The larvæ he described as the metatrochophores of Polydora (**6**, p. 46), following Claparède's figures (**4**, Plate VII, Figs. 4 and 5) were certainly not Polydora, but were very probably Sabellaria larvæ, as I shall have occasion to show in a future paper. Gravely (**7**) was the first to draw special attention to the complicated vestibule of these larvæ, and his figure of this has already been discussed. It must be remembered, however, that his species was probably a different one from either of mine. He bases a suggestion as to the way in which he supposed the vestibule to originate in development, partly on the trochophore figured by Claparède, as that of Polydora, and he repeats the latter's figure (**7**, Text-Fig. 3A), but, as has already been mentioned, this is not Polydora but is very likely Sabellaria. Söderström (**16**) has published a long account of the egg-sacs of the Spionidæ, to which the reader is referred for an account of his theory as to their formation, and for other interesting information. Of general interest is Gravier's fascinating paper (**8**) on the spawning and incubation of Polychætes.

In addition to these most important references to Polydora larvæ, there are a number of odd figures scattered through the literature. De Saint-Joseph (**15**, Plate III, Fig. 73), Mesnil (**12**, Plate XIV, Figs. 7 and 8), McIntosh (**11**, Plate XCIII, Figs. 6 and 7), Häcker (**9**, Taf. II, Figs. 16–18), Carazzi (**3**, Taf. II, Fig. 16), and one or two others, all figure one or more Polydora larvæ, usually from specimens caught in the plankton. Carazzi states that his larva is *P. hoplura*. I consider, however, that until the developments of several more species have been worked out it is futile to discuss them.

6. SUMMARY.

1. The developments of *Polydora ciliata* Johns. and *Polydora hoplura* Clap. are described from the egg to a very late planktonic stage in the case of the former, and to young metamorphosed individuals in the case of the latter. Only external characters are described.

2. In both species the eggs are laid in egg-sacs attached to the wall of the parent's burrow.

3. The larvæ of *P. ciliata* are released at a stage with three chætigerous segments and lead a long planktonic life.

4. The larvæ of *P. hoplura* are provided with special food in the form of yolk-masses ; they undergo most of their development while in the protecting burrow of their parent ; are released at a very late stage, and have only a short planktonic life.

5. The larvæ of both species have a complicated vestibule surrounding the mouth, and are provided with special sensory cilia on the head.

6. The larvæ are provided with a special kind of cilia, situated at the ends of every nototroch, which are used to take hold of the long provisional bristles in swimming. This suggests that one of the functions of the long bristles is that, in conjunction with these grasping-cilia, they increase the rigidity of the swimming larva, and hence the efficiency of its driving cilia.

7. Previous references to Polydora larvæ are briefly discussed.

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PLATE I.

Larvæ of *Polydora ciliata* Johnston. All drawings from life × 156.

FIG. 1. Early embryo from egg-sac. View of left side. Actual length approx. 135 μ (see page 569).

FIG. 2. Later stage from egg-sac. Dorsal view. Actual length approx. 173 μ (see page 570).

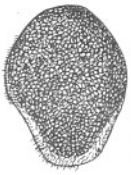
FIG. 3. Ventral view of the same larva as shown in Fig. 2.

FIG. 4. Early larva 24 hours older than the one shown in Figs. 2 and 3. Ventral view Actual length approx. 200 μ (see page 570).

FIG. 5. Larva from egg-sac 24 hours older than the one shown in Fig. 4. Dorsal view Actual length approx. 231 μ (see page 570.)

FIG. 6. Stage at which the larvæ are liberated from the egg-sac. A day or so older than the larva shown in Fig. 5. Dorsal view. Actual length approx. 256 μ (see page 571).

FIG. 7. Larva with four chætigerous segments, two nototrochs, and two pairs of dorsal black pigment spots. A few days after liberation from egg-sac. Dorsal view. Actual length approx. 300 μ (see page 573).



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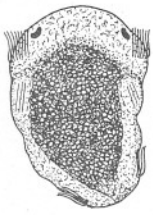

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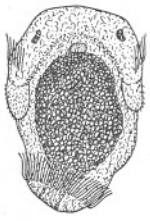

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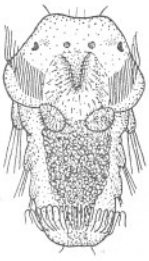

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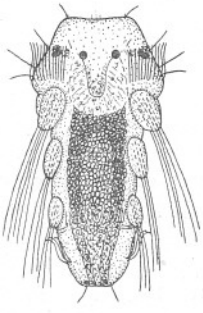

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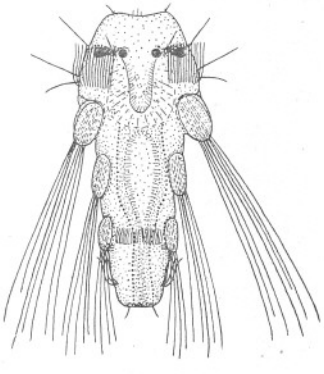

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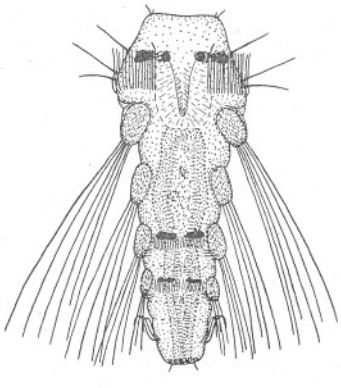

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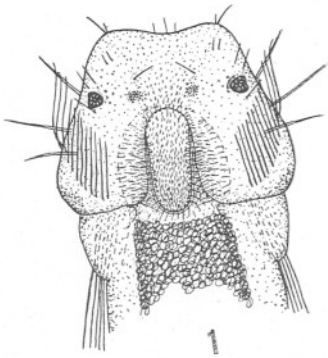
PLATE II.

Larvæ of *Polydora ciliata* Johnston. All drawings from life.

FIG. 1. Ventral view of head of same larva as shown in Plate I, Fig. 5. Developing vestibule open. × 312 (see pages 571 and 572).

FIG. 2. Larva about 10 days after liberation from egg-sac. Dorsal view. × 156. Actual length approx. 394 μ (see page 573).

FIG. 3. Larva about a week later. Dorsal view. × 156. Actual length approx. 605 μ (see page 573).



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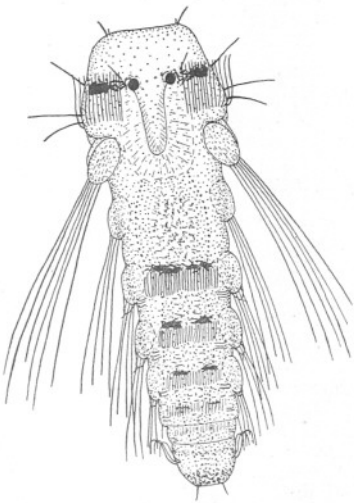

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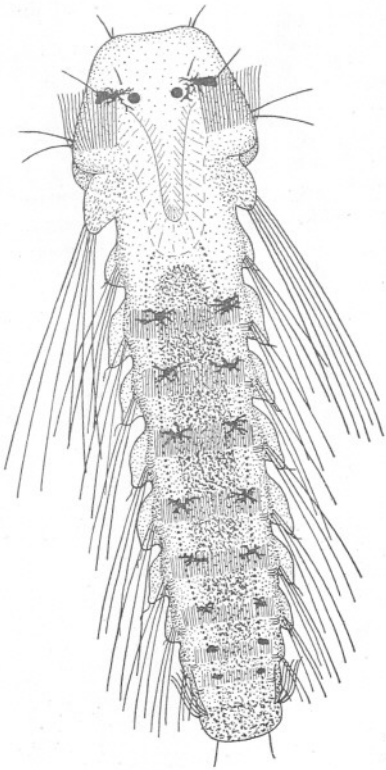

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PLATE III.

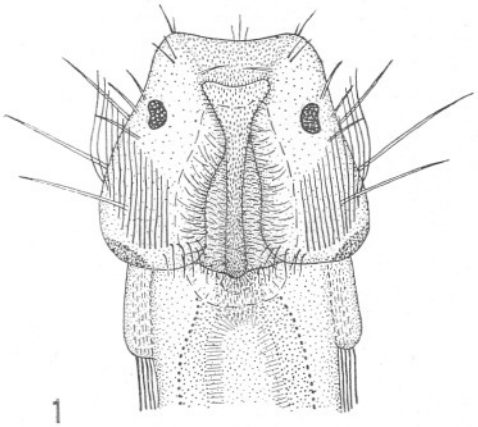
Larvæ of *Polydora ciliata* Johnston. All drawings from life.

FIG. 1. Ventral view of the head of a larva shortly after liberation from the egg-sac. Vestibule partially open. The position of the lateral eyes is indicated. × 312 (see page 572).

FIG. 2. Ventral view of the head of a larva at the same stage showing the vestibule wide open. × 312 (see page 572).

FIG. 3. Ventral view of the head of the larva drawn in dorsal and lateral views on Plate IV. Vestibule wide open. × 156 (see page 574).

FIG. 4. Lateral view of a larva about one month after liberation from the egg-sac. × 156. Actual length approx. 770 μ (see page 574).



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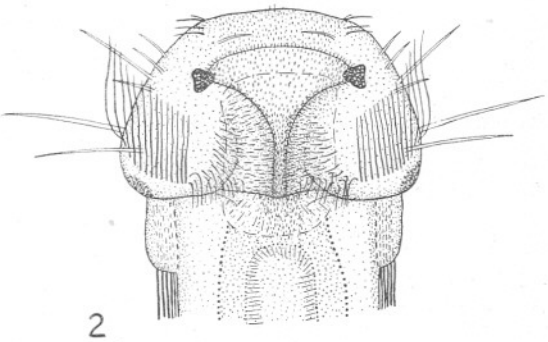

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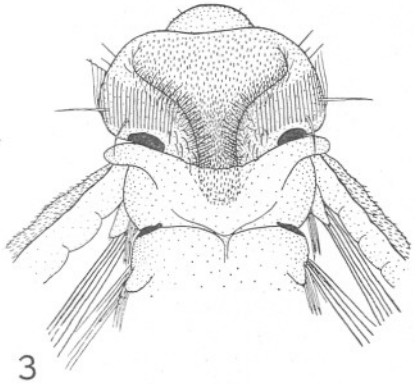

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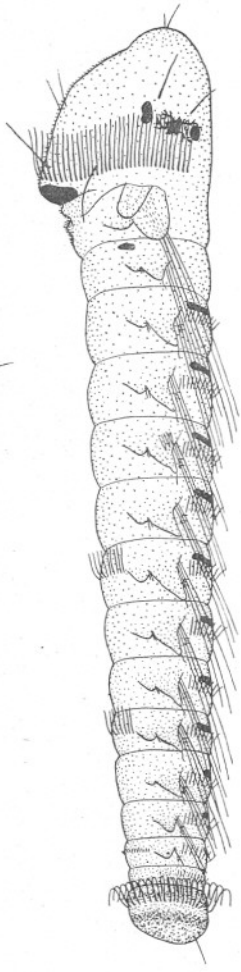

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PLATE IV.

Dorsal and lateral views of a larva of *Polydora ciliata* Johnston about six weeks after liberation from the egg-sac. From life × 104. [Actual length approx. 1340 μ (see pages 574–576).

PLATE IV.

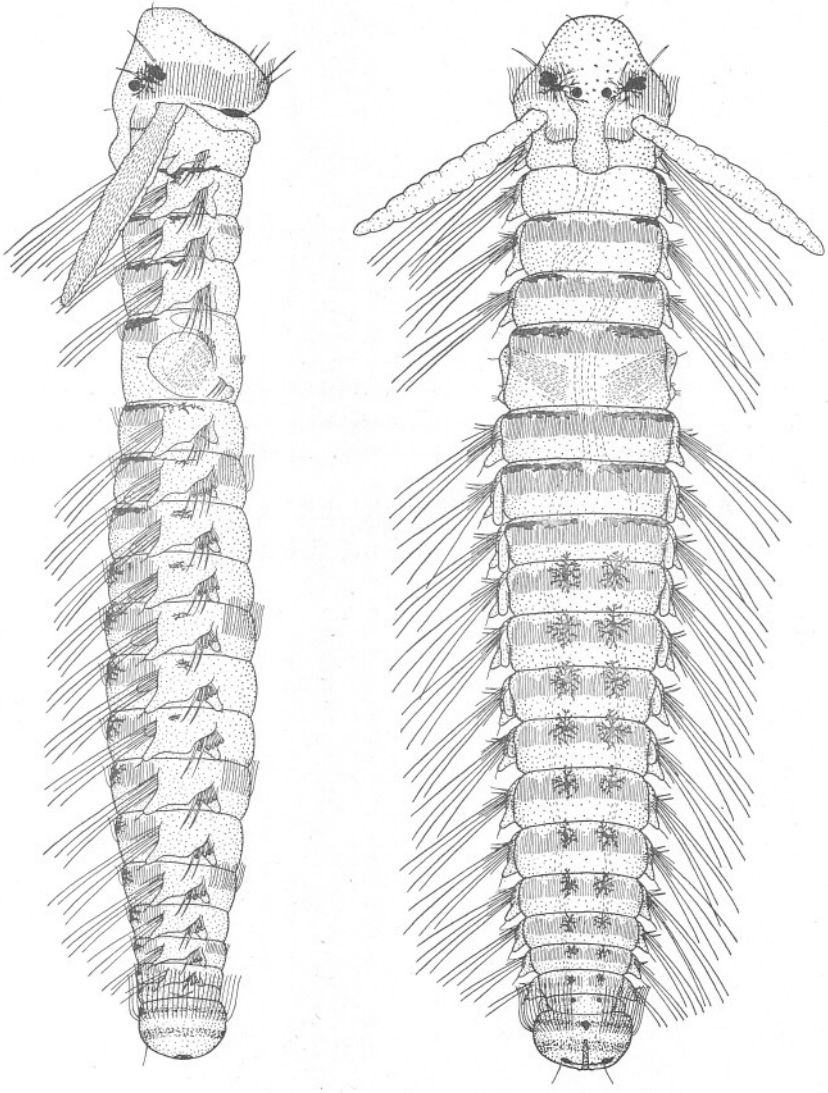


PLATE V.

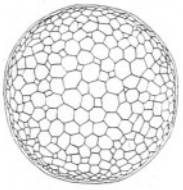
Larvæ of *Polydora hoplura* Claparède. All drawings from life × 156.

FIG. 1. Yolk mass from egg-sac. Actual diameter approx. 140 μ (see page 578).

FIG. 2. Early larva from egg-sac. Ventral view. Actual length approx. 305 μ (see page 580).

FIG. 3. Larva with three chætigerous segments from egg-sac. Dorsal view. Actual length approx. 355 μ (see page 580).

FIG. 4. Later larva from egg-sac. Dorsal view. Actual length approx. 500 μ (see page 581).



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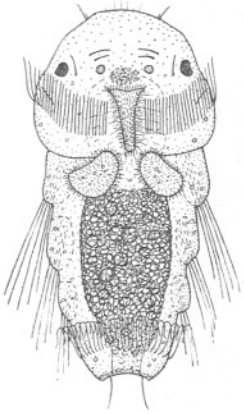

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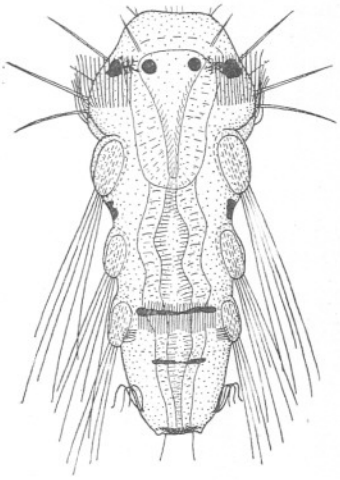

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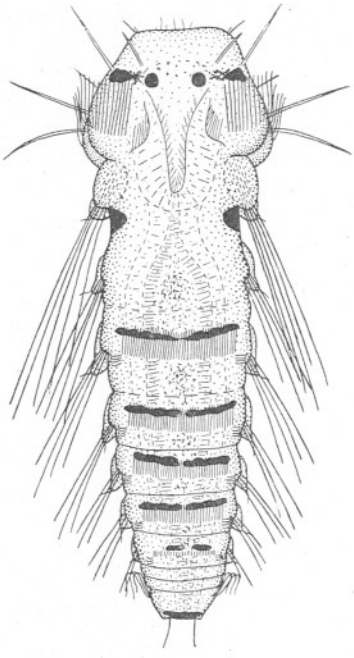

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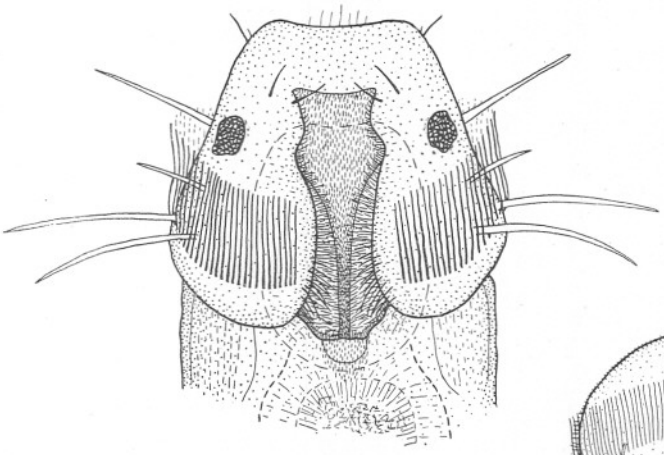
PLATE VI.

Larvæ of *Polydora hoplura* Claparède. All drawings from life.

FIG. 1. Ventral view of head of a larva a little older than that shown in Plate V, Fig. 3. Vestibule partially open. The position of the lateral eyes is indicated. × 312 (see page 581).

FIG. 2. Ventral view of the head of the larva drawn in dorsal view on Plate VII. Vestibule wide open. × 156 (see page 582).

FIG. 3. Lateral view of a fairly late larva from egg-sac. × 156. Actual length approx. 720 μ (see page 581).



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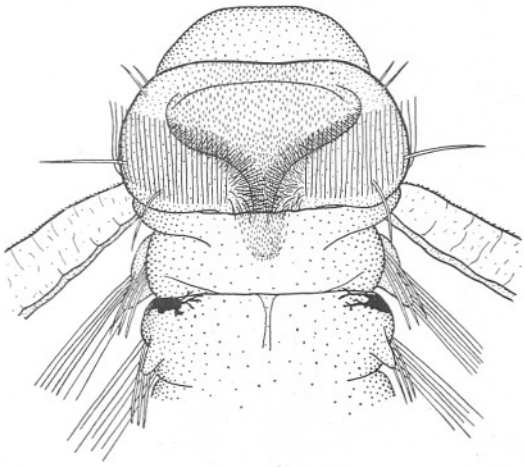

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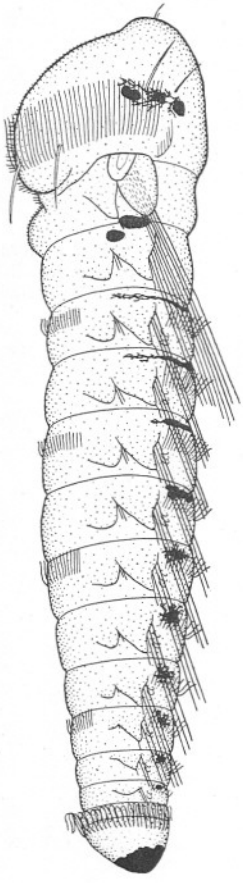

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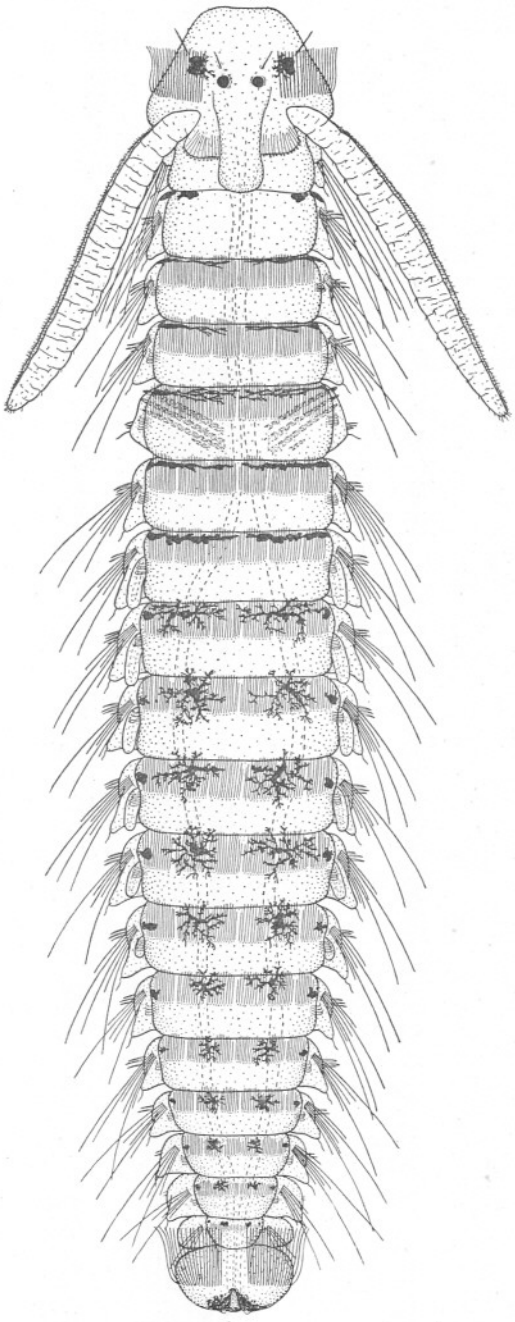
PLATE VII.

Dorsal view of a larva of *Polydora hoplura* Claparède, which, with others, was found free in the burrow of the parent. From life. ×104. Actual length approx. 1670 μ (see page 581).

PLATE VII.



On Lunar Periodicity in Reproduction of *Pecten opercularis* near Plymouth in 1927-28.

By

C. Amirthalingam, B.Sc.

With 5 Figures in the Text.

CONTENTS.

Introduction.

The belief that the moon has an effect on the life of animals and plants is found in the literature of ancient Greece and Rome, and is held to-day among the fishing population in the East as well as in the West. In Plymouth there is a general belief that queens (*Pecten opercularis*) get "full" and "empty" with the waxing and waning of the moon. To test the truth of this, systematic examinations of the gonads of *P. opercularis* were made, and the results are embodied in the following pages.

Material and Methods.

The material was obtained from the trawling grounds within an area of 25–30 miles radius of Plymouth, especially from the neighbourhood of Eddystone and of Mewstone, brought in either by the *Salpa* of the Marine Biological Association or by the commercial trawlers which came into port in the mornings. In both cases, the samples were kept under circulation and examined on the same day or the day following.

The right valve shell with the right mantle and the right gills was cut off and the following observations were made :—

(*a*) the size of the shell,
(*b*) the condition of the ovary and of the testis,
(*c*) the colour of the ovary and of the testis,
(*d*) the relative size of the ovary and of the testis,
(*e*) the condition of the eggs,
and (*f*) the presence or absence of ripe sperms.

The animals were then preserved in 5% formalin. The ovary of the preserved specimens was cut transversely at the point of the junction with the testis, and the major and the minor axes of the exposed face were measured. For sectioning, the specimens were fixed in Bouin's fluid and stained with iron hæmotoxylin and eosin by the usual method.

The Size of the Specimens.

From Table I (p. 607) it is clear that a large proportion of the individuals from the Eddystone and the trawling grounds was between 40 and 60 mm. in shell-length, whereas those from the Mewstone grounds were mainly of a smaller size ranging between 30–40 mm.

Although no definite information is available on the rate of growth of *Pecten opercularis*, yet by examining the shells it is possible to state the probable age of the animal by the vaguely-defined annular rings. The first year's growth can be seen clearly, especially in the right valve shell of small specimens, by the occurrence of a smooth surface in the furrows between the rays, and varies between 20–25 mm. in length. In some shells,

NOTES ON TABLE I.

The samples marked " Eddystone gds." were trawled from a region 10 miles S. × S.E. of Eddystone Lighthouse, and those marked " Mewstone gds." 4 miles S. of Mewstone ; both lots were brought in by s.s. *Salpa* of the M.B.A. The samples marked " Trawling gds." were obtained from the commercial trawlers working within an area of 25–30 miles of Plymouth. The same remarks apply to Table II.

[I am indebted to Capt. V. Lord of s.s. *Salpa* for the above information.]

The size of the specimens recorded was determined either by cardboard rings of 30, 40, 50, and 60 mm. diameter, or by direct measurement of the maximum length of the shell parallel to the hinge and the maximum height at right-angles to the hinge.

TABLE I.

THE RESULTS OF THE EXAMINATION OF THE SAMPLES FOR THE SIZE OF INDIVIDUALS FROM FISHING GROUNDS WITHIN A RADIUS OF 25–30 MILES OF PLYMOUTH.

Date. 1927	Locality.	Total No.	Shell 30–40 mm. Ring No. 1 No.	%	Shell 40–50 mm. Ring No. 2 No.	%	Shell 50–60 mm. Ring No. 3 No.	%	Shell 60–70 mm. Ring No. 4 No.	%
9th March	Trawling gds.	180	–	–	66	36·6	100	55·6	14	7·8
13th ,,	,,	170	2	1·1	78	43·8	94	52·9	4	2·2
18th ,,	,,	149	–	–	32	21·5	99	66·5	18	12·0
23rd ,,	,,	74	2	2·7	24	32·4	39	52·6	9	12·3
29th ,,	,,	100	–	–	5	5·0	82	82·0	13	13·0
7th April	,,	76	–	–	40	52·6	36	47·4	–	–
15th ,,	,,	104	–	–	29	27·9	72	69·2	3	2·9
22nd ,,	,,	109	–	–	2	1·8	105	96·3	2	1·8
6th May	Eddystone gds.	100	–	–	70	70·0	29	29·0	1	1·0
13th ,,	,,	100	–	–	72	72·0	27	27·0	1	1·0
18th ,,	,,	100	1	1·0	64	64·0	33	33·0	2	2·0
26th ,,	,,	125	2	1·6	86	68·8	34	27·2	3	2·4
1st June	Trawling gds.	100	–	–	41	41·0	56	56·0	3	3·0
8th ,,	Eddystone gds.	100	–	–	62	62·0	38	38·0	–	–
15th ,,	Trawling gds.	100	–	–	21	21·0	67	67·0	12	12·0
17th ,,	,,	100	1	1·0	44	44·0	53	53·0	2	2·0
21st ,,	,,	125	–	–	66	52·8	58	46·4	1	0·8
1st July	Mewstone gds.	100	75	75·0	22	22·0	3	3·0	–	–
6th ,,	,,	95	70	73·8	22	23·1	3	3·1	–	–
13th ,,	Eddystone gds.	100	–	–	44	44·0	52	52·0	4	4·0
21st ,,	Trawling gds.	144	1	0·7	28	19·4	115	79·9	–	–
26th ,,	,,	119	–	–	6	5·5	109	91·2	4	3·3
29th ,,	Mewstone gds.	86	57	66·3	29	33·7	–	–	–	–
5th August	,,	135	52	38·5	77	57·1	6	4·4	–	–
11th ,,	,,	100	65	65·0	33	33·0	2	2·0	–	–
16th ,,	,,	62	33	53·2	27	43·6	2	3·2	–	–
17th ,,	Eddystone gds.	100	1	1·0	32	32·0	66	66·0	1	1·0
23rd ,,	,,	35	–	–	30	85·8	4	1·14	1	2·8
30th ,,	Mewstone gds.	164	92	56·2	67	40·8	5	3·0	–	
9th September	Trawling gds.	165	–	–	34	20·7	130	78·7	1	0·6
14th ,,	Eddystone gds.	180	4	2·2	31	17·4	142	78·8	3	1·6
19th ,,	Mewstone gds.	37	23	62·2	13	35·1	1	2·7	–	–
27th ,,	Trawling gds.	170	2	1·2	56	32·8	112	66·0	–	–
4th October	,,	212	7	3·3	72	33·7	130	61·6	3	1·4
9th ,,	,,	200	4	2·0	51	25·5	142	71·0	3	1·5
11th ,,	,,	200	10	5·0	69	34·5	119	59·5	2	1·0
19th ,,	,,	200	7	3·5	80	40·0	112	56·0	1	0·5
24th ,,	,,	100	1	1·0	24	24·0	69	69·0	6	6·0
1st November	,,	120	–	–	32	26·6	88	73·4	–	–
8th ,,	,,	100	3	3·0	18	18·0	74	74·0	5	5·0
15th ,,	,,	130	–	–	20	15·4	103	79·2	7	5·4
22nd ,,	,,	100	–	–	15	15·0	80	80·0	5	5·0
2nd December	,,	100	–	–	25	25·0	68	68·0	7	7·0
9th ,,	,,	100	–	–	6	6·0	91	91·0	3	3·0
13th ,,	,,	100	–	–	12	12·0	81	81·0	7	7·0
22nd ,,	,,	100	–	–	14	14·0	80	80·0	6	6·0
30th ,, 1928.	Eddystone gds.	100	–	–	8	8·0	88	88·0	4	4·0
4th January	Trawling gds.	100	–	–	8	8·0	83	83·0	9	9·0
10th ,,	,,	100	–	–	1	1·0	88	88·0	11	11·0
18th ,,	,,	100	–	–	2	2·0	87	87·0	11	11·0
31st ,,	,,	100	3	3·0	16	16·0	80	80·0	1	1·0
3rd February	,,	100	1	1·0	8	8·0	88	88·0	3	3·0
7th ,,	,,	100	1	1·0	15	15·0	82	82·0	2	2·0
15th ,,	,,	95	–	–	11	11·5	81	85·3	3	3·2

either by the variation in the colour or by the thickness of the shell, two other rings can be seen. One occurring at a distance of about 40 mm. and the other at about 60 mm. from the umbo. It is from these observations the following suggestion is made that, in the second year, an additional shell-length of 20–25 mm. is secreted with the furrows now becoming roughened and continuing to be so with the further growth of the shell; in the third year, the shell reaching a length of 40–60 mm.; in the fourth year, more than 60 mm. By this method of reckoning it can be stated that the specimens from the Channel were 3–4 years old and those from the Mewstone 2–3 years old. Yet the periodicity of spawning (p. 614) is not affected by the age of the individuals.

Remarks on the Gonad.

The hermaphrodite organ is a tongue-like process situated ventrally and posteriorly to the rudimentary foot (Dakin, **8**, Fig. 1, Pl. 2). It forms a prominent mass stretching to the middle surface of the adductor muscle posteriorly, and to the under surface of the digestive gland close behind the mouth anteriorly. Slightly constricted behind the foot, it gradually increases in size until it attains its greatest breadth nearly opposite the posterior end of the organ of Bojanus, where the seminiferous part abuts against the ovigerous portion. From this point it tapers to a blunted end. The posterior part is the ovary and the anterior region the testis.

The Variation in the Condition of the Ovary and of the Testis.

(*a*) The spawned condition of the gonad="*spent.*"

After the discharge of the generative products or before the products have developed, both the ovary and the testis are in a collapsed condition, i.e. the lateral walls of the organ lie close to each other and the organ does not extend posteriorly beyond the point of attachment to the adductor muscle. At this stage, a transverse section at the junction of the ovary and of the testis reveals an ellipsoid shape whose minor axis is about half or less than half that of the major axis. This condition was observed in most of the individuals collected in September, October, and November, and in the spawned ones during the breeding season—January to June inclusive. This stage in the history of the development of the gonad is indicated in the records (p. 633) as "spent."

(*b*) The developing condition of the gonad="*Half-full.*"

As development begins, the walls of the organ become stretched in all directions; the anterior end being fixed, the tendency of the organ is to elongate posteriorly beyond the attached point, passing from a collapsed

form to a knee-shaped form, and to expand laterally into the mantle cavity. In transverse section the gonad has an elliptical shape whose minor and major axes tend to become equal ; an intermediate stage when the minor axis is not more than two-thirds that of the major axis is noted as " Half-full " in the records (p. 633). This condition was observed in most of the specimens obtained between the third quarter and the first quarter of the moon during the breeding season and in July, August and December.

(*c*) The ripening or the ripe condition of the gonad=" *Full.*"

In the mature condition, the reproductive organ is at its largest and is firm in consistency as if the contents were pressing against the walls laterally, so that a transverse section of the organ now reveals a phase which is more circular than elliptical. This stage when the minor axis is more than two-thirds that of the major axis is indicated as " Full " in the records (p. 633). The maximum number of individuals with ripening or ripe gonad was found in samples examined between the first quarter and the full moon during the breeding season.

The Variation in the Colour of the Ovary and of the Testis.

In the collapsed or undeveloped condition, the ovary exhibits a light brown colour (Klincksieck et Valette, **31**, Shade No. 117, e.g. Specimen No. 67, p. 633 of this paper). When the tissues become active the colour changes with the increase in size, first assuming a reddish tinge (*ibid.*, Shade No. 91, e.g. Specimen No. 35, p. 633) and then passing to bright scarlet (*ibid.*, Shade No. 81, e.g. Specimen No. 46, p. 633) or rich vermilion (*ibid.*, Shade No. 76, e.g. Specimen No. 25, p. 633), through a pale red phase (*ibid.*, Shade No. 86, e.g. Specimen No. 2, p. 633). A few individuals, however, were observed to possess a white ovary in developing and in mature conditions.

The spent or resting testis is transparent and colourless (e.g. Specimen No. 88, p. 634). As spermatogenesis starts, the organ becomes opaque and finally attains an opalescent (*ibid.*, Shade No. 0171, e.g. Specimen No. 1, p. 633) or a creamy colour (e.g. Specimen No. 15, p. 633). The creamy colour and the " full " condition of the testis is a sure indication of the mature products.

An additional feature of interest in connection with the pigmentation of the gonad has been observed in some individuals of *P. opercularis* from Mewstone grounds. In a small percentage of thin-shelled individuals, it was noticed towards the beginning of July that black pigment had been laid down on the ventral margin of the gonad at the junction of the ovary and of the testis. It seems probable that the pigment may have been

produced as a reaction to the penetration of the thin shell by actinic rays. A similar phenomenon had been observed in *Ostrea edulis* (**48**, p. 951) in which black pigment is laid down on the left side in the epithelium covering the visceral mass and also abundantly on the edges of the mantle ; in *Cucumaria saxicola*, whose skin becomes generally dusty black after prolonged exposure to light ; and in *C. normani*, in which the tentacles become black when exposed to light.

The Relative Size of the Ovary and of the Testis.

From the records (p. 633) it is clear that the absolute length of the full gonad is related directly to the size of the shell, i.e. the bigger the shell the longer the gonad, and vice versa.

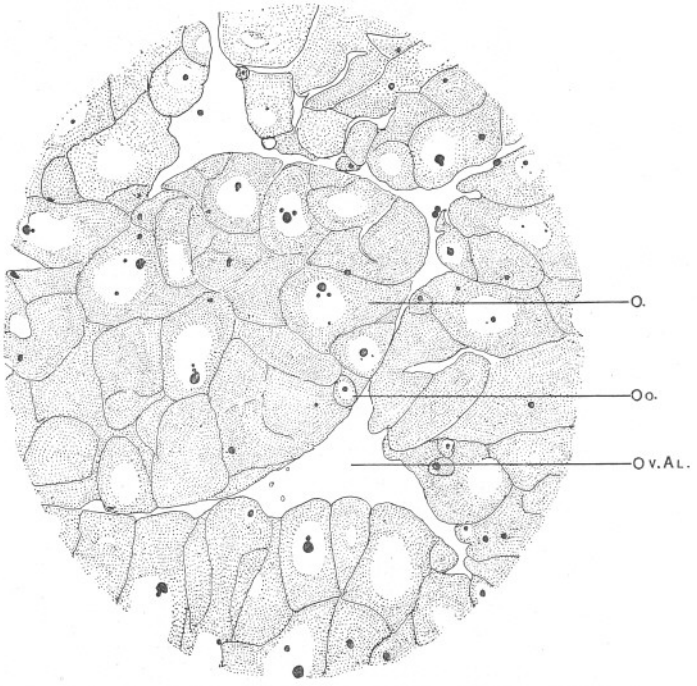


Fig. 1. A drawing (made with 2 eye-piece and $\frac{1}{6}$ objective. Leitz.) of a section through a ripe ovary of *Pecten opercularis*.

O.=nearly ripe or ripe egg.
Oo.=young oocytes.
Ov. Al.=Ovigerous alveolus.

After the discharge of the generative products, the ovary is very small, occupying about a fourth of the reproductive organ, whereas the testis forms the main mass of the organ. With the activity of the tissues the

ovary extends in length and may reach a size of about half of the gonad, but generally it occupies about a third of the mass and the testis two-thirds. The ovigerous tissues dovetail into the spermatiferous tissues so that the surfaces of contact are irregular in outline but quite sharp on account of their respective colours.

The Condition of the Eggs.

On teasing a mature ovary, the ripe ova (Fig. 1, p. 610) are liberated, which possess a spherical cell-wall with brown deutoplasm uniformly distributed round the periphery. These eggs are usually over 80μ in diameter, and the nucleus is hardly visible through the cell-wall. In some of these ripe eggs the nucleus can be seen, and it occupies about a third of the cell. When these cells are liberated they do not adhere to one another, but separate quickly into individual ova. The largest number of individuals with this class of eggs was found among the samples examined between the first quarter and the full moon during the breeding season and to a smaller degree in September and October.

When the ripe ova are discharged, a few eggs, however, remain within the ovary, and these very soon start cytolizing, with the result that there is no clear cell membrane to the eggs (50–70μ). On teasing such an ovary the smear shows a mass of naked nuclei in a brownish yolky matrix. This nutritive material is probably resorbed in the developing oocytes (Fig. 2, p. 612) in the follicles. The smallest oocyte observed was 30μ.

The young oocytes (30–50μ) are clear with a thin layer of light green-coloured yolk round the periphery, surrounded by an irregular cell-wall drawn out into spine-like processes. In these the nucleus, which is clear and vesicular, occupies nearly the whole of the cell and the nucleolus too is distinct. These young oocytes do not change their shape when artificially liberated. The greatest number of cases with this type of eggs was met with during the non-breeding season (July to January).

As development proceeds, the young oocytes pass through to an irregular polyhedral stage, in which the cells are between 50–80μ with a large quantity of nutritive material of a brown or brownish green colour, but not so much as to obscure the clear nucleus which is about half the size of the cell. If, at this stage, they be liberated artificially, a large number of the cells will adhere to one another for some time, though a few nearly ripe ones will separate. This stage in the development of eggs is, by far, the most frequent one found in the samples examined during the breeding season. As the oocytes become mature, the cell increases in size and the nucleus becomes obscured by the accumulation of yolk.

The Presence or Absence of Ripe Sperms.

When a full creamy testis is punctured, a viscous fluid is extruded which shows a mass of non-active sperms in a gelatinous matrix. On adding sea-water, the non-active sperms become active and swim in the field. After such ripe products are discharged, the testis becomes collapsed and transparent; in this state, if the testis be teased, it reveals a few

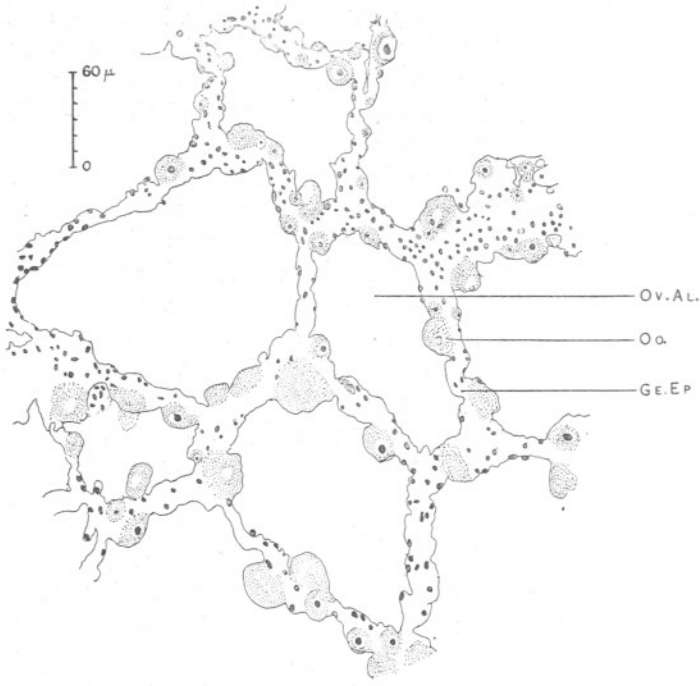


Fig. 2. A section through a spent ovary of *Pecten opercularis*.
Ge. Ep. = Germinal Epithelium.
Oo. = Young oocytes.
Ov. Al. = Ovigerous alveolus.

active sperms swimming in the liquid medium. This activity of the unspent sperms is due to the sea-water entering the spent testis. This is supported by the occurrence of a few turgid, transparent testes, which, on puncturing, collapse completely with the emission of a clear liquid.

As the tissues become active, the surface of the testis becomes honeycombed in appearance; this character is soon obliterated by the rapid development of the spermatocytes to form a white mass. At this stage there are no ripe sperms but spermatocytes only. With further develop-

ment the white mass attains an opalescent and often a creamy appearance, and the mature sperms are produced, which possess a small ovate head somewhat drawn out at the apex. (Fullarton, **14**, Fig. 2, Pl. 5.)

Criteria of Ripeness and Unripeness in Males and Females Defined.

The above-mentioned observations were made in order to fix a standard or standards by which an individual may be considered as ripe or as unripe. In the case of males, it is found that the collapsed and transparent or opaque testis contains few sperms and a large quantity of spermatocytes. This clearly indicates that such a testis is unripe. A full opalescent or creamy testis is considered as ripe as it contains sperms in abundance.

In the case of females, the distinction between the ripe and unripe is not clearly defined. The unripe individuals possess a " spent " or " half-full " ovary, light brown or red in colour with eggs not bigger than 80μ. The ripe ovary may be distinguished by the fact that the eggs are bigger than 80μ and, further, the eggs do not adhere to one another when artificially liberated.

For the present paper an individual was recorded as ripe (1) in the case of females when (*a*) the ovary was " full " *and* the eggs were over 80μ, a size at which the eggs would segment on artificial fertilisation, e.g. No. 1, p. 633 ; (*b*) when the ovary was " half-full " *and* the eggs were over 90μ, e.g. No. 3, p. 633 ; (2) in the case of males when (*a*) the testis was " full " *and* creamy, e.g. No. 15, p. 633 ; (*b*) the testis *and* the ovary were " full," e.g. No. 4, p. 633.

These were the criteria used. To test the validity of these properties as tests of ripeness, artificial fertilisations were made from samples of May 18th and 26th and June 17th. From each sample six different individuals were used as females with eggs varying from 80μ to 100μ and six others as males with opalescent or creamy testis. In all cases there were about 90–95% of segmenting eggs.

The products of the generative organs in the same individual do not always ripen at quite the same time, though the interval that separates the ripening of the eggs and the sperms is usually not more than a few days. When the ova are ready to be shed, the spermatozoa have either been shed or are not quite ripe. Some gonads—about 10% during the full-moon time—have been found with ova quite ripe and spermatozoa not ripe, while the others had ripe sperms and immature eggs. During the examination of all the samples, no individual was caught in the act of spawning.

The Periodicity in the Occurrence of Ripe Generative Products.

The numerical results of the examination of the gonad are given in Table II, below, and Fig. 3, p. 616, and the detailed records of six samples from 9th March to 7th April on page 633. The dates on which the samples were obtained, and also the locality and the total number of specimens in each lot, are noted in the table. As already pointed out in Table I, p. 607, the average size of the queens was about 50×50 mm. in all samples except those of 1st, 6th, and 29th July, 5th, 11th, 16th, and 30th August, and 19th September, in which the average was about 35×35 mm. On

TABLE II.

The Results of the Examination of the Samples for Ripe Individuals from the Fishing Grounds within a Radius of 25–30 miles of Plymouth.

Date. 1927.	Locality.	No. Total	Ripe females No.	Ripe females %	Ripe males No.	Ripe males %
18th February	Eddystone gds.	257	51	19·8	–	–
28th ,,	,,	151	37	24·5	–	–
9th March	Trawling gds.	180	84	46·6	95	52·8
13th ,,	,,	178	83	46·6	102	57·2
18th ,,	,,	149	13	8·7	31	20·8
23rd ,,	,,	74	4	5·3	11	14·8
29th ,,	,,	100	25	25·0	17	17·0
7th April	,,	76	27	35·5	25	32·8
15th ,,	,,	104	31	29·7	42	40·4
22nd ,,	,,	109	28	25·6	32	29·4
6th May	Eddystone gds.	100	28	28·0	21	21·0
13th ,,	,,	100	40	40·0	37	37·0
18th ,,	,,	100	18	18·0	16	16·0
26th ,,	,,	125	38	26·1	30	24·0
1st June	Trawling gds.	100	27	27·0	26	26·0
8th ,,	Eddystone gds.	100	37	37·0	23	23·0
15th ,,	Trawling gds.	100	58	58·0	44	44·0
17th ,,	,,	100	50	50·0	41	41·0
21st ,,	,,	125	1	0·8	1	0·8
1st July	Mewstone gds.	100	6	6·0	5	5·0
6th ,,	,,	95	7	7·3	4	4·2
13th ,,	Eddystone gds.	100	2	2·0	2	2·0
21st ,,	Trawling gds.	144	4	2·7	4	2·7
26th ,,	,,	119	18	15·1	19	15·9
29th ,,	Mewstone gds.	86	0	0	0	0
5th August	,,	135	2	1·4	0	0
11th ,,	,,	100	0	0	0	0
16th ,,	,,	62	1	1·6	1	1·6
17th ,,	Eddystone gds.	160	0	0	0	0
23rd ,,	,,	35	0	0	0	0
30th ,,	Mewstone gds.	164	0	0	1	0·6
9th September	Trawling gds.	165	5	3·0	5	3·0
14th ,,	Eddystone gds.	180	0	0	1	0·5
19th ,,	Mewstone gds.	37	0	0	0	0
20th ,,	Trawling gds.	200	0	0	0	0
27th ,,	,,	170	0	0	0	0

TABLE II—*continued.*

Date.	Locality.	No. Total	Ripe females No.	Ripe females %	Ripe males No.	Ripe males %
1927.						
4th October	Trawling gds.	212	6	2·8	6	2·8
9th ,,	,,	200	36	18·0	36	18·0
11th ,,	,,	200	6	3·0	12	6·0
19th ,,	,,	200	5	2·5	7	3·5
24th ,,	,,	100	11	11·0	17	17·0
1st November	,,	120	8	6·5	8	6·5
8th ,,	,,	100	0	0	1	1·0
15th ,,	,,	130	0	0	0	0
22nd ,,	,,	100	3	3·0	4	4·0
2nd December	,,	100	1	1·0	3	3·0
9th ,,	,,	100	1	1·0	3	3·0
13th ,,	,,	100	3	3·0	5	5·0
22nd ,,	,,	100	9	9·0	10	10·0
30th ,,	,,	100	13	13·0	13	13·0
1928.						
4th January	Trawling gds.	100	18	18·0	24	24·0
10th ,,	,,	100	6	6·0	6	6·0
18th ,,	,,	100	4	4·0	12	12·0
31st ,,	,,	100	17	17·0	21	21·0
3rd February	,,	100	45	45·0	48	48·0
7th ,,	,,	100	13	13·0	32	32·0
15th ,,	,,	95	16	16·8	18	18·9
23rd ,,	,,	100	27	27·0	38	38·0
28th ,,	,,	100	61	61·0	63	63·0
6th March	,,	100	28	28·0	29	29·0
13th ,,	,,	100	13	13·0	10	10·0

each occasion a fair number of individuals was examined ; on 9th April, 23rd August, and 19th September, only a small number could be obtained. Owing to bad weather an absence in sampling during the period from 8th to 16th April occurs, when no specimens were examined between the two dates. The results represent the ripe individuals in percentages of totals examined.

The curve (Fig. 3) can be conveniently divided into two sections : (*a*) February to June, 1927, and January to March, 1928 ; (*b*) June to December, 1927. The first section is for the breeding season and the second for the non-breeding season.

In the first half of the figure, the curves show :—

(1) a close correspondence between the male curve and the female curve, i.e. they rise and fall together.

(2) The four apices of the curve for March, April, May, and June, 1927, and the three for January, February, and March, 1928, occur during the full-moon time.

(3) The minima do not touch the zero ordinate till the breeding season approaches the end.

(4) The ripening of the sexual products seems to be correlated with the oncoming of the full moon.

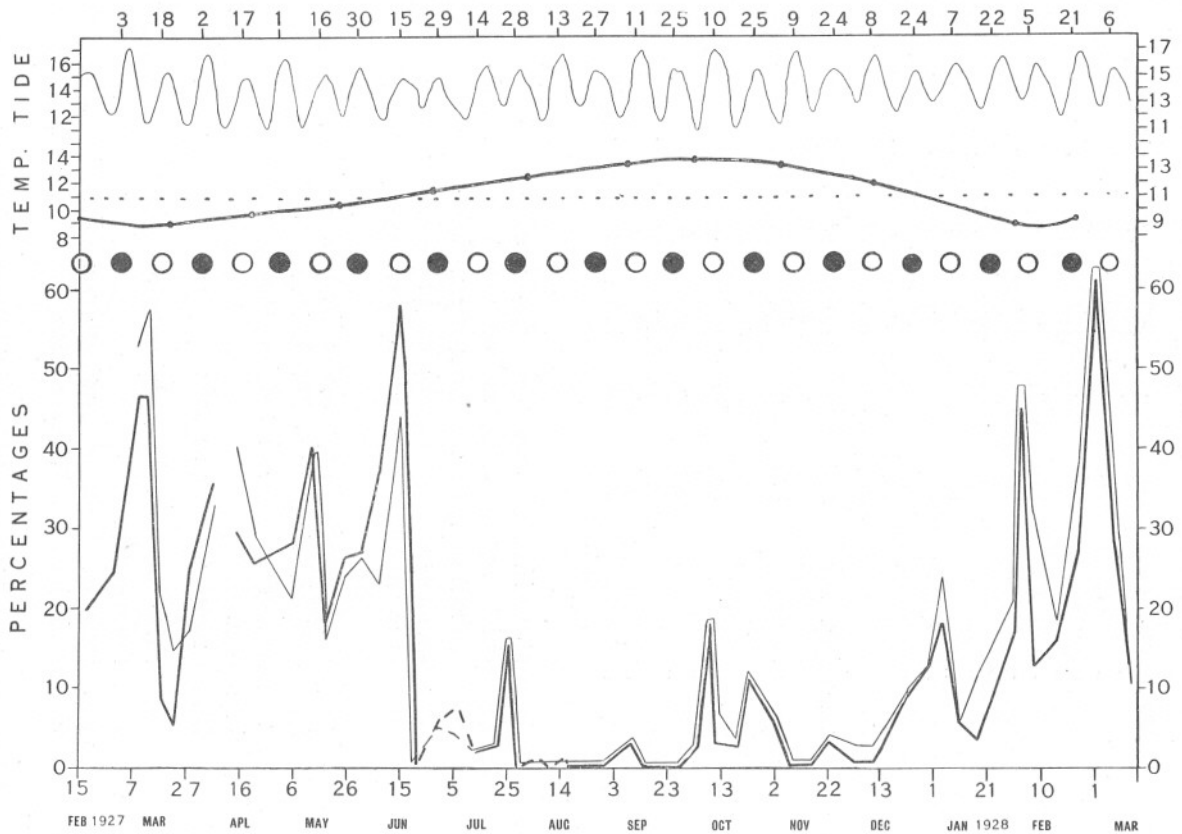


FIG. 3. Graph showing the percentages of nearly ripe or ripe specimens of *Pecten opercularis* in relation to the moon's phase, indicating a regular correlation between lunar periodicity and the breeding phenomenon. The samples of queens were obtained from the trawling grounds within a radius of 25–30 miles of Plymouth.

The thick continuous line denotes the frequency of ripe females ; the thin continuous line, that of the ripe males. The thick and the thin discontinuous lines represent the samples from Mewstone. Full moons are shown by circles and the new moons by the filled-in circles here and in Fig. 4.

At the top of the figure the tide—in feet—is shown by the thin line, and the curve for monthly temperature—in degrees Centigrade—at the bottom, at Station E1 (50° 02′ N. ; 4° 22′ W. ; depth 70 metres), is denoted by the thick line. [The temperatures at Station E1 were recorded by Mr. H. W. Harvey, to whom the writer is indebted for the data.]

(5) The temperature ranges between 8·9° C. and 11° C.

(6) No correlation between the new moon spring tides and the spawning time is shown.

Between the third quarter and the new moon in February, March, April, May, and June, 1927, and January, February, 1928, about 70% of the queens were found to contain large oocytes and spermatocytes; about 10% were in a collapsed condition with few, unspawned, degenerating eggs in the ovary; and the rest were found with gonads full of eggs and sperms.

Between the new moon and the first quarter, during the breeding season, there were about 5% of "spent" individuals; about 50% with developing eggs and sperms approaching maturity; and the rest contained eggs and sperms ready to be shed.

Between the first quarter and the full moon of the spawning season, the maximum number of ripe individuals occur. In addition to this there is about 35% of individuals with developing oocytes and spermatocytes. These will not reach maturity at the lunar period in question, but are those that have already spawned earlier in the year. At this stage, too, there are about 5% of "spent" ones present.

Between the full moon and the third quarter, the minimum number of mature individuals occurs. The percentage of "spent" gonads has increased, but the main bulk of the individuals contain developing oocytes and spermatocytes.

The second half of the curve from June to December shows: (1) A correspondence between the male curve and the female curve. (2) The breeding season approaches its end after June spawning. (3) The apices of the curve for July and the latter part of October occur during the new moon time; there is no spawning in August, November, and December; and the apices for September and the early part of October correspond with the full moon time. (4) The temperature has risen above 11° C.

It is interesting to note that at all times during the breeding season there is a large percentage of individuals with developing ovary. Further, the samples examined in July and in the early part of August were developing normally as if spawning was to occur at the August full moon; however, after the August full moon—sample taken on 17th August—the ovary of the specimens was still in a turgid condition, thus suggesting that no spawning had taken place.

In Table III (p. 618) and Fig. 4 the numerical results and the graphical representation of individuals with developing ovary for May, June, July, and August, are expressed in percentages of totals. The curve for each of the four months falls with the full moon, and hence the repetition of the same phenomenon for each of the months would be expected; but in nature, the developing eggs in May and in June reach maturity and are

TABLE III.

THE RESULTS OF THE EXAMINATION OF SAMPLES FOR INDIVIDUALS WITH DEVELOPING OVARY IN MAY, JUNE, JULY, AND AUGUST, 1927.

Date. 1927.	Total No.	Individuals with developing ovary. No.	%
6th May	100	56	56·0
13th ,,	100	50	50·0
18th ,,	100	73	73·0
26th ,,	125	80	64·0
8th June	100	39	39·0
15th ,,	100	37	37·0
17th ,,	100	41	41·0
1st July	100	93	93·0
6th ,,	95	88	92·5
13th ,,	100	35	35·0
26th ,,	119	34	28·6
29th ,,	86	40	46·5
5th August	135	124	91·8
11th ,,	100	20	20·8
17th ,,	160	30	18·7
23rd ,,	35	2	5·7
30th ,,	164	0	0

spawned, whereas those of July and of August are not spawned—as shown previously in Fig. 3, p. 616—but degenerate after the full moon. Hence this behaviour of the eggs in July and in August signifies the possibility of a physiological rhythm in the animal.

THE GUT CONTENTS OF THE QUEENS.

For the development of the genital products, a large amount of material is necessary. The source from which such material can be obtained is either from the tissues of the animal—as in the case of salmon's ovaries which develop at the expense of muscles (**21**)—or from the food that is taken into the gut by feeding.

Since no chemical analysis of tissues from weekly samples of *P. opercularis* has been made, it is not possible to state definitely whether the tissues are a source of nutrition or not to the developing gonad. However, it may be mentioned that "spent" individuals gape in a shorter time than those with developing or ripe gonad when left out of water. This seems to suggest that a certain amount of nutritive material is obtained

by the developing gonad at the expense of adductor muscles, or that during spawning the animal swims vigorously.

To test whether the quantity of food present in the gut varied during a lunar month, weekly examinations of fifty individuals—of approximately the same size—were made for two months. The gut contents were extracted by an apparatus similar to the one used by Moore for

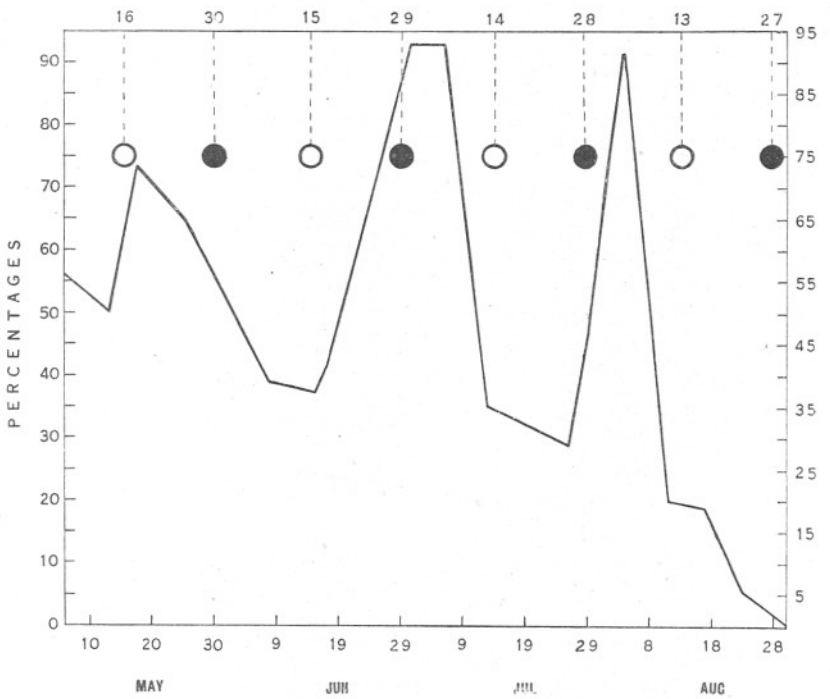


FIG. 4. Graph showing the percentages of individuals of *Pecten opercularis* with developing ovary for May, June, July, and August, 1927.

oysters (**42**, Fig. 6, p. 1305), preserved in 10% formalin and allowed to settle down. On roughly comparing the residue of all the samples, it was observed that there was no appreciable difference in quantity of the food. On microscopic examination of the residue it was noted that the same type of diatoms and flagellates occurred with a fair quantity of detritus, thus, suggesting that the nature of the food was the same.

THE EXPERIMENT ON QUEENS WITH MOONLIGHT.

Macht (**38**) and Garner and Allard (**17**) have shown that polarised light or the length of daylight has an influence on the growth of plants. Rowan (**52**, p. 183) has suggested that bird migration is due to an " environmental

controlling factor provided by the varying day lengths " among other factors. Mayer on Atlantic palolo (**41**, p. 110) states, " I had floating scows similar to those used in the previously described experiment, but they were provided with light-tight wooden covers, so that they could be closed at sunset every evening and exposed soon after sunrise every morning, thus preventing the moonlight from falling upon the rocks. Although I had at least 22 mature worms . . . but none of these worms showed any indication of swarming, and it appears that they could not respond owing to the absence of light." Treadwell (**60**) on the same annelid is of opinion that the presence of moonlight is not necessary for swarming reaction. Further, Grave, on the spawning habit of *Chætopleura apiculata* (**18**, p. 240),

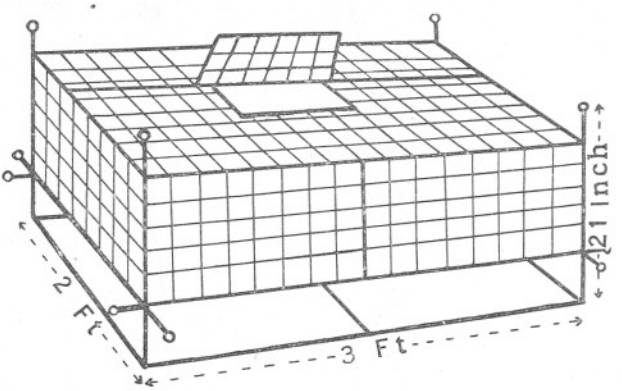


FIG. 5. A diagram showing the type of cage used for the experiment on queens with moonlight. The iron wire which forms the framework is represented by the thick line, and the galvanized wire by the thin line.

There are two bottoms to this cage, one true and the other false. The purpose of the false bottom is to prevent the cage from sinking into the sand and thus causing bad circulation in the cages that are covered by canvas.

states, " both sexes are apparently affected by the change of running to quiet water (tide changes), presumably also by the change in pressure between high and low tides (mechanical shock) *and most certainly by moonlight* " (italics not in the original). Since there are conflicting views in the literature on the effect of moonlight on spawning habits, the following experiment was carried out at Pier Cellars* in Cawsand Bay to find the influence of moonlight—if any—on the rhythmic reproduction of queens.

Specimens of *Pecten opercularis* were trawled from the Eddystone grounds on the 13th July, kept under circulation on board the s.s. *Salpa*

* Pier Cellars was selected for this experiment as the water is clean and the bottom sandy. Further, there is no dilution or change of pH due to rivers. At the lowest spring tides the cages were covered by about two fathoms of water and at the highest by 4 to 4½ fathoms.

and transferred into three cages—similar to those used by Dr. Orton in experiments on oysters (**45**)—at Pier Cellars. About 300 individuals were kept in each of the cages at the beginning of the experiment and 50 were taken out from each cage every week for examination.

The details of the cage are given in Fig. 5 (p. 620).

Cage A was left open to both sunlight and moonlight.

Cage B was left open to sunlight but not to moonlight.

This result was obtained by covering the cage with a tarred canvas hood every evening, and by removing it every morning just after sunrise.

Cage C was kept covered day and night by a canvas cover except when samples were required.

TABLE IV.

THE RESULTS OF THE EXAMINATION OF WEEKLY SAMPLES FROM EXPERIMENTAL CAGES SHOWING THE CONDITION OF THE EGGS.

		Young oocytes. 30–50 μ diameter			Developing eggs. 50–80 μ diameter			Degenerating eggs. 50–70 μ cytolizing		
	Date 1927	Cage A %	Cage B %	Cage C %	A %	B %	C %	A %	B %	C %
	13th July	71	71	71	37	37	37	2	2	2
○	14th ,,									
	20th ,,	68	98	96	20	2	2	12	none	2
☾	21st ,,									
	27th ,,	40	76	64	30	24	36	none	none	none
●	28th ,,									
	3rd August	20	60	24	80	40	76	none	none	none
☽	5th ,,									
	10th ,,	4	6	—	86	86	—	10	8	—
○	15th ,,									
	16th ,,	2	—	none	62	—	78	36	—	22

NOTE ON TABLE IV.

As there was heavy mortality in cages B and C due to predaceous crabs and gastropods, the stock was considerably reduced, and hence only five weekly samples were taken from each of these cages.

From Table IV it is evident that :—

(1) The development of the ovary under these conditions is independent of sunlight and moonlight.

(2) The individuals with degenerating eggs occur during the full moon time. It will be also noticed that the number of individuals with young oocytes throughout the period of experiment is predominant in Cage B. This result is probably due to the disturbance caused by the Cage B being

hauled up above the water every morning and evening to attend to the cover.

Although the experiment was carried out at the end of the breeding season—without the knowledge that June spawning was the last for *P. opercularis* in 1927—yet the experiment recalled the suggestion that in the animal there was a physiological rhythm which synchronised with the full phase of the moon.

Plants and Moonlight.

The belief in the beneficial effect of moonlight on plant-growth is world-wide and ancient. Musset (**43**) showed that flowering plants are positively phototropic to moonlight. Loftfield (**37**) states that the stomata open in moonlight. Wright (**64**) found that at new moon and at full moon practically none of the reflected light is polarised ; the greatest amount of polarisation is obtained about the end of the first and third quarters of the moon. Baly and Semmens (**3**) showed that plane-polarised light exercises a powerful acceleration on the hydrolysis of starch by diastase. Knaute's (**32**) figures show that the photosynthetic effect of moonlight with a ratio to that of sunlight is 2 : 9 although the intensity of the light of the sun is about 618,000 times greater than that of the full moon. Yoshii (**65**) found that the rate of growth is proportional to the length of daily exposure to light. Garner and Allard (**17**) state, " it is apparent that with the plants in which flowering is favoured by short days as well as with those in which the opposite is true, the general effect of the relatively short alternations of light and darkness on reproductive activity is much the same as that produced by long days or by continuous illumination." Kofoid (**33**) found that there was an algal maximum in the plankton in Illinois River during full moon time. Allen (**1**), too, found a similar increase in the number of green organisms in San Joaquin River as the light of moon increased. Among plants there are authentic cases of lunar rhythm in reproduction known. They are :—

(1) *Neoderma ;* Heligoland ; bilunar (neap tides). Kuckuck (**34**), 1901.
(2) *Dictyota dichotoma ;* Plymouth, Bangor ; bilunar. Williams (**63**), 1905.
(3) *Dictyota dichotoma ;* Beaufort, N. Carolina ; lunar. Hoyt (**25**), 1907.
(4) *Sargassum ;* Japan ; bilunar (neap tides). Tahara (**57**), 1909.
(5) *Dictyota dichotoma ;* Naples ; Bilunar (neap tides). Lewis (**35**), 1910.

It is interesting to note that *Dictyota dichotoma* at Bangor and Naples has two reproductive cycles per lunation, whereas the same species at

North Carolina has only one cycle per lunation. Yet the average tidal range at *Bangor is* 5·4 *metres*, at *Naples is* 0·3 *metres*, and at *Beaufort, North Carolina, is* 0·8 *metres*.

Lunar Periodicity already described in Animals.

Cœlenterata.

Obelia geniculata ; Millport ; full moon. Elmhirst (**10**), 1925.

Echinodermata.

Toxopneusthes variagatus ; Tortugas ; full moon. Tennett (**58**), 1910.

Centrechinus (*Diadema*) *setosus ;* Suez ; full moon. Fox (**12**), 1923.

Polychæta.

Leodice viridis * ; Samoa ; third quarter. Whitmee (**62**), 1875.

Leodice fucata ; Tortugas ; third quarter. Mayer (**39**), 1900.

Ceratocephale osawai ; Japan ; new and full moon. Izuka (**27**), 1903.

Convoluta roscoffensis ; Brittany ; new and full moon. Gamble and Keeble (**16**), 1903.

Lysidice œle ; Malay Archipelago ; second and third nights after full moon. Horst (**24**), 1905.

Amphritrite ornata ; Woods Hole ; within two days of new or full moon. Scott (**54**), 1909.

Nereis dumerilii ; Naples ; first and third quarter. Hempelman (**23**), 1911.

Odontosyllis enopla ; Flatt's Island ; third quarter. Galloway and Welch (**15**), 1911.

Nereis limbata ; Woods Hole ; between full moon and third quarter and third quarter and new moon. Lillie and Just (**36**), 1913.

Platynereis megalops ; Woods Hole ; between full moon and new moon. Just (**29**), 1914.

Eulalia punctifera ; Concarneau ; third quarter. Fage and Legendre (**11**), 1926.

Mollusca.

Chiton tuberculatus ; Bermuda ; full moon. Crozier (**7**), 1920.

Chætopleura apiculata ; Woods Hole ; between full moon and third quarter. Grave (**18**), 1922.

Ostrea edulis ; Falmouth ; full moon, 1925. Orton (**46**), 1926.

Cumingia tellinoides ; Woods Hole ; full moon. Grave (**19**), 1927.

* The Palolo worms have received several names. Tredwell's (**61**) identifications are followed in this paper.

PISCES.

Leuresthes tenuis ; California ; second, third, and fourth nights after full moon and after new moon. Thompsons (**59**), 1919, Clark (**5**), 1925.

MAMMALIA.

Homo sapiens. Arrhenius (**2**), 1898.

In the case of those animals with two reproductive cycles in each lunar month, the chief factor causing the rhythm is probably tidal as shown by Clark (**5**) in the case of *Leuresthes tenuis*. In those with only one cycle per lunation, various explanations have been put forward. Mayer (**41**), as already pointed out on p. 620 of this paper, stated that moonlight is the effective cause and that the tides are unnecessary but contributing factors for the swarming of the Polychæte *Leodice fucata*. In contradiction to this, Treadwell (**60**) showed that moonlight is not necessary for the swarming of this annelid. Lillie and Just (**36**) and Fox (**13**) have shown that males stimulate the females to spawn, and that, in the case of *Nereis limbata*, the males are stimulated by some chemical stimulus extruded from the eggs of ripe females. But this does not explain the lunar periodicity in reproduction.

Arrhenius (**2**) has shown statistically that there exists a low correlation between the frequency of human births and the sidereal lunar month of 27·32 days. The same periodicity was found for menstruation, but to a more pronounced degree.

DISCUSSION ON THE PROBABLE CAUSES OF PERIODICITY IN REPRODUCTION.

It has now been shown that there is a rhythmic periodicity in reproduction in *Pecten opercularis*, and that maximum spawning occurs about the full moon time. In order to explain satisfactorily why the queens spawn rhythmically, it would be necessary to detect the factors—internal or external—that would act periodically. Further, it would also be important to find out the factor that causes the queens to spawn at full moon time.

The rhythmic effect of the alternating spring and neap tides has already been described in some animals. In *Convoluta roscoffensis*, Keeble (**30**) has shown that the rhythm of egg-laying is so well established in this planarian that it keeps its habit of laying its eggs at neap tides even if reared in the Laboratory. *Leuresthes tenuis*, an atherine fish, spawns periodically on each series of high tides throughout the breeding season in California (Clark, **5**). *Pecten opercularis* has only one reproductive cycle each lunar month though there are two spring tides and two neap tides.

Nevertheless, it may be pointed out that spawning seems to occur at the beginning of the full moon spring tides after the neap of the first quarter. Further, the average excess tidal range of the new moon spring over that of the full moon spring, during the breeding season, was not more than two feet. This difference could scarcely effect the queens, especially as they are active migrants. In order to test whether the rhythmic habit of this mollusc was a well-established physiological rhythm or not—as in Convoluta—samples were kept in the Laboratory tanks. These individuals showed no signs of reproductive activity, but had the healthy eggs—which were present when they were captured in nature—degenerating, probably due to their captivity. This experiment, therefore, is not sufficient to state whether or not the spawning habit is a well-established cycle.

The presence of a large percentage of individuals with well developing gonad at all times during the breeding season, suggests that (1) the time taken for the production of a new crop of ripe sexual products is more than a lunar month, and (2) the early development of the oocytes and spermatocytes takes place in a relatively short time. Microscopic sections of mature ovaries (Fig. 1, p. 610) show that young oocytes are present in the walls of the follicles and ripe ova in the ducts. Sections of " spent " ovaries (Fig. 2, p. 612), too, possess similar young oocytes in the follicular wall. Hence it is suggested that both the above-mentioned factors contribute to the presence of a large proportion of individuals with developing eggs.

For the development of generative products, a large amount of nutritive material is necessary. The sources from which such material can be obtained are either from the tissues of the body or from the intake of the food or from both. It has already been indicated (p. 618) that the quantity of food in the gut is apparently constant, and hence does not contribute directly to the rhythmic ripening of the gonad.

The lunar periodicity of reproduction among plants is easily explained by the effect of polarised light on photosynthesis. But in the case of animals, the reason is not so clear, except in those which have two reproductive cycles per lunar month. Grave (**18**) states that moonlight has direct influence on both sexes of *Chætopleura apiculata*. The experiment described on p. 619 suggests, at least, that moonlight has no effect on the development of the sexual products of *Pecten opercularis*, although unfortunately the experiment was carried out at the end of the breeding season. Further, this species of Pecten normally occurs at a depth of 20 fathoms or more, where the amount of light from the moon is negligible, as the work of Poole and Atkins (**51**) on sunlight shows. They state that " the clearest water, 20 miles out in the English Channel, gave an absorption coefficient 0·110 for the upper 10 metres, 0·117 for the second and

0·133 for the third. This water with glassy surface transmitted 0·54% *of the vertical illumination to* 34·8 *metres* " (about 19 fathoms. Italics mine), " 28·3% to 8·3 metres, at which depth a white disc was just visible, and 71·2% to 1·5 metres." Lillie and Just (**36**) make the assumption that the maturity of the animals is dependent on some relation of the life-history to the phases of the moon, involving, probably through lunar tidal variations, rhythmical alternation of the condition of nutrition.

Conclusions regarding the Phenomenon Recorded.

It has been pointed out that the lunar periodicity in reproduction is not caused by (1) tidal effects, (2) food, and (3) direct light of the moon, individually, although the cumulative effect of these factors may be responsible ; but there is no proof to decide one way or the other.

The correlation between the cessation of spawning in *Pecten opercularis* and the rise of temperature or the beginning of the spawning with the fall of temperature (Fig. 3, p. 616) indicates that the temperature has a controlling effect on the spawning habits of this mollusc, i.e. as long as the temperature remains favourable to the animal the spawning will occur mainly at full moon time. Orton (**44**) has shown that the European oyster (*Ostrea edulis*) " begins to spawn in a mean temperature of 15°–16° C. throughout its geographical range. Further, this species continues to produce mature sexual products so long as the temperature remains above the figure." Fox (**12**), discussing the effect of temperature on *Centrechinus setosus*, states, " its breeding season begins at Suez some months previous to July at a temperature well below that of July and September. Yet from July onward, with the temperature still rising, the number of individuals reaching maturity declines, and in September all breeding ceases although the temperature is still above that at which the breeding season was initiated." In the case of *Pecten opercularis* the temperature seems to have the same effect as it has on Centrechinus. As long as the temperature remains below 11° C., spawning seems to occur normally ; but when the temperature rises above 11° C. breeding ceases. Hence it would appear that there is a maximum temperature limit of about 11° C. for *Pecten opercularis* above which the breeding of the species stops. This, with the work of Orton and Fox, suggests that there is a maximum and a minimum temperature limit for each species of the marine animals, between which temperatures breeding mainly occurs.

It may be mentioned here that the geographical distribution of *P. opercularis* is mainly confined to Europe. Bucquoy, Dautzenberg, and Dollfus (**4**) state, " Le *P. opercularis* est très abondant dans la Mediterranée et l'Adriatique sous la forme *Andouine ;* la forme typique est

au contraire très répandue dans l'océan, depuis le détroit de Gibralter jusqu'en Norvège, ainsi qu'aux îles Madère, Canaries, et Açores."

It has already been pointed out in Table III, p. 618, and Fig. 4, p. 619, that the ovary of *P. opercularis* was developing normally in early July and in the early part of August as if spawning was to take place with August full moon, but there was no spawning, and still the eggs were degenerating after the full moon of the 13th August. This seems to suggest that in the animal there is a physiological rhythm that causes the development of the gonad to coincide with the full moon phase of each lunar month.

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SUMMARY.

1. It has been shown that there is a lunar periodicity in reproduction of *P. opercularis* near Plymouth in 1927–28. The ripening of sexual products corresponds with the full phase of the moon.

2. The condition and shape of the gonad changes with the development of the tissues.

3. The colour, too, of the hermaphrodite organ changes with development.

4. Black pigmentation has been observed on the gonad in thin-shelled *P. opercularis*, a phenomenon apparently due to actinic rays penetrating the thin shell.

5. The breeding season is from January to June inclusive.

6. The gut contents seem to show no appreciable difference either in quantity or in the nature of the food during a lunar month.

7. The moonlight has apparently no effect on the lunar periodicity in reproduction.

8. It is suggested that in the animal there is a physiological rhythm that causes the development of the gonad to coincide with the full moon of each lunar month.

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RECORDS.

Trawled on 9th March, '27—Examined on 10th and 11th. Bought from Quay.

The following conventions are used in the records :—
Cr. = Creamy in colour. F. = Full.
H.F. = Half full. R. = Ripe.
H.Sp. = Half spent. Sp. = Spent.

No.	Size of shell. Length × Height in mm.	Ovary. Colour K+V No.	Ovary. Condition of.	Ovary. Size of in mm.	Ovary. Size of Eggs ×10μ	Ovary. Inference.	Testis. Colour. K & V No.	Testis. Condition of.	Testis. Size of in mm.	Testis. Inference.
	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.
1	45×45	91	F.	11	8–10	R.	0171	H.F.		
2	57×57	86	H.F.	14	7–9		151c	,,		
3	58×57	111	,,	12	9–10	R.	0171	,,		
4	62×58	86	F.	18	8–9	R.	,,	F.		R.
5	54×53	86	H.F.	13	8–9		0196	H.F.	15	
6	48×48	61	,,	13	6–7		,,	,,	12	
7	54×53	86	,,	13	8–10		,,	,,	18	
8	54×54	86	,,	16	8–10		0171	H.F. Cr.	17	
9	51×49	81	,,	10	8–9		0196	H.F.	15	
10	61×56	81	,,	11	9–10	R.	0171	,,	18	
11	63×60	86	,,	13	7–9		,,	F.	20	
12	61×56	61	,,	16	8–9		,,	,,	20	
13	50×48	81	Sp.	11	6–7		—	Sp.	15	
14	47×44	111	F.	16	8–9	R.	178a	H.F.	14	
15	54×51	86	H.F.	15	8–9		0171	F. Cr.	18	R.
16	44×44	81	,,	12	8–9		,,	H.F.	13	
17	59×55	81	,,	13	8–9		,,	F. Cr.	18	R.
18	50×48	106	,,	15	7–9		,,	H.F.	16	
19	53×51	81	F.	16	7–8		,,	F. Cr.	20	R.
20	44×44	86	H.F.	9	8–10		0196	H.F.	13	
21	47×47	86	,,	12	8–9		,,	F. Cr.	18	R.
22	59×55	81	,,	13	6–8		—	Sp.	18	
23	53×50	81	,,	12	7–8		0171	H.F. Cr.	15	
24	60×58	86	F.	15	8–9	R.	,,	F. Cr.	20	R.
25	49×46	76	,,	11	8–9	R.	,,	,,	15	R.
26	47×47	136	H.F.	14	8–9		,,	H.F.	14	
27	53×52	61	,,	15	9–10	R.	,,	,,	18	
28	62×59	81	,,	10	8–9		,,	,,	18	
29	53×52	86	,,	12	8–9		,,	H.F. Cr.	17	
30	49×47	86	,,	13	7–9		,,	F.	19	
31	48×48	81	,,	13	9–10	R.	,,	H.F.	13	

	1	2	3	4	5	6	7	8	9	10
32	50×50	81	H.F.	13	8–10		0171	H.F.	16	
33	56×52	86	,,	11	7–8		,,	,,	16	
34	56×53	81	,,	12	9–10	R.	,,	,,	16	
35	49×49	91	,,	13	7–8		,,	,,	15	
36	47×42	91	,,	10	9–10	R.	0196	H.Sp.	15	
37	58×55	86	,,	14	7–9		0171	F. Cr.	18	R.
38	46×45	81	,,	11	8–9		,,	F.	13	
39	47×47	86	,,	12	9–10	R.	,,	H.F.	15	
40	50×48	66	,,	10	8–9		,,	,,	13	
41	49×52	81	,,	13	9–10	R.	,,	,,	16	
42	55×52	91	F.	15	7–8		,,	F. Cr.	18	R.
43	50×50	86	H.F.	13	7–8		,,	H.F.	14	
44	52×49	76–81	F.	15	5–8		,,	,,	18	
45	48×49	86	H.F.	14	7–8		,,	,,	15	
46	52×51	81	F.	11	8–9	R.	,,	,,	15	
47	62×56	91	,,	16	8–10	R.	,,	F.	18	R.
48	43×43	81	H.F.	10	9–10	R.	,,	,,	12	R.
49	56×54	86	,,	13	8–10		,,	H.F.	17	
50	57×53	86	F.	15	9–10	R.	,,	F. Cr.	17	R.
51	53×50	111	,,	12	8–10	R.	,,	F.	15	R.
52	58×54	81	,,	15	8–9	R.	,,	F. Cr.	20	R.
53	51×49	121	Sp.	5	9–10		—	H.Sp.	13	
54	53×51	86	H.F.	13	9–10	R.	0171	H.F. Cr.	15	
55	56×54	81	,,	14	9–10	R.	,,	,,	20	
56	53×52	81	F.	14	9–10	R.	,,	F. Cr.	16	R.
57	49×47	86	,,	11	9–11	R.	,,	,,	13	R.
58	55×52	76–81	H.F.	11	9–10	R.	,,	,,	16	R.
59	60×57	86	F.	13	8–10	R.	,,	,,	18	R.
60	50×50	91	H.F.	14	9–10	R.	,,	F.	15	R.
61	49×47	86	,,	10	8–10		,,	H.F.	13	
62	59×56	96	F.	15	8–9	R.	,,	F.	15	R.
63	50×48	86	H.F.	10	8–9		,,	,,	15	
64	47×46	91	F.	10	9–10	R.	,,	H.F.	14	
65	57×53	86	,,	12	8–10	R.	,,	F. Cr.	15	R.
66	44×42	86	H.F.	10	9–11	R.	,,	,,	15	R.
67	57×53	117	Sp.	9			,,	Sp.	13	
68	52×50	81	F.	9	8–9	R.	,,	F. Cr.	12	R.
69	56×54	86	,,	13	8–10	R.	,,	,,	14	R.
70	59×55	81	,,	13	8–10	R.	,,	,,	15	R.
71	49×48	116	H.F.	8	8–10		,,	F.	14	
72	47×46	81	,,	10	8–9		,,	F. Cr.	14	R.
73	45×45	61	F.	14	7–8		,,	,,	17	R.

1	2	3	4	5	6	7	8	9	10
74	50×50	61	F.	11	8–10	R.	0171	F. Cr	15	R.
75	57×56	81	,,	14	6–7		,,	,,	20	R.
76	46×46	81	H.F.	11	8–9		,,	H.F.	12	
77	43×41	91	F.	12	9–10	R.	,,	F. Cr.	14	R.
78	53×53	81	H.F.	9	7–9		,,	H.F.	15	
79	52×50	81	F.	11	8–9	R.	,,	F.	14	R.
80	51×50	86	,,	13	9–10	R.	,,	F. Cr.	16	R.
81	49×47	111	,,	10	9–10	R.	,,	F.	13	R.
82	55×53	81	,,	10	6–7		,,	F. Cr.	18	R.
83	49×47	81	,,	11	8–9	R.	,,	H.F.	14	
84	51×48	86	,,	12	9–11	R.	,,	F. Cr.	15	R.
85	48×47	86	,,	12	9–11	R.	,,	,,	15	R.
86	48×47	86	H.F.	11	8–10		,,	H.F. Cr.	15	
87	56×53	86	,,	9	8–10		,,	H.F.	14	
88	48×45	142	Sp.	—	—		—	Sp.		
89	50×49	61	F.	14	8–10	R.	0171	F. Cr.	14	R.
90	63×60	81	,,	13	8–10	R.	,,	,,	20	R.
91	54×51	86	,,	14	8–10	R.	,,	F.	15	R.
92	46×44	111	,,	11	9–10	R.	,,	,,	15	R.
93	56×52	111	H.F.	11	7–8		,,	H.F.	13	
94	54×52	86	F.	10	7–9		,,	F. Cr.	16	R.
95	48×48	86	H.F.	11	9–10	R.	,,	H.F.	14	
96	55×53	91	F.	12	7–9		,,	F. Cr.	16	R.
97	49×48	111	,,	11	8–9	R.	,,	F.	14	R.
98	52×52	86	H.F.	9	9–10	R.	,,	H.F.	14	
99	49×47	86	,,	9	8–9		,,	,,	14	
100	48×46	81	F	12	7–9		,,	H.F. Cr.	15	
101	50×49	86	H.F.	11	8–10		,,	,,	16	
102	48×48	86	,,	10	8–9		,,	,,	14	
103	55×52	81	,,	10	8–9		,,	,,	15	
104	54×51	86	,,	10	8–9		,,	,,	15	
105	47×47	81	F.	10	9–10	R.	,,	F.	11	R.
106	50×49	66	H.F.	8	7–9		,,	H.F.	13	
107	56×53	91	F.	15	7–8		,,	F. Cr.	17	R
108	54×50	106	,,	11	8–11	R.	,,	F.	16	R.
109	48×45	76	H.F.	7	7–9		,,	H.F.	11	
110	58×54	81	F.	10	7–9		,,	F. Cr.	15	R.
111	46×46	86	,,	9	7–8		,,	F.	14	
112	57×53	106	,,	12	9–10	R.	,,	F. Cr.	16	R.
113	58×55	86	,,	15	7–9		,,	,,	15	R.
114	60×55	86	,,	12	9–11	R.	,,	,,	14	R.
115	43×43	81	H.F.	11	7–9		,,	H.F.	12	
116	47×46	76	F.	9	8–9	R.	,,	F.	12	R.
117	55×52	81	,,	15	8–10	R.	,,	F. Cr.	15	R.
118	53×49	76	,,	9	7–9		,,	H.F. Cr.	14	
119	56×56	91	,,	13	8–11	R.	,,	F.	15	R.
120	52×51	111	,,	13	9–10	R.	,,	H.F.	15	
121	49×48	86	,,	11	8–11	R.	,,	F.	15	R.
122	51×50	96	,,	12	8–10	R.	,,	,,	13	R.
123	49×48	76	,,	9	7–11		,,	H.F.	14	
124	60×58	81	,,	15	8–10	R.	,,	F. Cr.	17	R.
125	51×51	81	,,	10	9–10	R.	,,	,,	13	R.
126	47×47	111	,,	12	7–8		,,	F.	15	
127	58×56	81	,,	13	7–9		,,	F. Cr.	15	R.

1	2	3	4	5	6	7	8	9	10
128	55×53	81	F.	13	6–7		0171	F. Cr.	16	R.
129	45×46	81	,,	9	8–10	R.	,,	F.	12	R.
130	49×48	81	,,	11	7–9		,,	H.F. Cr.	15	
131	49×49	81	,,	13	8–10	R.	,,	H.F.	14	
132	49×47	91	,,	11	7–8		,,	F. Cr.	14	R.
133	56×55	76	,,	14	7–9		,,	,,	18	R.
134	52×50	81	,,	10	7–8		,,	F.	14	
135	45×45	86	,,	11	7–9		,,	,,	13	
136	47×46	86	H.F.	11	7–9		,,	H.F	14	
137	63×57	81	F.	15	5–8		,,	F. Cr.	16	R.
138	51×49	81	,,	14	8–10	R.	,,	,,	15	R.
139	51×49	81	,,	13	6–9		,,	,,	14	R.
140	59×55	86	,,	13	7–9		,,	,,	18	R.
141	55×52	76	,,	16	7–8		,,	,,	16	R.
142	45×45	78	,,	11	7–9		,,	,,	13	R.
143	60×55	81	,,	13	8–9	R.	,,	F.	15	R.
144	47×48	81	H.F.	7	9–11	R.	,,	H.F.	12	
145	48×47	81	,,	9	8–9		,,	H.F. Cr.	13	
146	59×55	81	F.	13	7–10		,,	F. Cr.	16	R.
147	50×48	86	,,	10	5–8		,,	F.	13	
148	60×57	81	,,	10	7–8		,,	F. Cr.	17	R.
149	51×50	106	,,	10	8–9	R.	,,	,,	14	R.
150	45×44	101	,,	10	9–10	R.	,,	H.F.	12	
151	48×48	81	H.F.	10	7–8		,,	H.F. Cr.	13	
152	45×45	76	F.	10	9–10	R.	,,	F.	15	R.
153	55×52	101	,,	13	7–10		,,	F. Cr.	17	R.
154	51×48	76	H.F.	10	7–9		,,	H.F.	15	
155	57×55	81	F.	10	8–10	R.	,,	F.	15	R.
156	47×47	81	,,	14	7–10		,,	F. Cr.	15	R.
157	56×53	66	,,	15	8–9	R.	,,	,,	15	R.
158	45×44	86	,,	10	8–10	R.	,,	F.	10	R.
159	58×55	91	,,	18	8–9	R.	,,	H.Sp.	14	
160	54×51	111	,,	14	8–10	R.	,,	F. Cr.	15	R.
161	50×50	86	,,	12	8–10	R.	,,	,,	15	R.
162	55×51	86	,,	11	8–9	R.	,,	,,	13	R.
163	52×50	81	,,	8	7–9		,,	H.F.	12	
164	58×55	86	,,	13	9–10	R.	,,	F. Cr.	17	R.
165	45×45	116	,,	10	8–10	R.	,,	F.	13	R.
166	49×49	106	,,	10	8–10	R.	,,	F. Cr.	15	R.
167	59×54	91	,,	15	9–10	R.	,,	,,	16	R.
168	55×52	86	,,	15	7–8		,,	,,	16	R.
169	46×46	76	,,	9	8–9	R.	,,	F.	12	R.
170	45×45	106	,,	9	8–11	R.	,,	F. Cr.	12	R.
171	53×52	76	,,	14	7–8		,,	F.	14	
172	43×43	86	,,	10	8–9	R.	,,	F. Cr.	10	R.
173	48×46	86	,,	10	7–10		,,	,,	12	R.
174	50×47	76	,,	8	6–9		,,	,,	15	R.
175	59×53	81	,,	11	6–8		,,	,,	16	R.
176	50×48	76	,,	12	7–8		,,	,,	14	R.
177	48×46	86	H.F.	10	7–10		,,	H.F.	12	
178	44×44	76	Sp.	7	5–7 (deg.)		,,	Sp.	11	
179	58×56	86	F.	13	8–9	R.	,,	F. Cr.	16	R.
180	58×53	86	,,	15	8–10	R.	,,	,,	17	R.

TRAWLED ON 13TH MARCH, '27—EXAMINED ON 14TH AND 15TH. BOUGHT FROM QUAY.

	1	2	3	4	5	6	7	8	9	10
1	51×50	81	F.	13	7–9		0171	F. Cr.	13	R.
2	45×44	81	H.F.	8	8–10		,,	H.F.	10	
3	43×43	81	Sp.	7	8–10		—	Sp.	11	
4	50×48	86	H.F.	8	9–10	R.	0171	H.F.	13	
5	54×52	66	Sp.	4	7–8		—	Sp.	11	
6	52×50	96	F.	14	9–11	R.	0171	F. Cr.	16	R.
7	49×47	86	,,	11	8–10	R.	,,	F.	13	R.
8	48×48	76	,,	13	8–10	R.	,,	,,	15	R.
9	57×55	86	,,	10	6–10		,,	H.F.	14	
10	51×51	81	,,	13	8–10	R.	,,	F. Cr.	14	R.
11	52×52	81	,,	10	8–10	R.	,,	F.	15	R.
12	53×53	86	Sp.	7	9–11		—	Sp.	12	
13	51×49	86	,,	8	6–8		0171	,,	13	
14	49×47	56	F.	7	7–9		,,	F. Cr.	12	R.
15	54×53	91	,,	11	9–11	R.	,,	,,	15	R.
16	47×47	121	Sp.	7	—		—	Sp.	11	
17	50×48	117	,,	—	—		0171	,,		
18	57×55	91	F.	12	8–10	R.	,,	F. Cr.	13	R.
19	58×54	86	,,	9	7–10		,,	,,	13	R.
20	54×50	86	Sp.	6	6–7		—	Sp.	13	
21	51×50	91	,,	8	7–8		0171	,,	10	
22	53×52	106	H.F.	11	7–9		,,	,,	15	
23	50×50	86	Sp.	9	8–9		,,	,,	15	
24	45×45	81	F.	13	9–10	R.	,,	F. Cr.	13	R.
25	47×47	81	,,	10	7–9		,,	,,	10	R.
26	49×48	101	,,	12	8–10	R.	,,	,,	17	R.
27	53×52	86	Sp.	11	7–8		—	Sp.	15	
28	44×44	86	F.	9	8–10	R.	0171	F.	16	R.
29	49×47	91	Sp.	8	7–8		—	Sp.	13	
30	53×49	81	F.	12	7–9		0171	F. Cr.	14	R.
31	51×49	86	H.F.	10	7–8		,,	H.F.	15	
32	49×49	81	,,	11	7–9		,,	,,	15	
33	47×47	81	F.	12	8–10	R.	,,	F. Cr.	15	R.
34	53×51	86	Sp.	7	7–9		—	Sp.	14	
35	46×45	91	F.	9	8–10	R.	0171	F.	15	R.
36	45×45	86	H.F.	8	6–8		,,	H.F.	12	
37	50×48	86	F.	12	6–8		,,	,,	16	
38	58×57	81	,,	11	8–9	R.	,,	F. Cr.	15	R.
39	49×48	117	Sp.				—	Sp.		
40	51×48	76	F.	8	7–9		0171	F. Cr.	12	R.
41	51×48	116	,,	7	6–8		,,	F.	15	
42	48×46	81	,,	11	7–10		,,	F. Cr.	13	R.
43	47×46	86	H.F.	8	6–8		,,	H.F.	13	
44	50×48	76	H.Sp.	7	8–9 (deg.)		,,	,,	13	
45	59×57	81	F.	13	9–10	R.	,,	F. Cr.	18	R.
46	52×50	91	Sp.	5			—	Sp.	12	
47	54×53	81	H.F.	9	9–11	R.	0171	H.F.	13	
48	52×50	91	H.Sp.	8	7–8 (deg.)		,,	F.	15	

	1	2	3	4	5	6	7	8	9	10
49	51×49	86	H.Sp.	8	6–8 (deg.)		0171	H.F.	12	
50	54×50	86	F.	13	9–10	R.	,,	F. Cr.	17	R.
51	54×54	86	,,	12	9–10	R.	,,	,,	15	R.
52	49×47	91	H.Sp.	7	6–7 (deg.)		,,	H.F.	13	
53	51×48	81	H.F.	8	7–9		,,	F.	15	
54	50×50	117	Sp.				,,			
55	48×46	86	F.	10	9–11	R.	,,	F. Cr.	15	R.
56	56×55	81	,,	11	8–10	R.	,,	,,	15	R.
57	52×50	116	Sp.	8	7–8 (deg.)		—	Sp.	13	
58	65×60	81	F.	11	9–10	R.	0171	H.F.	17	
59	48×47	76	,,	8	8–10	R.	,,	F. Cr.	13	R.
60	53×51	81	,,	15	6–9		,,	,,	18	R.
61	52×52	86	,,	11	8–9	R.	,,	,,	15	R.
62	48×47	86	,,	10	7–8		,,	,,	14	R.
63	48×48	86	,,	10	9–10	R.	,,	,,	13	R.
64	49×47	86	,,	11	9–11	R.	,,	,,	14	R.
65	55×50	81	,,	12	6–9		,,	,,	15	R.
66	44×44	76	,,	9	7–9		,,	H.F.	13	
67	49×49	81	,,	10	8–10	R.	,,	F. Cr.	15	R.
68	50×49	86	,,	11	8–10	R.	,,	,,	16	R.
69	49×48	86	H.Sp.	9	8–10 (deg.)		,,	H.F.	12	
70	48×47	81	H.F.	10	8–10		,,	H.F. Cr.	12	
71	50×50	76	F.	10	8–10	R.	,,	F. Cr.	15	R.
72	55×53	91	,,	10	8–10	R.	,,	,,	15	R.
73	48×47	86	,,	15	8–9	R.	,,	,,	12	R.
74	52×50	116	Sp.	5			—	Sp.	15	
75	45×45	86	H.F.	8	7–9		0171	H.F.	11	
76	49×47	86	F.	11	9–10	R.	,,	F. Cr.	15	R.
77	49×49	86	,,	11	8–10	R.	,,	,,	13	R.
78	50×47	117	Sp.				—	Sp.		
79	44×44	91	H.F.	7	5–7 (deg.)		0171	H.F.	12	
80	50×48	81	H.Sp.	9	8–9		,,	,,	12	
81	49×49	81	,,	8	9–10		,,	,,	14	
82	55×53	86	F.	11	7–9		,,	F. Cr.	16	R.
83	50×50	86	H.Sp.	9	7–9		,,	H.F.	14	
84	50×47	86	,,	8	5–8 (deg.)		,,	,,	16	
85	53×52	66	,,	9	8–10		,,	,,	14	
86	49×49	81	F.	13	8–10	R.	,,	F. Cr.	13	R.
87	49×47	81	,,	10	8–10	R.	,,	,,	15	R.
88	58×54	106	,,	14	8–9	R.	,,	,,	17	R.
89	50×49	86	,,	9	7–9		,,	,,	15	R.
90	54×51	81	,,	9	8–10	R.	,,	,,	15	R.
91	51×50	81	H.F.	11	7–10		,,	H.F.	13	
92	48×48	117	Sp.				—	Sp.		
93	57×56	86	F.	10	8–10	R.	0171	F. Cr.	17	R.
94	40×40	86	,,	8	8–10	R.	,,	,,	10	R.
95	52×49	81	,,	13	8–10	R.	,,	,,	14	R.
96	56×54	91	,,	12	5–6 (deg.)		,,	,,	14	R.

	1	2	3	4	5	6	7	8	9	10
97	53×50	81	F.	14	8–10	R.	0171	F. Cr.	16	R.
98	46×45	81	,,	9	8–11	R.	,,	,,	12	R.
99	52×52	66	,,	14	9–10	R.	,,	,,	18	R.
100	48×47	81	,,	10	8–10	R.	,,	,,	12	R.
101	50×49	86	H.Sp.	6	9–11		,,	H.F.	13	
102	43×42	86	F.	10	9–10	R.	,,	F. Cr.	10	R.
103	49×49	81	,,	12	9–11	R.	,,	,,	15	R.
104	48×47	86	,,	12	7–9		,,	,,	14	R.
105	48×47	81	,,	12	8–10	R.	,,	,,	13	R.
106	45×43	81	,,	10	9–10	R.	,,	,,	13	R.
107	53×50	81	,,	12	8–10	R.	,,	,,	15	R.
108	52×50	86	,,	9	8–10	R.	,,	H.F.	15	
109	51×49	86	H.Sp.	10	6–8 (deg.)		—	Sp.	12	
110	51×49	116	,,	9	6–7 ,,		0171	,,	14	
111	53×53	81	F.	12	8–9	R.	,,	F. Cr.	17	R.
112	47×47	81	,,	13	9–10	R.	,,	,,	13	R.
113	49×49	86	,,	10	9–10	R.	,,	,,	12	R.
114	48×47	91	Sp.	5	6–7 (deg.)		—	Sp.	10	
115	55×52	76	F.	12	8–9	R.	0171	F. Cr.	15	R.
116	54×52	81	,,	7	8–10	R.	,,	,,	12	R.
117	50×48	91	,,	10	7–9		,,	,,	12	R.
118	49×49	111	,,	10	9–11	R.	,,	,,	15	R.
119	61×57	116	H.F.	12	6–8 (deg.)		,,	H.F.	15	
120	44×44	81	F.	11	8–10	R.	,,	F. Cr.	13	R.
121	52×50	106	,,	12	8–10	R.	,,	H.F.	14	
122	55×52	66	,,	13	9–10	R.	,,	F. Cr.	13	R.
123	53×52	96	,,	12	6–9		,,	,,	14	R.
124	53×50	91	,,	12	8–10	R.	,,	,,	13	R.
125	51×48	103	,,	12	7–10		,,	,,	12	R.
126	58×55	86	,,	13	8–10	R.	,,	,,	16	R.
127	47×47	81	,,	11	8–10	R.	,,	,,	11	R.
128	51×50	86	H.F.	8	8–9 (deg.)		,,	H.F.	11	
129	56×55	81	F.	12	9–11	R.	,,	F. Cr.	16	R.
130	55×55	81	H.F.	8	8–10		,,	H.F.	15	
131	46×46	86	F.	12	9–10	R.	,,	F. Cr.	13	R.
132	42×42	81	H.F.	10	8–10		,,	H.F.	10	
133	47×47	76	F.	13	7–9		,,	F. Cr.	13	R.
134	49×48	81	H.F.	9	9–10	R.	,,	H.F.	13	
135	48×48	111	,,	8	7–8		,,	,,	12	
136	55×50	81	F.	12	9–10	R.	,,	F. Cr.	14	R.
137	47×47	—	Sp.				—	Sp.		
138	48×48	86	F.	11	9–10	R.	0171	F. Cr.	12	R.
139	54×51	86	,,	12	8–10	R.	,,	,,	15	R.
140	49×49		H.F.	12	8–10		,,	F.	10	
141	48×48	81	F.	12	8–10	R.	,,	F. Cr.	15	R.
142	51×50	91	,,	11	9–10	R.	,,	,,	12	R.
143	51×51	81	H.F.	10	6–8 (deg.)		,,	H.F.	13	
144	49×49	106	F.	12	8–9	R.	,,	F. Cr.	13	R.
145	51×50	81	H.F.	10	7–10		,,	H.F.	13	
146	30×30	—	Sp.	3			—	Sp.	7	
147	38×36	—	,,				0171	,,		
148	53×51	91	F.	13	8–10	R.	,,	F. Cr.	15	R.
149	45×44	81	,,	8	8–10 (deg.)	R.	,,	F.	11	R.
150	48×45	91	H.F.	11	6–7 ,,		,,	H.F.	13	
151	40×40	91	Sp.	6	7–8 ,,		—	Sp.	12	
152	49×47	81	F.	11	7–8		0171	F. Cr.	14	R.
153	48×46	81	,,	12	8–10	R.	,,	,,	14	R.
154	57×55	86	H.Sp.	12	6–7 (deg.)		,,	H.F.	15	
155	43×42	86	,,	6	6–7 ,,		,,	,,	9	
156	42×41	111	,,	9	7–10 ,,		,,	,,	10	
157	48×48	86	F.	14	7–9		,,	F. Cr.	13	R.
158	50×49	86	,,	10	8–10	R.	,,	,,	13	R.
159	48×47	81	H.Sp.	6	7–8		,,	H.F.	11	
160	43×43	86	F.	9	8–9	R.	,,	F. Cr.	11	R.
161	51×51	86	,,	13	8–11	R.	,,	,,	15	R.
162	52×51	111	H.Sp.	8	7–9 (deg.)		,,	H.F.	12	
163	47×47	86	F.	10	7–10		,,	F. Cr.	15	R.
164	47×45	81	,,	10	7–9		,,	,,	15	R.
165	51×50	81	,,	9	8–10	R.	,,	,,	10	R.
166	44×43	86	H.Sp.	9	6–7 (deg.)		—	Sp.	10	
167	50×50	76	F.	14	9–11	R.	0171	F. Cr.	13	R.
168	63×58	81	,,	15	8–10	R.	,,	,,	16	R.
169	50×50	76	,,	15	9–10	R.	,,	,,	15	R.
170	48×48	86	,,	10	7–10		,,	,,	15	R.
171	61×57	81	,,	12	8–9	R.	,,	,,	15	R.
172	51×49	81	,,	12	7–9		,,	,,	13	R.
173	43×43	86	,,	10	9–11	R.	,,	,,	13	R.
174	48×47		Sp.	7	6–7 (deg.)		—	Sp.	10	
175	48×48	86	F.	10	7–9		0171	F. Cr.	14	R.
176	47×47	91	,,	7	8–10	R.	,,	,,	13	R.
177	52×52	91	H.Sp.	11	8–10		,,	H.F.	13	
178	53×51	111	,,	10	5–6 (deg.)			,,	13	

Trawled on 18th March, '27—Examined on 19th and 20th. Bought from Quay.

Ring No.	1	2	3	4	5	6	7	8	9	10
1	2*	91	F.	10	9–11 (deg.)	R.	0171	F. Cr	15	R.
2	3	86	,,	14	6–8		,,	F.	15	
3	2	86	H.F.	13	7–8 (deg.)		,,	H.F.	13	
4	3	86	H.Sp.	10	4–7 ,,		—	Sp.	12	
5	2	116	F.	11	7–8		0171	F. Cr.	15	R.
6	3	66	,,	8	9–11	R.	,,	,,	15	R.
7	2	91	H.F.	9	6–8 (deg.)		,,	,,	10	R.
8	3	86	,,	11	6–8 ,,		,,	F.	15	
9	2	111	,,	9	8–11 ,,		,,	,,	13	
10	3	91	H.Sp.	9	7–8 ,,		,,	,,	13	
11	3	86	,,	7	6–8 ,,		,,	H.F.	11	
12	3	86	,,	13	5–8 ,,		,,	,,	15	
13	2	86	,,	10	8–10 ,,		,,	,,	12	
14	3	116	F.	11	7–9 ,,		,,	F. Cr.	16	R.
15	4	91	,,	16	6–8 ,,		,,	,,	16	R.
16	2	91	,,	10	7–9 ,,		,,	F.	11	
17	3	86	H.F.	10	6–10 ,,		,,	F. Cr.	13	R.
18	3	111	F.	14	9–10	R.	,,	F.	16	R.
19	4	86	H.Sp.	13	7–10		,,	H.F.	20	
20	3	86	H.F.	12	7–8 (deg.)		,,	H.F. Cr.	12	
21	3	86	H.Sp.	15	6–8 ,,		—	Sp.	10	
22	3	86	H.F.	10	9–11	R.	0171	H.F.	15	
23	3		Sp.				—	Sp.		
24	3	86	H.Sp.	9	9–10		—	,,	12	
25	3	86	,,	11	7–8 (deg.)		0171	,,	14	
26	2	86	,,	8	7–8 ,,		,,	,,	10	
27	2	91	,,	9	8–9		,,	,,	12	
28	3	86	,,	7	6–10 (deg.)		,,	,,	15	
29	3	81	,,	9	5–7 ,,		,,	,,	13	
30	3	81	H.F.	10	5–7 ,,		,,	H.F.	15	
31	3	66	H.Sp.	12	6–8 ,,		,,	,,	15	
32	2	81	Sp.	5			—	Sp.	7	
33	3	86	F.	13	5–7 (deg.)		0171	F. Cr.	13	R.
34	2	76	,,	11	7–9		,,	,,	13	R.
35	2	91	H.Sp.	8	7–8		—	Sp.	12	
36	3		Sp.	7			0171	,,	12	
37	2	76	F.	15	9–11	R	,,	F. Cr.	15	R.
38	3	86	H.F.	10	7–10 (deg.)		,,	H.F.	15	
39	3	86	,,	8	9–10	R.	,,	,,	14	
40	3	81	F.	12	8–10	R.	,,	F. Cr.	15	R.
41	3	86	H.F.	13	5–7 (deg.)		,,	H.F.	13	
42	3	81	F.	18	9–10	R.	,,	F. Cr.	20	R.
43	3	86	,,	12	5–7 (deg.)		,,	,,	15	R.
44	3	116	,,	12	5–7 ,,		,,	,,	15	R.
45	2		Sp.				—	Sp.		
46	3	116	F.	12	5–7 (deg.)		0171	F.	13	
47	4	76	,,	15	7–8 ,,		,,	F. Cr.	20	R.
48	3	86	H.Sp.	12	7–8 ,,		—	Sp.	16	

Ring No.	1	2	3	4	5	6	7	8	9	10
49	3	81	H.F.	11	9–10	R.	0171	H.F.	16	
50	4	86	,,	14	5–7 (deg.)		,,	F. Cr.	15	R.
51	2	86	,,	11	6–8		,,	H.F.	14	
52	4	81	,,	12	6–8		,,	,,	15	
53	3	86	,,	12	7–8		,,	,,	17	
54	3	81	,,	10	5–7 (deg.)		,,	,,	15	
55	4	86	,,	14	6–7 ,,		,,	,,	19	
56	3	86	,,	11	7–9		,,	,,	16	
57	3	86	,,	12	6–8		,,	,,	15	
58	3	86	,,	14	6–9		,,	,,	14	
59	3	86	,,	12	7–9		,,	,,	15	
60	3	86	,,	15	6–9		,,	,,	15	
61	3	86	,,	12	6–9		,,	,,	14	
62	2	106	F.	12	7–9		,,	,,	14	
63	2	86	,,	10	6–8		,,	,,	14	
64	3	86	,,	12	6–8		,,	,,	15	
65	3		Sp.	10			—	Sp.	15	
66	2	86	H.F.	10	7–10		0171	H.F.	13	
67	2	91	F.	9	7–9 (deg.)		,,	F.	10	
68	3	86	,,	12	8–10	R.	,,	F. Cr.	13	R.
69	2	91	,,	9	6–10 (deg.)		,,	H.F.	12	
70	3		Sp.	8	5–6 ,,		—	Sp.	12	
71	3	86	F.	11	8–10	R.	0171	H.F. Cr.	12	
72	3	66	,,	13	5–7 (deg.)		,,	F. Cr.	17	R.
73	4	81	,,	15	6–8 ,,		,,	,,	18	R.
74	4	116	H.F.	13	7–8 ,,		,,	,,	16	R.
75	3	86	,,	12	6–9		,,	H.F.	13	
76	3	81	,,	13	8–10		,,	,,	17	
77	3	86	,,	12	7–9		,,	H.F. Cr.	16	
78	3	66	,,	13	7–9		,,	,,	13	
79	3	76	,,	12	7–9		,,	H.F.	13	
80	3	86	,,	10	5–8 (deg.)		,,	,,	14	
81	3	111	,,	11	7–9		,,	,,	13	
82	3	86	,,	11	5–7 (deg.)		,,	,,	10	
83	4	86	,,	13	5–7 ,,		,,	,,	15	
84	2	86	,,	11	6–8 ,,		,,	H.F. Cr.	13	
85	3	86	,,	11	4–8 ,,		,,	,,	14	
86	3	76	,,	11	6–8		,,	H.F.	14	
87	3	106	,,	10	7–9		,,	H.F. Cr.	14	
88	3	76	,,	11	7–9		,,	,,	15	
89	2	76	,,	9	5–7 (deg.)		,,	H.F.	12	
90	3	86	H.Sp.	9	7–9 ,,		—	Sp.	13	
91	3	81	F.	12	7–9 ,,		0171	H.F.	17	
92	3	96	,,	14	6–10 ,,		,,	F. Cr.	15	R.
93	3	76	H.F.	11	6–8 ,,		,,	H.F.	13	
94	3	81	,,	10	6–9		,,	,,	13	
95	2	86	,,	11	8–10		,,	H.F. Cr.	15	
96	3	76	,,	11	8–10		,,	H.F.	16	

	1	2	3	4	5	6	7	8	9	10
97	3	116	H.F.	13	5–9 (deg.)		0171	H.F. Cr.	14	
98	2	86	,,	10	7–9		,,	,,	14	
99	2	91	,,	12	7–10		,,	,,	15	
100	3	81	,,	10	7–9		,,	H.F.	13	
101	3	91	,,	12	7–9		,,	,,	15	
102	2	86	,,	10	6–8		,,	,,	14	
103	2	91	,,	10	7–9		,,	,,	11	
104	3	86	,,	12	7–9		,,	,,	15	
105	2		Sp.	8			—	Sp.	10	
106	4	86	H.F.	15	6–8		0171	H.F. Cr.	18	
107	3		Sp.	7			—	Sp.	13	
108	3	86	H.F.	13	6–7		0171	H.F.	15	
109	3	86	F.	11	7–8		,,	F.	13	
110	2	76	H.F.	11	6–8		,,	H.F.	13	
111	3	86	,,	11	7–8		,,	,,	13	
112	3	76	H.Sp.	9	8–9		,,	,,	15	
113	3	86	,,	13	6–7 (deg.)		,,	,,	13	
114	3	76	H.F.	13	6–7 ,,		,,	,,	14	
115	4	91	,,	14	7–9		,,	,,	18	
116	3	96	,,	12	6–8		,,	,,	16	
117	2	76	F.	13	6–8		,,	F. Cr.	15	R.
118	3	76	H.F.	16	7–10		,,	H.F.	13	
119	3	81	F.	15	8–10	R.	,,	F. Cr.	16	R.
120	4	81	H.F.	14	6–7 (deg.)		,,	H.F.	16	
121	3	71	,,	15	6–8		,,	,,	13	
122	3	81	,,	9	6–8 (deg)		,,	,,	15	
123	3	76	,,	15	7–8 ,,		,,	,,	17	

	1	2	3	4	5	6	7	8	9	10
124	3	91	H.F.	12	8–9 deg.		0171	H.F.	13	
125	3	76	F	19	8–10	R.	,,	F. Cr.	17	R.
126	3	86	H.F.	10	6–8		,,	H.F.	15	
127	4	86	,,	15	7–8		,,	,,	15	
128	3		Sp.	11	3–5 (deg.)		—	Sp.	11	
129	3	86	H.F.	12	6–9		0171	H.F.	15	
130	4	91	,,	15	5–7 (deg.)		,,	,,	15	
131	3	106	F.	11	6–8		,,	F. Cr.	15	R.
132	3	86	H.F.	8	8–10 (deg.)		,,	H.F.	10	
133	3	76	F.	14	7–9		,,	F. Cr	14	R.
134	4	121	,,	15	5–7		,,	,,	18	R.
135	3	86	H.F.	10	7–10		,,	H.F.	14	
136	3	86	,,	13	7–9		,,	,,	14	
137	3	81	,,	11	7–9		,,	,,	13	
138	3	86	,,	13	7–8 (deg.)		,,	,,	13	
139	3	76	,,	10	7–9		,,	,,	15	
140	2	86	,,	11	7–9		,,	,,	15	
141	2	86	,,	9	5–7 (deg.)		,,	H.F. Cr.	13	
142	4	91	F.	15	5–7		,,	F. Cr.	17	R.
143	2	81	,,	10	6–8		,,	,,	12	R.
144	3	116	H.F.	15	6–8		,,	H.F.	15	
145	3	86	,,	15	7–8		,,	,,	13	
146	4	76	F.	15	5–6 (deg.)		,,	F. Cr.	20	R.
147	3	91	H.F.	10	5–8		,,	H.F.	15	
148	3	66	F.	13	6–7		,,	F.	17	
149	3	91	H.F.	14	6–7		,,	H.F.	14	

Ring No. 1=30–40 mm.; Ring No. 2=40–50 mm.; Ring No. 3=50–60 mm.; Ring No. 4=60–70 mm.

Trawled on 23rd March, '27—Examined on 24th and 25th. Bought from Quay.

	1	2	3	4	5	6	7	8	9	10
1	4	91	H.F.	11	6–8		0171	H.F.	18	
2	4	81	,,	9	7–10		,,	H.F. Cr.	25	
3	2	81	,,	10	8–10		,,	H.F.	16	
4	3	81	F.	16	6–9		,,	F. Cr.	16	R.
5	3	76	H.F.	12	7–10		,,	H.F. Cr.	17	
6	3	86	,,	11	7–8		,,	H.F.	14	
7	3		Sp.	8			—	Sp.	12	
8	3	86	H.F.	13	9–10	R.	0171	H.F.	16	
9	4	86	,,	15	7–8		,,	F. Cr	17	R.
10	3	116	F.	12	7–9		,,	,,	14	R.
11	3	101	,,	15	8–11	R.	,,	,,	14	R.
12	4	76	,,	13	7–8		,,	,,	18	R.
13	3	76	H.F.	9	7–10		,,	H.F. Cr.	9	
14	3	81	,,	12	5–9		,,	,,	15	
15	4	91	,,	15	7–9		,,	H.F.	18	
16	3	81	H.Sp.	9	5–7 (deg.)		—	Sp.	15	

	1	2	3	4	5	6	7	8	9	10
17	4	116	H.Sp.	11	7–8		0171	Sp.	16	
18	3	81	F.	13	8–11	R.	,,	F. Cr.	15	R.
19	3	81	H.F.	14	7–10		,,	H.F. Cr.	13	
20	2	81	,,	6	6–9		,,	H.F.	11	
21	2	111	,,	10	6–8		,,	,,	13	
22	3	91	,,	12	5–7 (deg.)		,,	,,	13	
23	2	76	F.	10	7–8		,,	F. Cr.	12	R.
24	3	66	H.F.	12	7–11		,,	H.F. Cr.	13	
25	3	81	,,	12	7–9		,,	,,	14	
26	2	86	,,	9	7–9		,,	,,	11	
27	3	106	,,	11	7–10		,,	H.F.	11	
28	2		Sp.				—	Sp.		
29	2	86	H.F.	12	7–9		0171	H.F. Cr.	13	
30	4	86	,,	14	7–9		,,	H.F.	14	
31	3	76	,,	19	8–10		,,	H.F. Cr.	15	
32	4	81	,,	14	7–10		,,	,,	17	

	1	2	3	4	5	6	7	8	9	10
33	3	86	H.F.	12	6–10		0171	H.F.	14	
34	3	76	,,	12	7–8 (deg.)		,,	,,	15	
35	3	81	,,	10	7–9		,,	,,	15	
36	2	81	,,	13	7–9		,,	,,	15	
37	3	86	,,	12	7–9		,,	H.F. Cr.	15	
38	2	86	,,	12	6–7 (deg.)		,,	H.F.	14	
39	2	106	,,	13	6–7		,,	,,	15	
40	3	111	,,	13	6–8		,,	,,	15	
41	2		Sp				—	Sp.		
42	3	111	F.	12	7–9		0171	F. Cr.	15	R.
43	2	81	H.F.	12	7–8		,,	H.F. Cr.	12	
44	2	81	,,	11	7–9		,,	,,	13	
45	3	106	,,	12	8–10		,,	H.F.	14	
46	3	91	,,	11	7–8 (deg.)		,,	,,	15	
47	3	86	H.Sp.	10	7–8		—	Sp.	15	
48	3	76	F.	14	8–11	R.	0171	F. Cr.	16	R.
49	2	White	H.F.	10	7–8		,,	H.F. Cr.	14	
50	2	86	,,	10	7–9		,,	,,	10	
51	3	86	,,	10	8–9		,,	H.F.	16	
52	3	106	,,	13	5–6 (deg.)		,,	,,	17	
53	3	111	,,	13	7–9		,,	,,	15	

	1	2	3	4	5	6	7	8	9	10
54	4	106	H.F.	15	7–8		0171	H.F.	16	
55	3	81	H.Sp.	9	6–7 (deg.)		—	Sp.	13	
56	3	81	F.	14	6–8		0171	F. Cr.	14	R.
57	2	86	H.F.	11	6–8		,,	H.F. Cr.	14	
58	2	86	H.Sp.	8	7–8		—	Sp.	12	
59	2		Sp.				—	,,		
60	3	76	F.	8	7–9		0171	F. Cr.	13	R.
61	3	91	H.F.	10	7–9		,,	H.F. Cr.	13	
62	3	106	,,	12	6–8		,,	,,	13	
63	3	86	,,	13	7–8		,,	,,	15	
64	2	106	,,	10	8–10		,,	,,	12	
65	3		Sp.				—	Sp.		
66	3	86	H.F.	12	6–8		0171	H.F.	15	
67	2	86	H Sp.	10	7–9		—	Sp.	13	
68	1	86	,,	7	7–9		0171	,,	7	
69	1	106	,,	8	7–9		,,	,,	8	
70	2	86	,,	8	8–9		—	,,	12	
71	3	111	,,	10	6–7 (deg.)		0171	,,	12	
72	2	86	,,	9	7–9		,,	,,	11	
73	2	86	,,	10	7–8		,,	,,	12	
74	2	111	,,	9	7–8		,,	,,	13	

Trawled on 29th March, '27—Examined on 30th and 31st. Bought from Quay.

No.	Ring No.	Ovary. Colour K & V No.	Ovary. Condition of	Ovary. Size of Eggs ×10⁴	Ovary. Inference.	Testis. Condition.	Testis. Inference.
	1	2	3	4	5	6	7
1	3	91	F.	8–9	R.	F. Cr.	R.
2	4	81	,,	8–9	R.	,,	R.
3	3	81	H.F.	8–9		H.F. Cr.	
4	3	81	,,	8–9		,,	
5	3	81	,,	9–10	R.	,,	
6	3	86	,,	8–11		,,	
7	3	86	,,	8–9		,,	
8	2	81	,,	7–9		,,	
9	3	86	,,	7–10		,,	
10	3	White	,,	8–9		,,	
11	3	86	,,	8–9		H F	
12	3	81	,,	8–10		H.F Cr.	
13	3	86	,,	7–9		,,	
14	2	81	,,	8–9		,,	
15	3	86	,,	7–10		,,	
16	3	81	,,	8–9		,,	

	1	2	3	4	5	6	7
17	3	81	H.F.	8–10		H.F. Cr.	
18	2	81	,,	8–10		,,	
19	3	81	,,	8–9		,,	
20	3	86	,,	7–10		,,	
21	3	91	,,	7–9		,,	
22	3	61	,,	8–10		,,	
23	3	81	,,	9–11	R.	,,	
24	4	86	,,	7–9		H.F.	
25	3	116	,,	5–7 (deg.)		,,	
26	3	81	,,	8–9		,,	
27	3	81	,,	7–10		,,	
28	3	81	,,	7–9		,,	
29	3	66	,,	8–10		,,	
30	4	86	,,	9–10	R.	H.F. Cr.	
31	3	91	,,	9–10	R.	,,	
32	3	86	,,	8–9		,,	
33	3	81	,,	8–10		H.F.	
34	3	81	,,	8–9		H.F. Cr.	
35	3	86	,,	8–10		,,	
36	3	81	,,	8–10		,,	
37	3	86	F.	9–10	R.	,,	
38	3	91	H.F.	8–9		,,	
39	3	86	,,	8–10		,,	
40	3	81	Sp.	6–9 (deg.)		Sp.	

	1	2	3	4	5	6	7
41	3	81	H.F.	7–9		H.F. Cr.	
42	2	86	F.	8–10	R.	F. Cr.	R.
43	3	106	H.F.	9–10	R.	H.F. Cr.	
44	3	86	F.	8–10	R.	,,	
45	3	86	H.F.	6–7 (deg.)		,,	
46	3	76	F.	9–10	R.	F. Cr.	R.
47	4	81	H.F.	8–9		H.F. Cr.	
48	3	86	,,	8–9		,,	
49	3	86	Sp.	6–7 (deg.)		Sp.	
50	3	81	Sp.	5–6 ,,		Sp.	
51	3	81	F.	8–10	R.	F. Cr.	R.
52	3		H.F.	8–9		H.F. Cr.	
53	3	86	,,	8–10		H.F.	
54	3	91	,,	9–10	R.	,,	
55	4	81	,,	8–9		,,	
56	3	76	F.	8–9	R.	,,	
57	3	81	H.F.	8–11		,,	
58	3	86	,,	7–9		H.F. Cr.	
59	3	91	,,	7–8		H.F.	
60	3	86	F.	8–10	R.	F.	R.
61	3	81	,,	9–10	R.	F. Cr.	R.
62	3	86	,,	8–10	R.	H.F.	
63	4	81	,,	8–10	R.	F. Cr.	R.
64	3	86	H.F.	8–9		F.	
65	2	86	Sp.	7–9		Sp.	
66	3	86	H.F.	8–9		H.F.	
67	4	91	F.	9–10	R.	F. Cr.	R.
68	3	86	,,	7–9		,,	R.
69	3	81	H.F.	7–9		H.F. Cr.	
70	3	106	,,	7–10		,,	
71	3	121	Sp.	6–8 (deg.)		Sp.	
72	4	81	F.	9–11	R.	F. Cr.	R.
73	3	81	H.F.	7–8		H.F.	
74	3		Sp.	7–8 (deg.)		Sp.	
75	3	86	H.F.	7–9		H.F.	
76	4	86	,,	7–8		,,	
77	3	86	,,	7–9		H.F. Cr.	
78	3	81	,,	8–10		,,	
79	3	81	F.	8–10	R.	F.	R.
80	3	86	,,	7–9		F. Cr.	R.
81	3	76	,,	8–10	R.	,,	R.
82	3	86	H.F.	8–10		H.F.	
83	4	86	F.	8–11	R.	F. Cr.	R.
84	3	86	,,	8–10	R.	,,	R.
85	3	81	H.F.	7–8 (deg.)		H.F.	
86	3	81	,,	7–10		,,	
87	3	91	,,	7–9		,,	
88	4	86	,,	7–9 (deg.)		,,	
89	4	81	,,	8–10		,,	
90	3	81	,,	8–10		,,	
91	3		Sp.	7–8 (deg.)		Sp.	
92	3	86	F.	7–9		F. Cr.	R.
93	4	81	H.F.	7–10		H.F.	
94	3	81	F.	8–10	R.	,,	
95	3	86	H.F.	7–9		,,	
96	3	86	,,	7–9		,,	
97	3	81	,,	8–10		,,	
98	3	86	,,	8–10		,,	
99	3		Sp.	5–6 (deg.)		Sp.	
100	3	81	H.F.	7–9		H.F.	

Trawled on 7th April, '27—Examined on 8th. Bought from Quay.

	1	2	3	4	5	6	7
1	3	106	H.Sp.	9–10		Sp.	
2	2	81	H.F.	9–10	R.	H.F. Cr.	
3	2	81	,,	7–9		H.F.	
4	2	91	,,	9–11	R.	,,	
5	2	86	F.	9–11	R.	,,	
6	2	76	H.F.	7–9		,,	
7	3	86	,,	7–9		,,	
8	3	81	F.	8–9	R.	F. Cr.	R.
9	3	81	H.F.	9–10	R.	H.F.	
10	3	86	F.	5–6 (deg.)		F.	
11	2	91	,,	5–6 ,,		,,	
12	2	86	H.F.	6–9		H.F. Cr.	
13	3	106	,,	7–9		H.F.	
14	2	81	,,	7–9		,,	
15	3	86	,,	7–9		,,	
16	2	86	H.F.	7–9		H.F.	
17	3	81	,,	7–8		,,	
18	3	86	F.	9–10	R.	F. Cr.	R.
19	2	81	,,	10–11	R.	F.	R.
20	2	81	H.F.	7–9		H.F.	
21	3	106	F.	9–11	R.	F. Cr.	R.
22	3	86	,,	7–9		,,	R.
23	3	81	H.F.	7–8		H.F.	
24	3	71	,,	8–9		,,	
25	2	76	,,	7–8		F. Cr.	R.
26	3	86	F.	7–9		,,	R.
27	2	81	,,	8–9	R.	F.	R.
28	2	86	,,	7–8		F. Cr.	R.
29	2	106	,,	8–9	R.	H.F.	
30	3	86	H.F.	7–9		,,	

	1	2	3	4	5	6	7
31	2	76	H.Sp.	6–8		H.F.	
32	3	81	H.F.	7–9		,,	
33	2	86	,,	7–9		,,	
34	2	81	,,	7–9		,,	
35	3	81	,,	6–7		,,	
36	2	76	F.	8–10	R.	F. Cr.	R.
37	3	81	H.F.	9–11	R.	H.F.	
38	3	81	,,	8–9		,,	
39	2	86	,,	6–8 (deg.)		,,	
40	2	81	,,	9–11	R.	,,	
41	3	86	F.	8–9	R.	F. Cr.	R.
42	3	76	,,	9–10	R.	,,	R.
43	2	81	H.F.	7–9		H.F.	
44	2	81	,,	7–9		,,	
45	2		Sp.	9–10		Sp.	
46	2	86	F.	5–6 (deg.)		F. Cr.	R.
47	2	81	H.Sp.	5–6 ,,		Sp.	
48	3	76	H.F.	5–6 ,,		H.F.	
49	3	81	,,	9–10	R.	,,	
50	2	81	,,	7–9		H.F. Cr.	
51	3	81	,,	8–9		,,	
52	2	86	F.	8–10	R.	F. Cr.	R.
53	3	86	H.F.	8–9		,,	R.

	1	2	3	4	5	6	7
54	3	86	F.	9–11	R.	F. Cr.	R.
55	3	81	H.F.	7–8		H.F.	
56	2	86	,,	9–11	R.	H.F. Cr.	
57	2	86	,,	7–9		H.F.	
58	3	81	F.	7–9		F.	
59	2	81	H.F.	8–9		H.F. Cr.	
60	3	86	F.	7–9		F. Cr.	R.
61	2	76	,,	7–9		,,	R.
62	3	76	,,	7–9		,,	R.
63	2	91	,,	7–9		F.	
64	2	86	,,	6–7		F. Cr.	R.
65	2	86	,,	7–8		F.	
66	3	91	,,	7–9		F. Cr.	R.
67	2	81	H.F.	9–11	R.	H.F.	
68	3	76	F.	9–11	R.	F. Cr.	R.
69	2	86	H.F.	9–10	R.	H.F.	
70	2	86	,,	9–11	R.	,,	
71	3	86	,,	9–11	R.	,,	
72	3	81	F.	9–10	R.	F. Cr.	R.
73	3	76	H.F.	8–9		H.F.	
74	3	76	,,	9–11	R.	,,	
75	3	76	F.	9–10	R.	F.	R.
76	3	81	,,	6–8 (deg.)		F. Cr.	R.

The Absorption of Glucose by *Ostrea edulis.*

By

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With 1 Figure in the Text.

CONTENTS.

1. Introduction and Literature.

In a series of papers Ranson (1924, 1925, 1926, 1927) has put forward the view that in Lamellibranchs soluble matter is absorbed directly by the epithelia of the gills, palps, mantle and other exposed surfaces in the mantle cavity. It is in this manner, he considers, that the greening of oysters is brought about, the oily green pigment (Marennin) from the diatom *Navicula ostrearia* being excreted into the water in which it is dissolved and from which it is absorbed in the manner described. He is opposed to the view that the pigment is absorbed in the alimentary canal and then deposited in the epithelium as a result of leucocytic excretion.

Ranson gives very unsatisfactory evidence in support of his views; he has failed to follow the process of absorption in any detail, while he lays great stress on the work of Carazzi (1896, 1897) and Churchill (1915, 1916). Since in my own work on feeding and digestion of Lamellibranchs, I failed to observe the assimilation of soluble matter in the form of iron saccharate elsewhere than in the digestive diverticula (or occasionally in phagocytes) in Nucula, Cardium, Mya, Teredo (1926a), in larval, spat, and adult *Ostrea edulis* (1926b), and in Cuspidaria and Poromya (1928), I find it difficult to accept the conclusions of Ranson.

Carazzi thought that Marennin was taken up by the epithelial cells of the gills, palps, and gut, and then passed on to the " liver " where it was assimilated and stored, basing his views on evidence obtained by keeping

oysters in a solution in sea-water of iron sulphate. But his experimental methods, as List (1902) originally pointed out, are open to the gravest criticism. He kept oysters for *four months* in three litres of sea-water containing 20 grams of a 10% solution of iron sulphate in distilled water, and then in clean sea-water for 1–2 weeks before fixing them. By this time the animals were thoroughly permeated with iron which he found in the epithelium of the gills, palps and gut, and in the " liver " ; but he had no better reason for assuming that it had been absorbed by the former and passed on to the latter than that the reverse process had taken place. Churchill, who worked on freshwater mussels, found that after animals had been kept in very dilute solutions of soap, egg albumen, and soluble starch stained with iodine, these substances were found in the epithelial cells of the body, mantle, foot, gills and palps, some being carried away by the blood cells which he observed on occasion between the epithelial cells. Although his experiments were kept up for from 2 to 58 days, yet absorption clearly took place through the mantle surface, because he plugged the mouths of many of his animals with wax, thus preventing the passage of material into the gut and digestive diverticula.

This evidence Ranson accepts as conclusive, while he considers that he has completed Carazzi's evidence. He found that the epithelia in the mantle cavity of white oysters became charged with Marennin, or iron sulphate, after animals from which the stomach had been cut away were kept for 48 hours in sea-water containing these substances in solution. Moreover, he suspended oysters, of which the two valves were held open, in water so that the gills and mantle were under water but the mouth and anus were not, and got similar results.

With the exception of the carnivorous Septibranchs (1928) which feed on large food masses, I have found that in the Lamellibranchs a very important rôle in the absorption of food is played by phagocytes which pass into the gut and ingest food particles (e.g. diatoms, or blood corpuscles of fish on which the animals had been experimentally fed) laden with which they return through the epithelium into the underlying tissues and blood stream (1926a, 1926b). On occasion these phagocytes may also be extruded in great numbers in the mantle cavity, a phenomenon known as " bleeding " (see Orton (1924) p. 55). After an emulsion of olive oil stained red with Nile blue sulphate was injected into the mantle cavity of oysters, it was found (1926b) that the oil had been taken in by phagocytes (and changed to blue in the process, showing that the neutral fats had been converted by the digestive enzymes into fatty acids). Some phagocytes lay free on the surface of the epithelia, but many others had passed back into the epithelia and underlying tissues of the gills, palps, mantle, and other exposed surfaces. In no case was there any evidence of direct absorption by the epithelial cells. Absorption may, therefore,

occur in the mantle cavity but only, in my opinion, *by the intervention of phagocytes*. In a letter to me on this subject Prof. E. P. Churchill says, "I suspect your finding, carrying out the details of the behaviour of the phagocytes farther than I was able to do then (i.e. in his work of 1915, 1916) is correct."

It appeared to me necessary that this problem should be approached from a new aspect, and that the capacity of oysters for removing material from solution in sea-water should be tested *quantitatively* both before and after their mouths had been plugged, and also when they were "bleeding" profusely in the mantle cavity. It was hoped to experiment with a number of substances, proteins and fats as well as carbohydrates, but, owing to lack of time, only glucose has been employed. Mitchell (1916) has already shown that oysters (*O. virginica*) which have been kept in sea-water containing dissolved glucose greatly increase their reserves of glycogen, the optimum conditions being "(a) duration of glucose feeding 2–3 days: (b) concentration of glucose equal to about 0·25%: and (c) water density not greatly different from that in which the oysters have previously been." He did not attempt to determine how and where the glucose was absorbed.

2. Methods.

Ostrea edulis was used for these experiments as it is an animal of exceptional hardiness amongst Lamellibranchs. Since it was necessary for comparative results that a continuous stream of water should be passing through the mantle cavity and through the alimentary canal during the entire course of the experiments, the inhalent and exhalent chambers were opened by means of a drill, a wide semicircle of shell being cut away opposite the palps and anterior end of the gills, and a smaller opening made in the exhalent cavity, care being taken not to damage the tissues. After the operation and subsequent washing, the presence of a through current of water, in by way of the opening in the inherent cavity and out by way of that in the exhalent cavity, was in every case demonstrated by means of carmine. It was also found that after such animals had been kept for one hour in water coloured deeply with methylene blue the stomach contents were blue, showing that a stream of water was passing into the alimentary canal. Animals treated in this way live indefinitely in the Laboratory tanks.

In all experiments the glucose solution was approximately 0·2%. In the first experiments tank water was used, and the experiments were kept going for 48 hours; but there was a great growth of bacteria at the end of this period. By using outside sea-water and running the experiments for 36 hours, this difficulty was overcome, the production of bacteria being

only slight at the end of that period. The experiments were carried out in five straight-sided aquarium jars in each of which was placed four litres of sea-water containing glucose. Two oysters were placed in each jar (it was difficult to get significant differences in 36 hours when one oyster was used) and the water was kept well aerated for the full period of the experiments. Control experiments (to check the possible decomposition of glucose by bacteria), consisting of one litre of glucose solution without oysters, accompanied each set of experiments.

In the first set of experiments normal animals were used, in the second the mouths of the oysters were plugged by covering the palps (the mouth in Ostrea is not exposed) with hot wax which immediately solidified without damaging the tissues. To prevent the wax floating away when the animals were placed in water it was held in place with plasticine, which in turn was secured (and the oysters prevented from moving the plugs by flapping their valves) by string tied tightly round the oyster. In the third set of experiments plugged oysters " bleeding " profusely in the mantle cavity were employed. It was found in the preliminary experiments, where the great growth of bacteria caused the pH of the water to fall to 6·8, that the oysters " bled " profusely ; the attempt was made to repeat this experimentally by lowering the pH with acid, but without satisfactory results ; instead, *plugged* oysters were induced to " bleed " by leaving them in the Laboratory tanks for 8 days, at the end of which period the mantle cavity contained great masses of leucocytes.

The glucose, both before the experiments and after 12, 24, and 36 hours, was estimated by means of Benedict's solution in both experiments and controls, samples of 50 c.c. being removed for that purpose. The results were later converted into grams of glucose per litre. The pH was taken at the same time, though only the first and last readings are given in the tables. In every case five experiments and one control were run.

3. Experimental Results.

The results are most easily understood by reference to Tables I, II, and III, referring to experiments with normal, plugged, and plugged and " bleeding," oysters respectively. In no case was any decrease in glucose observed in the controls, showing that, in the 36 hours, there is no appreciable action by bacteria. The pH never fell lower than 7·3 and seldom as low as that. In the case of normal oysters there was a progressive diminution in the amount of glucose : but when the *same* oysters were plugged there was *no* change in the amount of glucose present in two experiments and only a slight diminution in the other three, while, after testing the stomach contents of all oysters with Fehling's solution, glucose was detected in one oyster from each of the three latter experimental jars, but not in any of

TABLE I.

Normal Oysters in Glucose Solution.

Five experiments (A–E) and control (K), each experiment consisting of 2 oysters, opened in inhalent and exhalent chambers, in 4 litres of sea-water containing about 0·2% glucose in solution.

	pH	Glucose in grams per litre.				Total	pH
	before.	before.	12 hrs.	24 hrs.	36 hrs.	decrease	after 36 hrs.
A	8·0	2·041	2·0	1·951	1·886	0·155	7·4
B	8·0	2·041	2·0	1·887	1·835	0·206	7·3
C	8·0	2·051	2·02	1·961	1·923	0·128	7·4
D	8·0	2·051	2·01	1·932	1·878	0·173	7·3
E	8·0	2·062	2·02	1·942	1·887	0·175	7·3
K	8·0	2·062	2·062	2·062	2·062	0	7·8

TABLE II.

Plugged Oysters in Glucose Solution.

Same procedure as in Experiment I, same animals used, but mouths plugged with paraffin wax held in place by plasticine and string.

	pH	Glucose in grams per litre.				Total	pH
	before.	before.	12 hrs.	24 hrs.	36 hrs.	decrease.	after 36 hrs.
A	8·0	1·961	1·961	1·942	1·932	0·029*	7·5
B	8·0	1·961	1·961	1·961	1·961	0	7·5
C	8·0	2·02	1·98	1·98	1·961	0·059*	7·6
D	8·0	2·02	1·98	1·98	1·961	0·059*	7·6
E	8·0	1·99	1·99	1·99	1·99	0	7·7
K	8·0	1·99	1·99	1·99	1·99	0	7·8

TABLE III.

Plugged and "Bleeding" Oysters in Glucose Solution.

Same procedure as in Experiments I and II, but oysters plugged for 8 days before and, as a result, "bleeding" profusely in mantle cavity.

	pH	Glucose in grams per litre.				Total	pH
	before.	before.	12 hrs.	24 hrs.	36 hrs.	decrease.	after 36 hrs.
A	8·0	2·083	2·041	2·0	1·942	0·141	7·85
B	8·0	2·083	2·041	1·942	1·914	0·169	7·5
C	8·0	2·083	2·03	2·0	1·961	0·122	7·8
D	8·0	2·083	2·041	1·961	1·896	0·187	7·9
E	8·0	2·083	2·02	1·951	1·932	0·151	7·8
K	8·0	2·083	2·083	2·083	2·083	0	8·0

* Glucose detected by means of Fehling's solution in stomach of one oyster in each of these experiments ; no sugar in stomachs of other seven oysters.

the other seven oysters. Thus there is evidence that the slight diminution was due to the passage of glucose into the alimentary canal and its subsequent absorption in the digestive diverticula. There was no evidence of " bleeding " in these oysters after 36 hours. In the case of plugged and " bleeding " oysters a very marked diminution in the quantity of glucose was noted, almost as great as in the case of normal oysters, but in no case did an examination of the stomach contents reveal the presence of sugar.

TABLE IV.

Comparison of Percentage Amounts of Glucose removed from Solution in 36 hours by Oysters under Different Conditions.

	Same Oysters.		
	Normal.	Plugged.	Plugged and " Bleeding."
A	7·59	1·48	6·77
B	10·09	0	8·12
C	6·24	2·92	5·86
D	8·43	2·92	8·98
E	8·49	0	7·25
Average	8·17	1·46	7·40
K	0	0	0

In Table IV the experimental results are compared, and the differences in the percentage amounts of glucose removed from solution by oysters under different conditions shown. In the graph shown in Fig. 1, on page 649, the percentage decrease in glucose is plotted against the time for all five sets of experiments (A–E) under the three different experimental conditions, and the differences very strikingly displayed. The results of the normal and plugged experiments are directly comparable as the same animals were employed, but, though different animals had to be used for the plugged and " bleeding " experiments, the results are introduced into the graph for the sake of completeness.

The results given above are those of final experiments which confirmed the results obtained from a series of preliminary experiments.

4. Discussion.

The above results show clearly that, though two normal oysters may remove from 6·24 to 10·09 per cent of the glucose in 36 hours, either no glucose or very slight quantities are absorbed after the mouths of the oysters have been plugged, and the slight degree of absorption in three

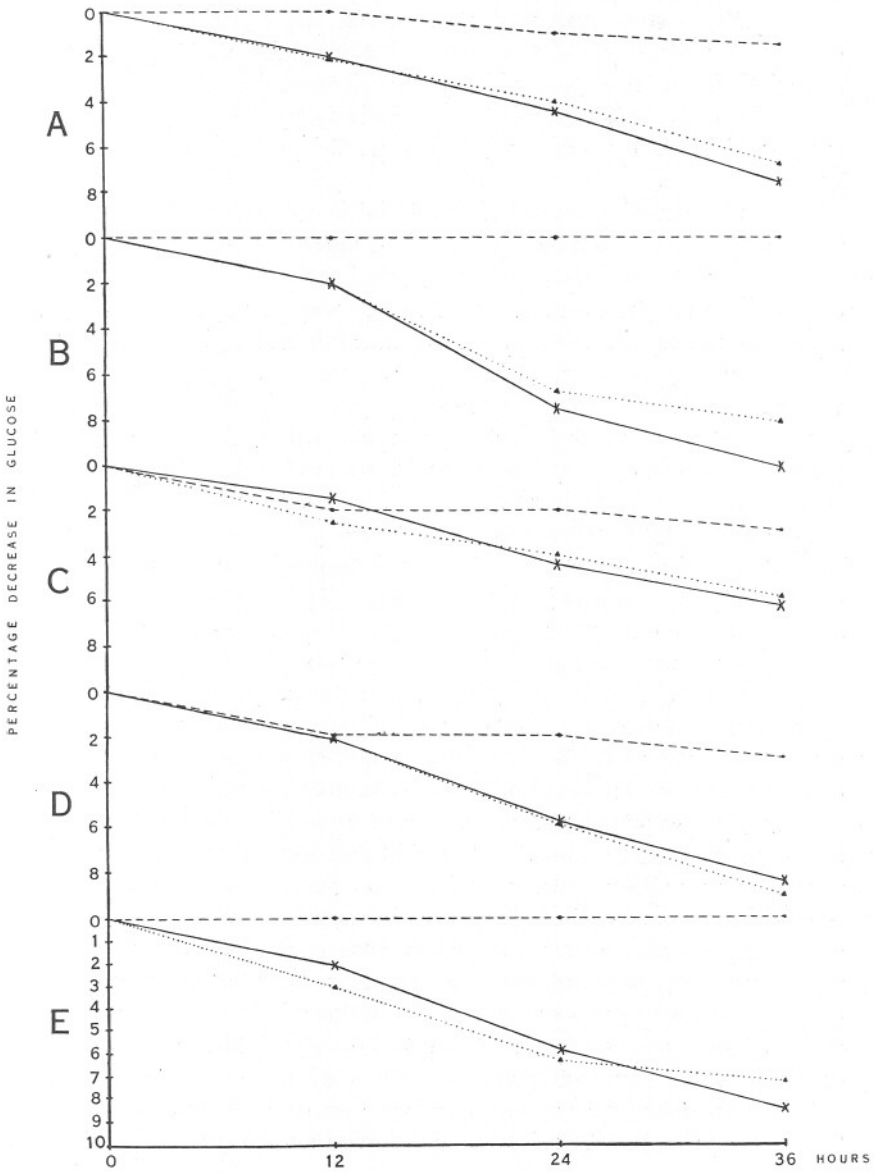

FIG. 1. Graph showing percentage decrease in dissolved glucose up to 36 hours in five sets of experiments (A–E), two oysters being used in each, under three different conditions, normal, plugged, and plugged and "bleeding," the *same* oysters being used in the normal and plugged experiments.

—×— Normal. - - -•- - - Plugged. ·····▲····· Plugged and "Bleeding."

cases is probably due to incomplete blocking of the mouth. These results are entirely in agreement with previous feeding experiments with iron saccharate, which showed that absorption of soluble matter takes place *exclusively* in the tubules of the digestive diverticula. Absorption in the remainder of the gut is carried on exclusively by the agency of phagocytes, which are concerned with solid particles rather than matter in solution.

From the digestive diverticula material is transported by leucocytes throughout the body especially, if it be of nutritive value, to the gonads. But if it is waste material (such as Marennin) then, if absorbed in large quantities, it may not all be disposed of by way of the excretory organs (which do not appear very efficient in Lamellibranchs), but be deposited in the epithelial cells lining the alimentary canal and mantle cavity. The presence of pigmented granules in such cells is *no* indication that they have been absorbed by the cells. Thus the stomach epithelium of Nucula (1926a) is frequently found gorged with them although iron saccharate is absorbed exclusively in the digestive diverticula, while in Cuspidaria and Poromya (1928), where the stomach cells are invariably packed with brown or yellowish granules, absorption is impossible owing to the thick cuticle which everywhere lines the stomach. In the Gastropod, Trochus, also, I have found the epithelium of the stomach packed with green globules, but, there again, iron saccharate was absorbed exclusively in the digestive diverticula. In all cases, probably, these granules represent excretory matter deposited in the epithelial cells by leucocytes in much the same way as the products of the digestion of the blood corpuscles fed to oysters are passed on to the epithelial cells from the phagocytes (1926b).

Nevertheless material may be absorbed directly in the mantle cavity, as shown by the experiments of Churchill and Ranson where the alimentary canal was either securely blocked, removed, or else raised above the solution. The explanation of this, as I indicated above, is to be found in the presence of phagocytes free in the mantle cavity. This view receives the strongest support from the experiments on plugged and " bleeding " oysters. In no case was sugar detected in their stomachs, yet from 5·86 to 8·98% of glucose was removed by two oysters in 36 hours. In every case the mantle cavity contained countless millions of extruded phagocytes which formed whitish masses on the surface of the mantle and gills. There is good reason, therefore, for assuming that the glucose is absorbed by these phagocytes, since the epithelia in the mantle cavity have been shown to be incapable of absorbing. We know little, unfortunately, of the conditions causing " bleeding " in Lamellibranchs, but unfavourable conditions, such as high temperature, being kept for a day or more out of water—especially in warm weather (Orton (1. c.) p. 59)—or in water of low pH, or with their mouths plugged for long periods, undoubtedly cause

it. In the experiments of Churchill (where freshwater bivalves were kept for long periods with their mouths plugged) and of Ranson (where the alimentary canal was cut away, or oysters suspended half out of water) the conditions were so abnormal that " bleeding ", to a greater or less extent, most probably occurred. The phagocytes so extruded would ingest solid material or absorb soluble matter (as I found in the case of olive oil), and some of them would make their way back into the tissues. This I consider to be the true explanation of these experimental results. It is not impossible that Marennin may be absorbed in this manner in the " claires " at Marennes, where the temperature and salinity of the water both become exceptionally high in the periods between spring-tides, thus possibly causing extensive " bleeding " in the oysters. In other cases the Marennin is probably absorbed in the digestive diverticula and thence transported to all free surfaces by the leucocytes.

The great importance of leucocytes in the mantle fluid of Lamellibranchs has recently been emphasised by Jatzenko (1928), who has approached the problem from the very different aspect of respiration and found that an important part in the process of respiration in freshwater Lamellibranchs is played by the leucocytes. Gorka (1916) stated that the gill mucus of Anodonta and Unio contains enzymes capable of digesting a variety of substances and, as previously pointed out (1926b), the enzymes he found were probably derived from phagocytes in the mucus.

Reference may be made, in conclusion, to the work of Hatt (1926), who states that Indian ink is taken in phagocytically by the epithelium of the gills and palps of Lamellibranchs. Indian ink undoubtedly appears in the epithelia after animals have been in a suspension of ink for several weeks, but this was observed by List and attributed by him, probably correctly, to the action of leucocytes which carried it from the digestive diverticula where it is freely absorbed, as recently confirmed by Vonk (1924). Hatt, however, claims that the ink is taken in directly by the ciliated epithelium because, when he cut off pieces of gill and palp and placed them in water containing Indian ink, he found this in the cells after some six hours. I have repeated his experiments, using the tissues of *Ostrea edulis*, and found that, under these circumstances, many phagocytes appear on the surface of the epithelium, a large number of them gorged with Indian ink. Others, similarly laden, were seen, after sectioning, between the cells of the epithelium and in the blood stream. Ink was occasionally to be seen in the epithelial cells, but there was no evidence that it was directly ingested ; it is, in view of the evidence outlined in this paper, far more probable that it was deposited there by phagocytes.

Acknowledgments are due to the Director and Staff of the Plymouth Laboratory for the provision of facilities for this research, and especially

to my wife, without whose constant help it would have been impossible, in the limited time at my disposal, to have completed the experiments and prepared the manuscript for the Press.

5. SUMMARY.

1. Normal healthy oysters with openings drilled in both inhalent and exhalent chambers, remove considerable amounts of glucose from solution. The average diminution in 5 experiments, each consisting of two such animals kept in 4 litres of sea-water containing about 0·2% of glucose, was 8·17% at the end of 36 hours.

2. In similar experiments, using the same oysters after their mouths had been plugged with wax and plasticine, there was only an average diminution of 1·46% in the glucose at the end of 36 hours. In two of the experiments there was no diminution, and in the three others there was evidence that one of the two oysters in each had been incompletely plugged and glucose had passed into the alimentary canal.

3. Oysters which had been plugged for 8 days so that they were "bleeding" profusely, the mantle cavity containing vast numbers of leucocytes, were used for a third set of experiments in which the average diminution was 7·4% at the end of 36 hours.

4. There was no evidence of bacterial decomposition of glucose within the experimental period.

5. These results, taken with those of previous investigations, show that the ciliated epithelia of Lamellibranchs cannot absorb (nor ingest phagocytically). Absorption takes place in the tubules of the digestive diverticula within the alimentary canal, and, in the mantle cavity, only through the agency of phagocytes which are extruded in great numbers when Lamellibranchs "bleed" as a result of bad conditions.

6. The opinion of Ranson that Marennin and other soluble matter is absorbed directly by the ciliated epithelia in the mantle cavity cannot be upheld, this material being deposited in the cells by the phagocytes which either absorb it directly from the mantle cavity and gut, or transport it from the digestive diverticula.

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Contributions to the Study of Relative Growth in *Gammarus cheureuxi.*

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With 18 Figures in the Text.

Introduction.

The following two sections represent two preliminary communications to the study of relative growth in a small Crustacean admirably adapted for use as a laboratory animal in all studies involving growth and development.

It is not proposed to discuss the significance of the results in detail at the present moment. For this, more data will be necessary. But one or two points may be mentioned.

One of the results of work on relative growth has been to show (Huxley, 1927) that in Crustacean appendages, showing disharmonic (heterogonic) growth, there exist *growth-centres* where the growth-rate is at a maximum. In the appendages so far studied the growth centre appears to be not at but close to the distal end (propodite). A distal growth-centre for heterogonic organs also exists in the antlers of deer, in the legs of mammals (unpublished work of J. Hammond, to whom we would like to express our thanks for allowing us to mention the fact), and in the abdomen of female Inachus (unpublished observations of Miss M. E. Shaw).

The studies of the present paper do not throw further light on this particular aspect of the problem. They do, however, throw some light upon the problem of growth-centres in the main trunk-region of the animal. For instance, the facts concerning the growth of the fifth free segment (see later) indicate that in females there is here a growth-centre (presumably part of a larger region of rapid growth) associated with the development of ovary and brood-pouches in this segment. In the two sexes the whole relative rate of growth of trunk (including head) and

appendages is also different, the partition of growth-potential being more in favour of the appendages in the male, of the trunk in the female.

Another general fact appears to be that excess growth of appendages as a secondary sexual male character is predominantly in *length*, even in parts which (like gnathopod propodite) are broad and massive. All appendages (as would be expected, since they are outgrowths from the body) grow more in length than in breadth in both sexes ; and apparently it is natural that this tendency should be still the underlying one in the sexual heterogonic growth of secondary sexual characters.

Finally, when a part shows marked enlargement in one sex, it appears often to show relative decrease in the opposite sex, instead of remaining constant (isogonic) in its growth as might perhaps be expected. This appears to be the case with the ♂ fifth free segment, the ♀ uropod, and the ♀ gnathopods. Even in details, the growth-processes appear often to be reversed in the two sexes when the organ is an enlarged sex character in one sex (see under gnathopods).

It is hoped that by the accumulation of studies such as these a detailed knowledge of the growth-centres in the body, or, we may say, the partition of growth-potential in different species, may be gradually acquired. If so, it would pave the way for interesting biochemical studies in growth.

PART I.

By

B. W. KUNKEL.

(*A*) FOREWORD, MATERIAL, AND METHODS.

The work done recently on heredity in the brackish-water Gammarus, *G. chevreuxi*, especially that which indicates that certain eye mutations are in the nature of retardations in the development of normal characters (Ford & Huxley, 1927), has made the study of the growth-changes of this animal seem highly desirable. On Professor Huxley's suggestion, therefore, while working in his laboratory at King's College, London, in 1925, I undertook to study the changes in bodily form of this species under normal circumstances. It gives me great pleasure at this time to express my appreciation of the many courtesies and suggestions of Professor Huxley in connection with this study.

The material used in the study consisted of some two hundred wild specimens from Plymouth, England, where the species was first found, together with about fifty which had been reared in the laboratory at Oxford. These latter were used to fill out certain gaps in the material procured at Plymouth. In order to measure the appendages it was found

necessary to dissect them off carefully and mount them in glycerine to render them transparent. The gnathopods especially showed so strong a tendency to be bent medially that without dissection they were greatly foreshortened and so incapable of accurate measurement. It was found most convenient to project the magnified image of the appendages on a glass plate over which co-ordinate paper ruled to millimetres could be moved about freely. The paper was sufficiently thin to allow the image to show through readily. At the magnification used, namely, 61 diameters, it was impossible to read the measurements closer than one millimetre apparent—i.e. about 17 μ absolute.

The following measurements were made: breadth and length of the second joint of the peduncle of the first antenna; breadth and length of the propodite of the first and the second gnathopods and of the first pereiopod. In addition to these measurements, the joints of the flagellum of the first antenna were counted. This last-named character was exceedingly irregular, probably because of the frequency with which the flagellum is injured and joints of the flagellum autotomized. For the sake of brevity, the second peduncular joint of the first antenna will be referred to simply as "the antenna" and the propodites of the gnathopods and pereiopod will be referred to simply as "the gnathopods" and "pereiopods" respectively.

It is fully realized that the method of studying growth of an organism by measuring a population, as has been done in the present study, is open to certain objections from which the study of successive ecdyses of the same individual is free. Mrs. Sexton's (1924) paper, however, shows that Gammarus can be examined in this way only with the greatest difficulty, because of the tendency of the animal to eat its own skin very shortly after shedding it.

The propodite of the first pereiopod was selected as the index of the size of the individual throughout because of its uniformity in the two sexes and because of the fact that in the course of growth the pereion does not suffer the conspicuous changes which the cephalon does.

The growth in total size of the female Gammarus ceases much earlier than that of the male. This has been observed already in *G. chevreuxi* in the paper referred to above by Mrs. Sexton, and in other species by a number of observers. After sexual maturity is reached, the female's growth becomes very slow, while that of the male continues high. I did not meet with any male as large as Mrs. Sexton reported, but even so, in my largest male the pereiopod attained a length 164% of that of the largest female in my collection.

In general, the sexual differences could not be determined at as early a stage as Mrs. Sexton has shown in the careful drawings of successive moults of the same individual. The characteristic curved hairs of the

second antenna of the male do not appear generally as early as she has figured them. The smallest individuals whose sex I could be sure of had a pereiopod length when projected of 11, and the flagellum of the first antenna in one case had only ten segments, which would correspond with Mrs. Sexton's fourth stage; but generally when the sex could be determined in so small an animal, there were from fourteen to sixteen flagellar segments, which would indicate a fifth or sixth stage.

(*B*) Results:—1st Antenna; Gnathopods; 1st Pereiopod.

The changes in the relations of certain dimensions with age can be expressed in several ways. One of the simplest is by plotting the ratio of

TABLE I.

Ratios to Pereiopod Length, expressed as %.

Pereiopod length mm.	Ant. length.					Gn. 1 length.			Gn. 2 length.		
	no.	sex ? %	no.	sex ♀ %	no.	sex ♂ %	sex ? %	sex ♀ %	sex ♂ %	sex ? %	sex ♀ %	sex ♂ %
·08	6	83·3					80			96·7		
·098	11	72·8					84			84·5		
·11	6	76					85·2			85·2		
·13	6	85·7					91·5			91·5		
·15	6	77·8					83·5			83·5		
·16	10	84					90			90		
·18	11	84·2	3	82	2	91	89·7	91	103	89·7	95·5	106
·197	4	87·5	1	83	3	86	91·7	100	102·7		100	91·7
·21			1	77	4	86·5		92	102		100	102
·23			1	100	7	90			97			104·4
·25			5	90·6	2	90		100	100		101·2	106·5
·26			2	94	7	89·9		100	102·3		100	102
·28			5	87·2	2	91		102·4	103		104·5	104·8
·29			9	95·7	5	95·6		99·8	122·4		103·6	117·5
·31			6	89·3	3	96·7		98·3	119·7		95·7	128
·33			10	90	7	97·9		100·2	116·4		100	127·9
·34			2	88	1	86		95	124		93	138
·36			3	91·	4	101·2		95·3	136·2		104·7	150·5
·38			2	95·5	6	105·5		98	138·3		102·5	150·8
·39			1	96	5	101·6		100	142·2		104	155·8
·41			2	84	8	106·5		92	150·2		94	166·5
·43					7	107·9			153·3			163·3
·44					9	109·8			149·1			162·4
·46			1	64	7	108·1		75	146·9		75	162·4
·48					4	107·5			148·2			166·7
·49					5	105·6			143·8			158·6
·51					2	108			148			162
·525					3	103			139·7			151·5
·54					1	115			145			164
·56					8	107·5			144·1			158·2
·57					1	108			146			157
·59					2	108·5			140			154·5
·61					2	104			135			170
·62					2	116			145			166
·64					2	106			136			155
·66					2	110			146·3			149
·67					1	112			146			151

the part in question to the standard against the standard itself. The ratios of length of antenna and of first and second gnathopods to length of pereiopod are shown in Table I, and have been plotted against pereiopod length in Figs. 1 and 2. In spite of the size of the groups upon which these graphs are constructed, they exhibit certain irregularities whose significance has not yet been interpreted. It is obvious that in the early stages, before sexual differentiation is apparent, there is an elongation

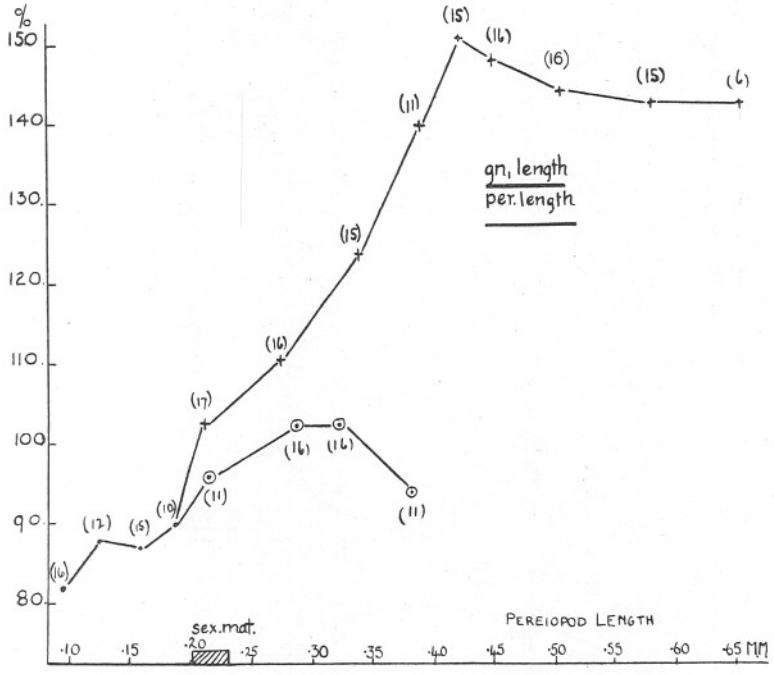


FIG. 1. Ratio of the length of the first gnathopod to the pereiopod expressed as % plotted against the pereiopod length. The figures in parentheses indicate the number of individuals in each class. The young in which the sex was indeterminate are indicated in all the diagrams by a ●, the males by a +, and the females by a ⊙.

of the antenna and the two gnathopods which is more rapid than that of the pereiopod; furthermore, that of the antenna is more uniform than either of the gnathopods, in which appendages the sexual differences are more marked. In the female, from the time sexual differences are evident, there is practically no further relative elongation of the antenna, as is indicated by the nearly horizontal position of this portion of the curve. The antenna of the male, on the other hand, increases more rapidly in length relatively to the pereiopod, until the latter attains a length of about 0·44 μ, which is beyond the maximum size attained in the female.

From this time on, although actual growth does not cease, the male antenna simply keeps pace with the pereiopod, maintaining a proportion of 106 to 109% of the latter.

The changes in the length of the first gnathopod with reference to the pereiopod are similar, but rather more irregular. During adolescence there is a gradual increase, as in the case of the antenna. While the latter

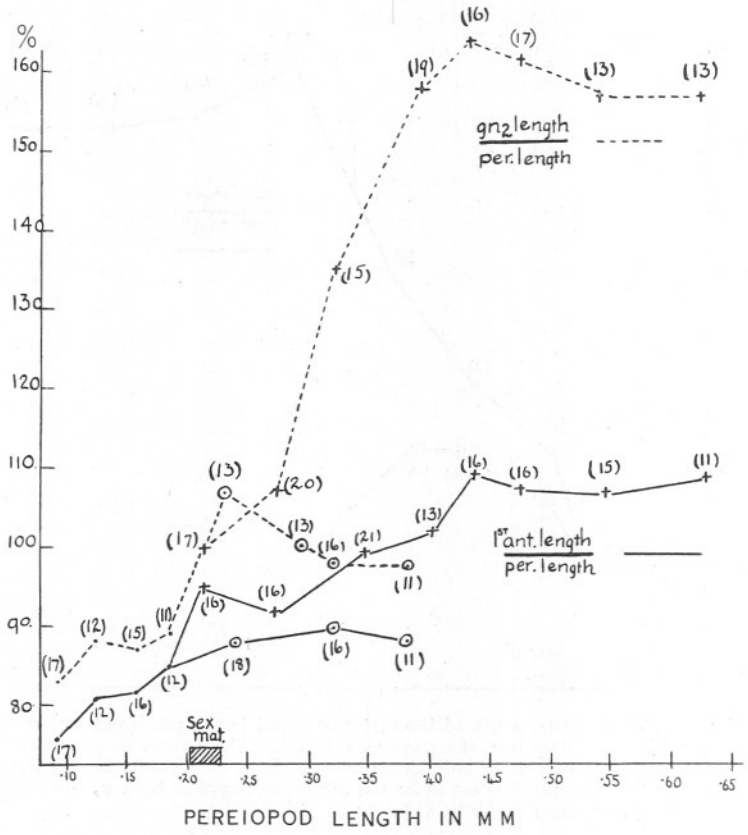


FIG. 2. Ratios of the length of the antenna and of the second gnathopod to the pereiopod expressed as % plotted against the pereiopod length. The graph of the antenna is represented by a solid line, that of the second gnathopod by a broken line.

increases from 75% to 85%, the elongation of the first gnathopod is from 83% to 90%. The gnathopod of the mature female elongates for a short time more rapidly than the pereiopod, then for a very brief period at the same rate, and then when older it lags markedly behind the pereiopod. The changes in the length of the first gnathopod of the male are quite different from those of the female. From the size at which sexual

differences are first discern'ble, up to about the size finally attained by the female, elongation is very rapid. In very large males, however, the growth falls somewhat behind that of the pereiopod, until the gnathopod proportional length finally becomes constant at 143% of the pereiopod. In comparing the growth changes of the male gnathopods and the antenna, it would seem as if the former gained a certain momentum of growth and then lagged behind the pereiopod, while the antenna during the period in which the gnathopods are growing so rapidly, grows at a lower rate but maintains its relative size, instead of falling behind like the more markedly heterogonic appendages when comparative old age has been reached.

The changes in length of the second gnathopod with reference to that of the pereiopod are more marked than those of the first gnathopod, and of the same character, but a little less regular. During immaturity, before the sexes can be distinguished, there is a slight irregularity similar to that of the first gnathopod, but more marked. In general, the second gnathopod-length shows a more marked relative increase during this period than does the first, the relative growth-rate being highest just before maturity.

The second gnathopod of the female shows at first a very rapid relative rate of elongation, and at about ·225 mm. pereiopod-length actually surpasses that of the male. This is followed, however, by a longer period, during which the relative length of the gnathopod grows less, until finally the ratio becomes constant at about 97%. The second gnathopod of the male exhibits essentially the same changes in elongation that the first gnathopod does. There is a very rapid rising of the curve from 100% to a maximum of 164% during the time between the attainment of sexual maturity and the time that the body-size of the largest female is reached. In the largest males there is a slight relative retardation of the gnathopod and then a constant ratio of 157% is maintained. The second gnathopod is thus relatively longer than the first in large males, but smaller in small males. *Per contra*, the female second gnathopod is relatively longer than the first in small animals, but then decreases more rapidly, though not to a finally lower level.

A better index of growth than the increase in a single dimension of a flattened structure is the increase in its area. Accordingly the product of length and breadth has been calculated for the joints measured. This will not be far from being proportional to the actual area of the surface; and for brevity's sake is hereafter referred to as " the area " of the joint in question. The areas of the projection of the antenna and of the gnathopods, thus found, were then plotted against the area of the pereiopod, on a double logarithmic graph. Table II gives the data upon which graphs in Figs. 3, 4, and 5 have been constructed. The graph illustrating

the growth of the antenna shows that the antenna area increases at a rate only slightly greater than that of the pereiopod area. In the simple heterogony formula, $y=bx^k$, k expresses the ratio of the two growth-rates considered, and is here between 1·1 and 1·2. The general tendency is for the relative growth-rate to be higher at first (k=1·2 to 1·3) during adolescence and early maturity, and then to decrease, earlier in females than in males, to a rate actually below that of the pereiopod area (k=about 0·8 and 0·9 in females and males respectively). In other words, the breadth of the antenna cannot be increasing relatively as fast as that of the pereiopod. This is brought out in Fig. 4. The slight irregularities

TABLE II.

Ratios of Breadth to Length, expressed in %.

	Per.					Ant.			Gn. 1.			Gn. 2.		
Per length mm.	No.	Sex ind. %	No.	♀ %	No.	♂ %	Sex ind. %	♀ %	♂ %	Sex ? %	♀ %	♂ %	Sex ind. %	♀ %	♂ %
·08	6	23·3					60·3			80			63·3		
·098	11	33					65·4			62			71·5		
·11	6	29					59·5			75·3			71·7		
·13	6	25					55·8			66			69		
·15	6	23·8					54			63·2			64·3		
·16	10	21					52·7			69·1			61·2		
·18	7	20·5	4	22·5	3	21	51·7	50·2	48·3	68·1	65	63	66·7	59·5	63·3
·197	4	21	1	25	3	25	48·2	50	52·5	70	58	58·7	66·7	58	57
·21			1	23	4	23		50	51·5		67	64·2		54	60·2
·23					7	23			43			65·4			62·4
·25			5	24·2	2	23·5		43	48		55·2	66·5		62·2	59·5
·26			2	19	7	22·4		43·5	48·1		62·5	64·2		59·5	60·3
·28			5	22·8	3	20		46·8	39·7		62·6	60·7		58	55
·29			9	20·9	5	21·2		38·8	43·8		61·8	61·7		58·8	62
·31			5	19	3	19·7		39·6	41·2		63·9	62		62·6	62·7
·33			10	20·5	7	20		40·2	39·7		65	61·9		59·7	58·7
·34			2	22·5	1	19		38	44		61·5	54		61·5	57
·36			3	21·3	4	21·7		43·3	36		65·3	58·2		64	60
·38			2	19·5	6	20·3		38·5	35·3		64·5	54		55·5	56·7
·39			1	21	5	20·2		39	34·6		58	55		56	56·6
·41			2	20	8	19		38	33·9		63	52·4		62	56·1
·43					7	18·4			35·1			50			57
·44					9	19·3			32·9			48·9			55·2
·46			1	18	7	18·4		44	32·6		62	49·9		62	57·3
·48					4	19			34·2			49·5			56·2
·49					5	19·4			33·4			48·6			55·4
·51					2	19			40			47			54·5
·525					4	19			32			51·7			59·2
·54					1	18			29			46			54
·56					8	20·2			33			49·5			58·4
·57					1	20			34			51			60
·59					2	18			32			44·5			54·5
·61					2	19			29·9			47			58·5
·62					2	18			29·5			48			57·5
·64					2	19			33			51			57
·66					3	19·3			29			50·7			57·7
·67					1	17			26			47			66

are essentially the same as those exhibited in the growth in length with respect to the pereiopod length.

The increase in the area of the first gnathopod relative to that of the pereiopod is shown in Fig. 4. It is comparable to what had been found in a number of secondary sexual characters, as has recently been pointed out by Huxley (1926). During adolescence, before the sex can be determined,

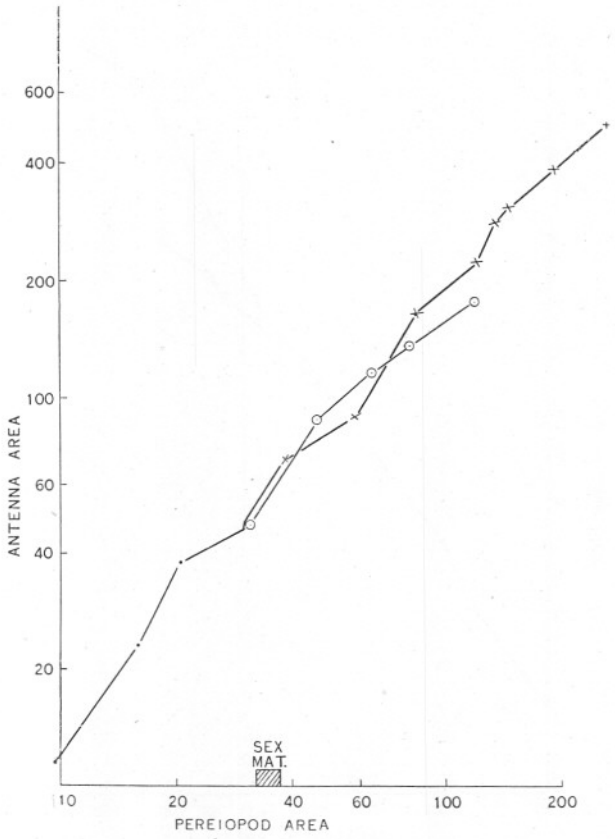


FIG. 3. The area of the antenna is plotted against the area of the pereiopod, on a double logarithmic grid.

the gnathopod area increases more rapidly than that of the pereiopod, so that the slope of the graph is greater than 45 degrees ; k, as read from the tangent of the angle made by the graph with the x axis, is nearly 1·4. The rate is on the whole greater at first, less (k=about 1·2) later. In the female, this decrease is gradually accentuated, k being at first close to 1·0, dropping later to 0·8. On the other hand, in the male the gnathopod increases much more rapidly from soon after the moment of sexual differentiation up to the time that the maximum female size is reached. During

this period k is almost equal to 2·0. At the close of this period, the increase of the area of the gnathopod slows down to a little below that of the pereiopod.

The second gnathopod area (not figured) increases with somewhat greater uniformity than that of the first gnathopod, as well as at a greater

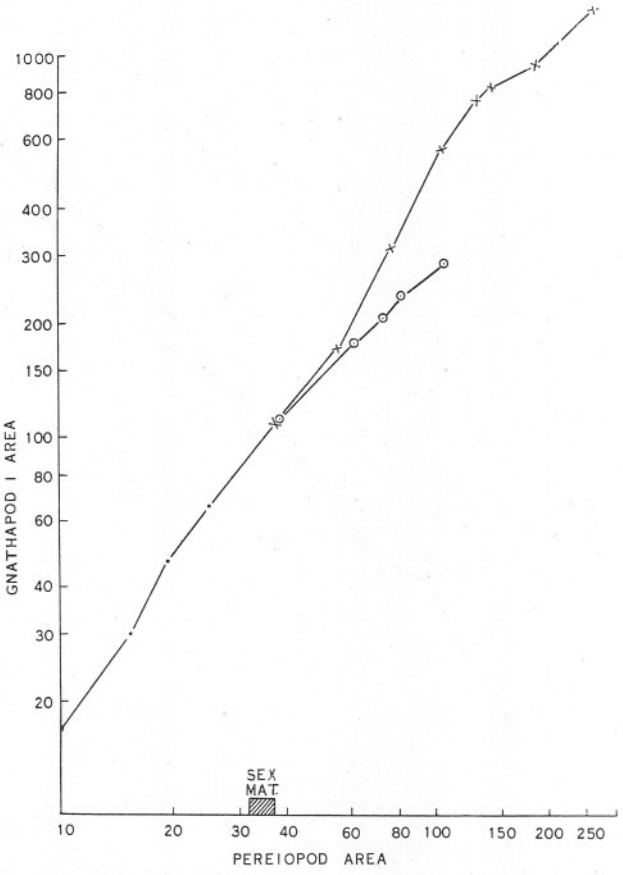


FIG. 4. The area of the first gnathopod is plotted against the area of the pereiopod, on a double logarithmic grid.

rate. During adolescence the gnathopod increases in area faster than the pereiopod. Throughout the period of sexual differentiation the female exhibits great regularity, the graph being a straight line and k being a little over 1·1. This is peculiar in view of the irregularities in length percentages ; presumably the area is much more constant than the length or breadth taken singly. This is corroborated by Fig. 5. The second gnathopod of the mature male grows very rapidly in respect to the

pereiopod. Up to approximately the time when the maximum size of the female is reached, k averages a little over 2·0, with a maximum value of nearly 2·5. In very old males, however, the gnathopod and pereiopod areas increase at about the same rate.

Changes in the form of the appendages with growth are shown in Fig. 5, which is constructed from the data shown in Table II. These changes in form are indicated by the ratio of the breadth to the length of the appendages in question. These ratios in the diagram have been plotted

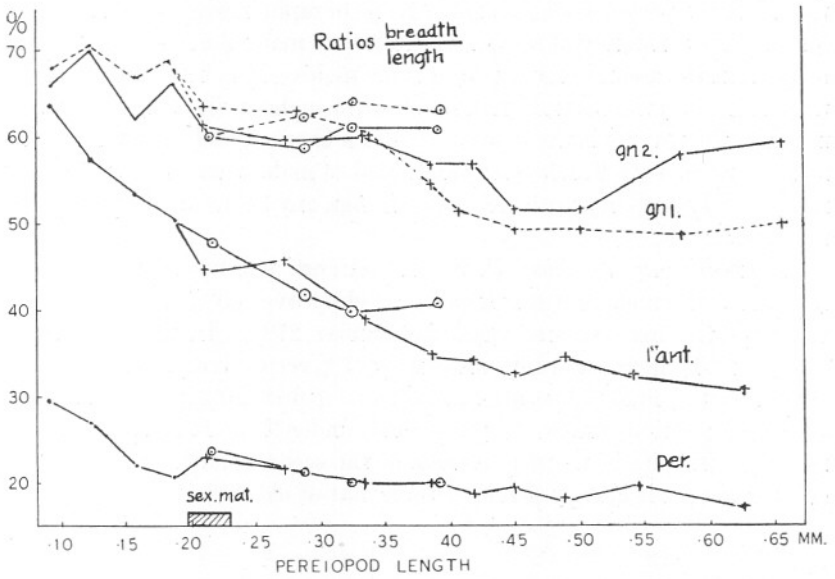


FIG. 5. The ratios of the breadth to the length, expressed as a %, are plotted against the length of the pereiopod. The graphs of the pereiopod, antenna, and second gnathopod are shown with solid lines, that of the first gnathopod by a broken line.

against mean pereiopod length. In the very early stages the pereiopod becomes rapidly more slender, but before sexual maturity is reached the form becomes more established and from that time on in both sexes the increase in slenderness is slighter (somewhat over 20% decrease in the relative breadth). The total decrease of the relative breadth is under 40% of its original value. The antenna of the male shows in general an increase in slenderness, more marked at first, but evident in even the oldest males. The total decrease of relative breadth is over 50% of its original value, and the decrease after maturity is over 30% of its value at maturity. In females there is a similar increase in slenderness until they become fairly old, when the ratio becomes constant. The male ratio never

becomes constant, but there is a definite slowing up of the decrease in this sex, as in the females.

The changes in the form of the gnathopods are less regular than in the antenna or the pereiopod. During immaturity there is an increase of slenderness, but with marked oscillations. This cycle is repeated before the period of sexual differentiation is reached, but the general tendency is definitely toward an increase of slenderness. In the female, both gnathopods during the period of sexual maturity tend to increase in relative breadth, the first more so than the second. In mature males, there is first a period of slight, and then one of rapid increase of slenderness, followed by constancy of ratio in the first, but marked increase of relative breadth in the second gnathopod of large males. It is interesting to note that in females the second gnathopod is throughout the slenderer, while in males the reverse is the case except for a short period after the attainment of maturity. The second gnathopod of males then grows relatively more rapidly both in length and breadth than any of the other appendages measured.

The maximum decrease (between extreme points) of the relative breadth of the male first gnathopod is slightly over 30% of its maximum value, of the male second gnathopod under 27%. In the female the corresponding figures are 15% and under 17% respectively. The decrease from initial to final values are as follows :—♂ first, 20% ; ♂ second, just over 10% ; ♀ first, under 8% ; ♀ second, under 9%. It is interesting to note that in spite of the massiveness of the second gnathopod propodite of old males, it is always slenderer than that of old females.

PART II.

By

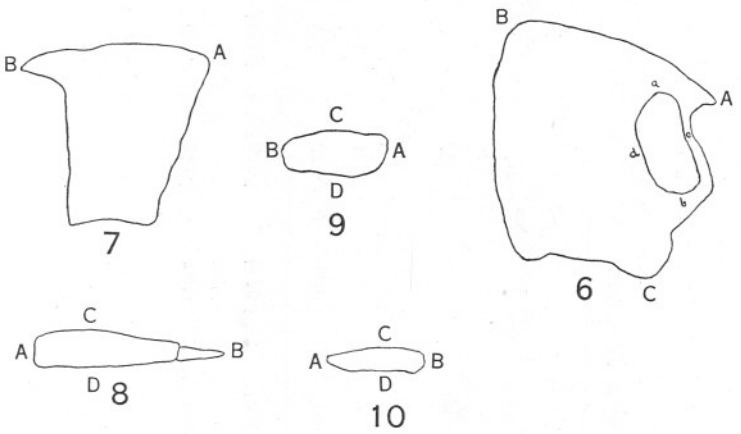
J. A. Robertson.

(*A*) Foreword and Methods.

It was suggested to me by Professor J. S. Huxley that some investigation of the comparative rates of growth of various appendages of *Gammarus chevreuxi* would be of interest, especially in view of the knowledge recently acquired of its genetic constitution. Since Professor B. W. Kunkel had already investigated the growth of the first antenna, first and second gnathopods, and the first pereiopod in this species (see Part I of this paper), it was decided that further measurements of head, eye, second antenna, uropod, and fifth body-segment would render the account of the growth-phenomena more comprehensive. I accordingly undertook the latter measurements, together with those of the first pereiopod

as a standard whereby the two sets of results might be compared ; the only other measurement common to the two investigations is the record of the number of flagellar joints in the first antenna.

The measurements were made by means of a screw-micrometer-eyepiece, and the combination of lenses was such that one division of the screw-vernier equalled ·00213 mm. The readings for each animal



FIGS. 6–9. Camera lucida drawings of parts of one animal.

FIG. 6. *Head.*
AB=Head length.
AC=Head depth.
ab=Eye length.
cd=Eye breadth.

FIG. 7. *Fifth Body-segment.*
AB=Fifth segment length.

FIG. 8. *Uropod, last two joints.*
AB=Uropod length.
CD=Uropod breadth.

FIG. 9. *Second antenna, first large joint.*
AB=Second antenna length.
CD=Second antenna breadth.

FIG. 10. Freehand drawing of a first pereiopod propodite (approximately same scale).
AB=Pereiopod length. CD=Pereiopod breadth.

separately, and also in the tables of sums and means (or averages), were expressed in terms of unit divisions of this screw-vernier. I measured 121 animals.

The actual measurements taken were the length and depth of the head (Fig. 6), the length of the fifth body segment (Fig. 7), the lengths and breadths of the last two joints of the uropod (Fig. 8), of the first large joint of the second antenna (Fig. 9), and of the propodite of the first pereiopod (Fig. 10). The length and width of the eye was taken in some cases, but since the stock was of the genetic constitution known as " colourless," in which the ommatidia are unpigmented and frequently scattered, these measurements were not sufficiently numerous or accurate to warrant inclusion in the results. The number of joints in the flagellum

TABLE III.

The Mean Absolute Values for the Various Measurements Taken, Arranged in Classes According to First Pereiopod Propodite Length.

Average Measurements in Millimetres.

	Group by Pereiopod length in Micrometer divisions.	No. of Individuals in group.	Head L	Head Depth (Anterior border).	2nd Antenna 1st large joint L	2nd Antenna 1st large joint B	1st Antenna No. of joints in flagellum.	Uropod L (last 2 segments).	Uropod B (penult. segment).	1st Pereiopod propodite L	1st Pereiopod propodite B	5th Body segment L
Indeterminates.	Taken together. 34–59	5	·285	·238	·098	·049	6·80	·193	·040	·092	·026	·133
	12	·388	·340	·164	·070		·272	·060	·136	·036	·243	
	72–85	7	·462	·412	·211	·084	14·1	·330	·075	·167	·043	·324
	86–102	7	·511	·448	·232	·086	15·1	·422	·080	·200	·044	·360
	♂, ♀ and indeterminates 103–122	20	·574	·509	·285	·106	17·3	·492	·101	·243	·052	·435
	123–146	26	·692	·595	·338	·117	21·1	·631	·122	·288	·057	·531
Females.	(72–85 omitted from graphs)	[1]	[·679]	[·574]	[·311]	[·113]	[20·0]	[·601]	[·102]	[·179]	[·055]	[·575]
	147–175	7	·784	·682	·379	·129	21·6	·709	·136	·336	·064	·653
	176–210	5	·955	·805	·464	·150	28·0	·794	·152	·426	·084	·876
Males.	147–175	16	·790	·679	·477	·151	25·2	·860	·149	·345	·072	·586
	176–210	6	·859	·730	·533	·163	27·8	1·02	·162	·405	·081	·634
	211–252	10	1·02	·937	·683	·199	29·9	1·34	·194	·494	·100	·788
	253–362	11	1·19	1·02	·814	·234	33·0	1·53	·221	·601	·111	1·04

of the first antenna was also recorded, but in several cases the flagellum was broken. The lengths of the longest hairs on the first large joint of the second antenna, and on the uropod, were also taken, but discarded owing to the prevalence of curling, which rendered accurate measurement impossible.

The animals were arranged in groups according to the length of the propodite of the first pereiopod, the two sexes and indeterminate (indistinguishable) animals being separated. It is impossible to take age as the criterion for grouping, since temperature, nutrition, and genetic factors all have a profound effect upon the rate of growth, and careful standardisation of these conditions was not feasible with the means at my disposal at the beginning of this investigation. Since, however, *relative* growth was being investigated, and relative appendage-size seems to be almost or wholly a function not of age but of total size, this does not matter. Each group had a pereiopod length 20% greater than the previous one. It was found necessary, in order to compare significant numbers of animals, to combine some of these groups. Tables giving the sums, and means (averages) of these groups (in terms of unit divisions of the screw-vernier) for each measured character were compiled, and from them a table giving the ratios of the various parts, expressed as percentages of the "first pereiopod length" (propodite) of the group taken as standard. A table giving the ratios of various characters to each other was also drawn up. Finally, a table of means (averages) reduced to absolute measurements in millimetres was obtained. (Table III.) Since the numbers of sexually distinguishable animals in some of the earlier groups were small in comparison to the number of indeterminates, the last two groups of indeterminates were recombined with the corresponding sexed individuals and indiscriminately called indeterminates. Thus the last two groups of indeterminates in the graphs (with the exception of Fig. 13) include some distinguishable males and females. The single female falling into the first group of its sex was so atypical in its proportions that it was omitted from the graphs.

From the data provided by the tables referred to, three types of graphs were constructed; firstly, average-graphs (Figs. 11–13) in which the average measurement under consideration was plotted as ordinate against the average pereiopod propodite (or other) measurement of the group in the abscissæ. These graphs gave the *absolute size* attained by the organs of the three classes (males, females, and indeterminates) at the same stages of pereiopod growth. Secondly, a graph showing the proportions of the lengths of various organs to the pereiopod length (expressed as percentages of the latter) was drawn; from this the growth-changes in the *relative proportions* of the various organs can be most readily observed. The percentages were plotted in the ordinates and the

pereiopod-lengths of the groups in the abscissæ (Fig. 14); had the curve for the pereiopod propodite length been drawn it would, of course, have been a straight line of 100%. Finally, a series of log-log graphs (Figs. 15–18) were constructed, in which the logarithms of the size-averages of

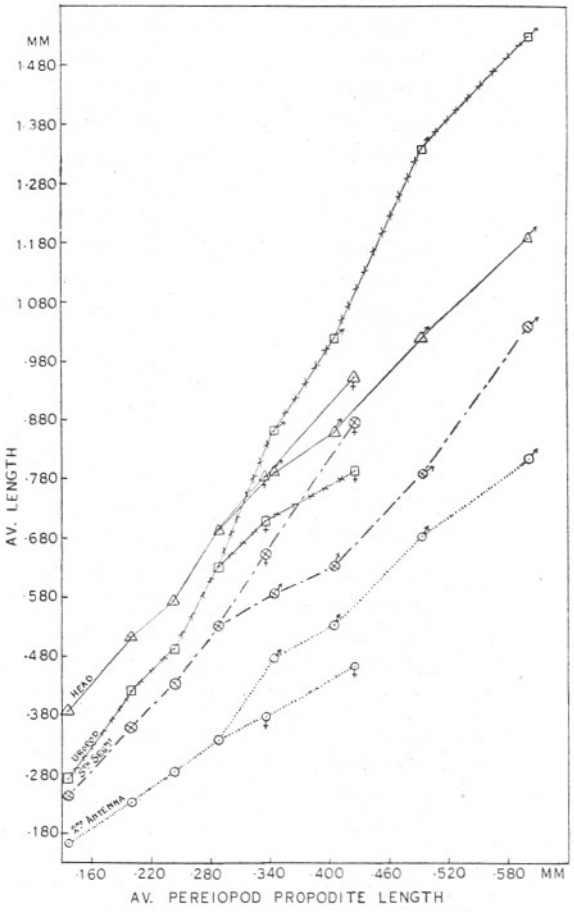


FIG. 11. The mean absolute lengths of the head, uropod (last two joints), fifth body segment, and second antenna (first large joint), plotted against mean absolute length of the first pereiopod propodite.

various organs (in the ordinates) were plotted against the logarithm of some other average measurement (in the abscissæ) as standard. In this way the relative *rates of growth* of the various organs in their different dimensions could be compared (see below).

From these three types of graphs, showing respectively the actual

progress of growth and absolute size attained, the relative proportions, and the comparative rates of growth found in the various organs examined, some understanding of the quantitative relations of the processes at work in the different parts may be extracted.

The formula for simple heterogony put forward by Professor J. S. Huxley ('27); viz. $y=bx^k$, where y=organ measurement, x=standard

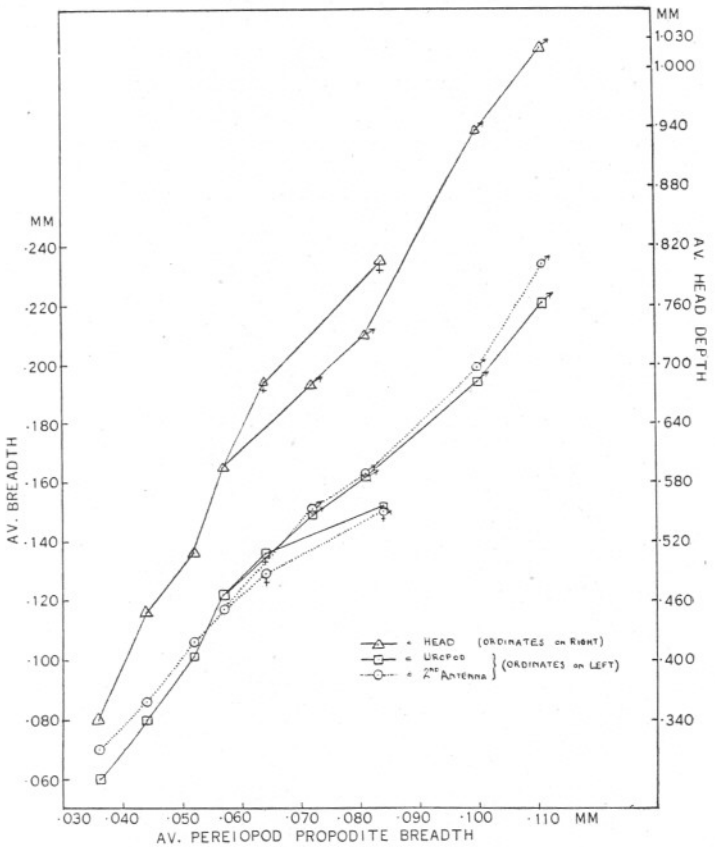


FIG. 12. The mean absolute depth of the head, and breadths of the uropod (last two joints) and second antenna (first large joint), plotted against mean absolute breadth of the first pereiopod propodite.

measurement, and b and k are constants, may be applied in this paper. I have calculated the values of k in Table III, these being equal to the tangents of the angles made by the log-log graphs with the abscissæ; k expresses the ratio of the two growth-rates concerned. Thus, where k=1 the compared rates of growth are equal; where $k > 1$ the organ in the ordinates is growing faster (positive heterogony), and when $K < 1$

the standard in the abscissæ has the higher relative growth-rate (negative heterogony). The values of k given are approximate; they do not pretend to accuracy beyond the first decimal place.

Such statistical data as do not actually appear in this paper are deposited for reference at the British Museum.

(*B*) Results and Description of Graphs.

Appendages.

(*a*) *First Antenna.* The number of joints in the flagellum is smaller in females than in males of the same pereiopod-size group.

(*b*) *Second Antenna, first large joint.* (i) It can be seen from Figs. 11

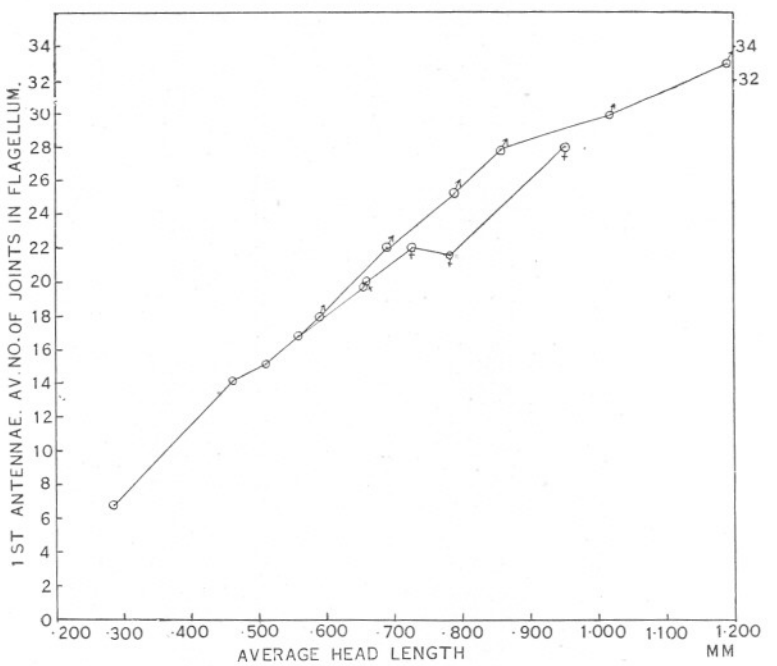


Fig. 13. The mean number of joints in the flagellum of the first antenna, plotted against mean absolute head-length.

and 12 that the actual size attained both in length and breadth is always greater in males than in females of corresponding groups.

(ii) From Fig. 14 it may be seen that the proportions remain more or less unaltered in the indeterminates and females, though in the latter a slight tendency to relative decrease is observable, while in the males a relative enlargement occurs early and remains fairly constant.

(iii) The relative rate of growth *in length* in indeterminates and females is slightly less than that of the fifth segment, being especially noticeable in the case of the females. (Fig. 15 : k=·91 and ·62 respectively.) The relative rate is very nearly the same as that of the pereiopod in the indeterminate (k=·94), but lower in the females (k=·72). In males the relative rate is very markedly greater than that of fifth segment at first (Fig. 15 : k=3·7), but tends to equal it later, while its rate is about twice as high as that of the pereiopod (k=2·0).

The relative rate of growth *in breadth* (Fig. 18) is somewhat higher in indeterminates than that of the pereiopod, decidedly lower in the females, and somewhat higher again in males (k=1·1, ·81, 1·1 respectively).

(iv) In males, females, and indeterminates the rate of growth in length is somewhat greater than that in breadth (Fig. 17 : k=1·35) ; i.e. the joint in question is becoming longer and relatively narrower with growth.

(*c*) *Uropod, last two joints.* (i) From Fig. 11 it can be seen that the actual length attained in corresponding groups is very much greater in males than in females, but in breadth (Fig. 12) the males are only slightly larger than females. This difference in length between the sexes is much more marked than the divergence found in the second antenna, but the sex-differences in breadth are very similar in the two appendages and their curves follow each other remarkably closely.

(ii) The relative (length) proportions of the indeterminates (Fig. 14) show a variable tendency to enlargement ; this is continued as a definite and considerable increase in the males, which is progressive, until a slight decrease occurs in the last group. The females show a decided decrease in proportion relative to the pereiopod propodite length.

(iii) The relative rate of growth *in length* (Figs. 15 and 16) in indeterminates about equals that of the fifth segment (k=1·06) and is slightly greater than that of the pereiopod (k=1·12). The relative rate *in breadth* is markedly higher than that of the pereiopod (k=1·5 to 1·6 ; Fig. 18). The length-rate in females is decidedly lower than that in either fifth segment (k=·63) or pereiopod (k=·74) ; the breadth-rate is also markedly lower than that of the pereiopod (k at first=1·05, but much lower later ; Fig. 13). In males the relative rate in length is very much greater than that of the fifth segment at first (k=2·8), but tends to equal the rate of the females later (k<·63), resembling the second antenna in this peculiarity ; the length-rate is considerably greater than that of the pereiopod (k=1·4), and though it falls off in the last groups this does not occur to so great an extent as it does relative to the fifth segment. Fig. 18 shows that the *breadth* growth-rate in males is somewhat lower than that of the pereiopod (k=·82) ; it should be noted that the males and females have lower relative rates than have the indeterminates in this respect (cf. Table IV).

(iv) Fig. 17 shows that in indeterminates and females the rate of growth in length is slightly greater than that in breadth (k=1·1 to 1·2), whereas, in males, the length-rate is markedly higher (k=1·6). Thus, the male uropod tends to become relatively longer and thinner than that of an indeterminate or female.

(*d*) *First Pereiopod, propodite.* (i) In Fig. 15 it can be seen that the

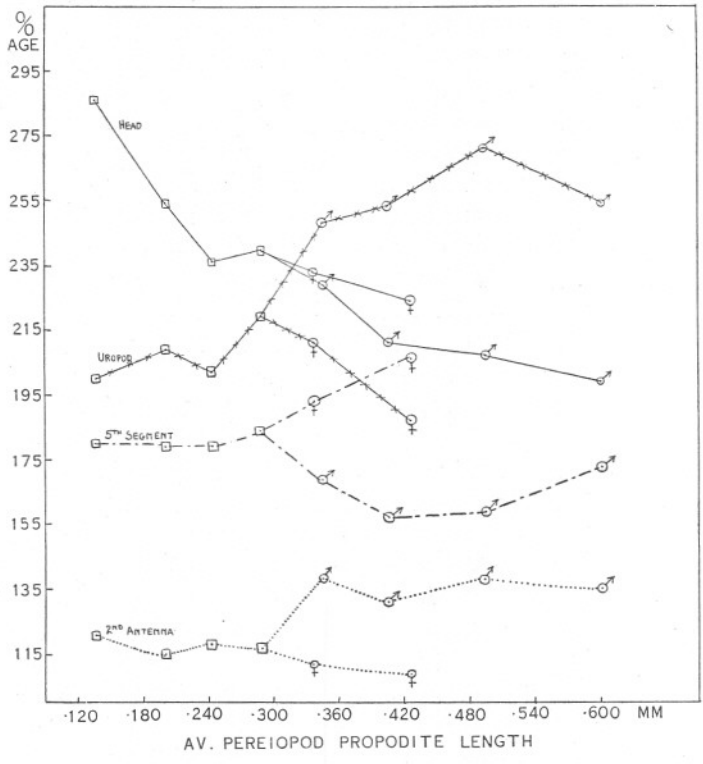


FIG. 14. Ratios of lengths as percentages of pereiopod propodite lengths (standard).

□ Indeterminates. ♂ Males. ♀ Females.

rate of growth in length is approximately equal to that of the fifth segment in the indeterminates (k=1·0), in the females it is slightly lower (k=·77), but in the males is considerably higher at first (k=1·8), approaching the female rate later. In this respect the male pereiopod resembles the male second antenna and uropod, but in this case the sex difference in comparative growth-rates is not so pronounced.

(ii) Fig. 17 shows that the rate of growth in length is slightly higher, for all classes, than that in breadth (k=1·2 for ♂, ♀, Indets.). This positive heterogony in length is less marked than in the case of the second antenna.

Body Segments.

(*e*) *Head.* (i) The actual size attained both in length and depth in corresponding groups is slightly greater in females than in males (Figs. 11 and 12). This is the reverse of the relationship in the appendages.

(ii) From Fig. 14 it can be seen that the proportionate size of the head decreases rapidly at first among the indeterminates, then becomes more stable, and finally the decrement is continued more gently in both males and females. In the former the decrease is greater than in the latter, presumably owing to the faster growth of the male appendages, the pereiopod included.

(iii) The relative *length* growth-rate is markedly less, in indeterminates

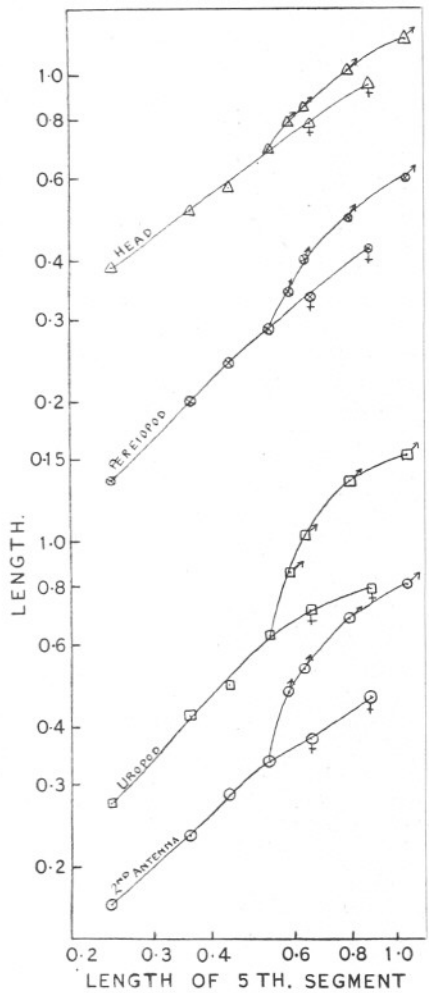


FIG. 15.

FIG. 15. The mean lengths of head, first pereiopod propodite, uropod (last two joints), and second antenna (first large joint), plotted against the length of the fifth body segment, on a double logarithmic grid.

FIG. 16. The mean lengths of uropod (last two joints), and fifth body segment, plotted against first pereiopod propodite length, on a double logarithmic grid.

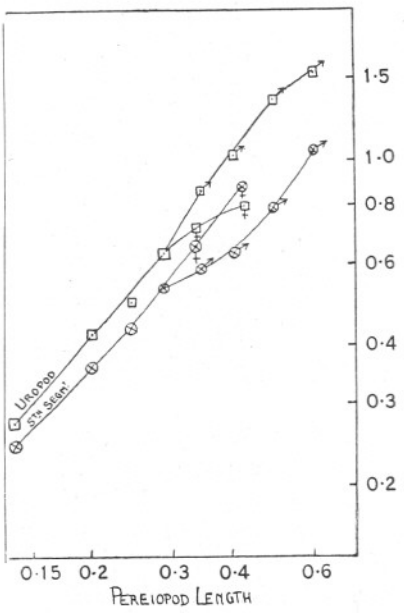


FIG. 16.

and females, than that of the fifth segment (Fig. 15 : k=·71 in both classes), and also of the pereiopod (k indet.=·74, k ♀=·82). The relative *breadth* growth-rate is somewhat higher in indeterminates (k=1·2), and though higher at first in the females (k=1·2), later becomes lower than the breadth-rate of the pereiopod (Fig. 18).

In males the *length*-rate is somewhat higher than that of the fifth segment at first (k=1·3), but approximates to the female rate later ; on the

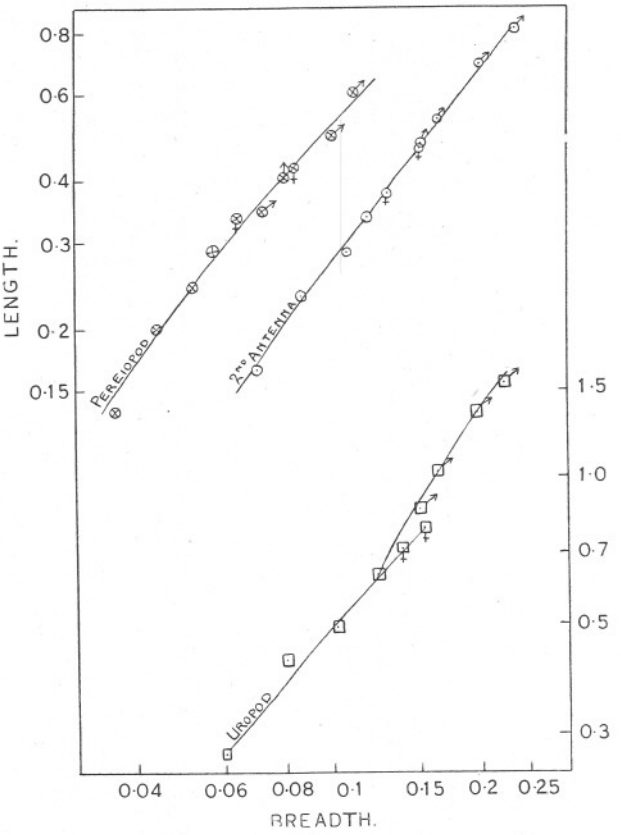


FIG. 17. The mean lengths of first pereiopod propodite, second antenna (first large joint), and uropod (last two joints), plotted against their respective breadths, on a double logarithmic grid.

other hand, the male length-rate is even lower than that of indeterminates and females in comparison to that of the pereiopod (k=·72). The relative rate in *breadth* is very markedly lower in the males at first (k=·6), but later becomes somewhat higher than the corresponding rate in the pereiopod.

N.B.—That the head, in Fig. 15, shows males with a higher rate of

growth relative to the fifth segment than females, is the reverse of the usual relation in body-segments ; this appears to be due to the fast growth of the fifth segment in females pulling their line down towards the abscissæ (probably associated with the growth of the brood pouches) ; such an occurrence is not found in the male, since its fifth segment is not particularly fast-growing ; when the growth-rate is compared with that of the pereiopod (Table IV) the relations are quite different. (For values of k see Table IV.)

TABLE IV.

Approximate Values of the Exponent k in the Heterogony Formula.

	Part.	Indeterminates.	Females.	Males.
Lengths vs. length of 5th segment (Fig. 15)	Head	·71	·71	1·3 at first (about =♀ later)
	1st Pereiopod	·95–1·0	·77	1·8 at first (about =♀ later)
	Uropod	1·1	·63 but considerably lower later	2·8 at first (but less than ·65 later)
	2nd Antenna	·9	·6	3·7 at first (but about=♀ later)
Lengths vs. length of pereiopod (Fig. 16)	Uropod	1·1	·75 but considerably lower later	1·4 (tendency to become lower later)
	5th Segment	1·0	1·3	·5 (but increases to about = ♀ later)
Lengths vs. length of pereiopod	Head	·75	·8–·85	·72
	2nd Antenna	·95	·7–·75 somewhat higher later	2·0 at first (about = indeterminates later)
Lengths vs. respective breadths (Fig. 17)	1st Pereiopod	1·2 all classes (approx. ; somewhat higher at first and somewhat lower later)		
	Uropod	1·1 (approx.)	1·1 (approx.)	1·6 (tendency to become lower later)
	2nd Antenna	1·3–1·4 (approx.) all classes		
Breadths vs. breadth of pereiopod (Fig. 18)	Head	1·2	1·2 at first, considerably lower later	·6 (later about= indets.)
	Uropod	1·6	1·0, much lower later	·8–·85 (tendency to become higher later)
	2nd Antenna	1·1	·8 at first, considerably lower later	1·1 at first (then lower, then gradually higher)

(*f*) *Fifth Body-segment.* (i) Inspection of Fig. 11 reveals the interesting fact that the actual length attained in corresponding groups is very much greater in females than in males. This is the reverse of the relation holding in appendages and similar to that for the head, but more marked. It seems possible that this considerable growth in the females is correlated with the formation of the brood-pouch, for the third pereiopod (attached to fifth segment of body) carries a brood-plate (Sexton, '24).

(ii) The indeterminates maintain their original relative proportions; in the females there is a marked increment, while the males decrease at first, become stable, and finally increase in proportion once more (Fig. 14).

(iii) Fig. 15 shows that the growth-rate *in length* of the fifth segment is somewhat faster than that of other organs in the females; in indeterminates it varies, but is on the whole equal to or slightly lower than the rate of females. In the males the fifth segment lags markedly at first, but later its rate approaches or surpasses those of the other organs (cf. Table IV).

From Fig. 16 it can be seen that the indeterminates have a length growth-rate of the fifth segment about equal to that of the pereiopod (k=1·05), in the females it is higher (k=1·3), while in the males the rate is very much lower at first (k=·5), but eventually becomes decidedly higher. This curve should be compared with that of the uropod in the same graph, since it shows distribution of positive and negative heterogony to opposite sexes in the two cases. In both the length growth-rate of the indeterminates *approximately* equals that of the pereiopod (somewhat higher in the uropod). Positive heterogony occurs in the male uropod and female fifth segment, while the female uropod and male fifth segment (at first) show negative heterogony with respect to the pereiopod.

(*C*) Conclusions.

From the above data we may, with some degree of confidence, draw the following conclusions:—

1. It appears that in each group (classified by pereiopod propodite length) the male appendages and female head and body-segments show the greater absolute size (Figs. 11, 12, and 13), and therefore the greater proportionate length (Fig. 14), and the higher relative rate of growth (Figs. 15, 16, and 18). The relative increase of the female fifth segment is considerably greater than that of the female head.

2. The greatest divergence between the sexes is shown by the length of the uropod among the appendages, and by the fifth segment among the body-measurements (Figs. 11, 14, 15, and 16).

As regards breadth, however, the uropod does not show greater sex-divergence than other appendages (Figs. 12 and 18).

3. (i) In the appendages selected, there is positive heterogony in males relative both to fifth segment and to pereiopod, while in females there is negative heterogony. These facts, or at least the positive heterogony in the male, would be expected, since both the appendages measured show positive secondary sexual characters (curved sensory hairs) in the male.

(ii) In the case of the fifth segment at least, the length of body-segments shows in the females positive and in the males negative heterogony relative to pereiopod length (Fig. 16) : this again is to be expected

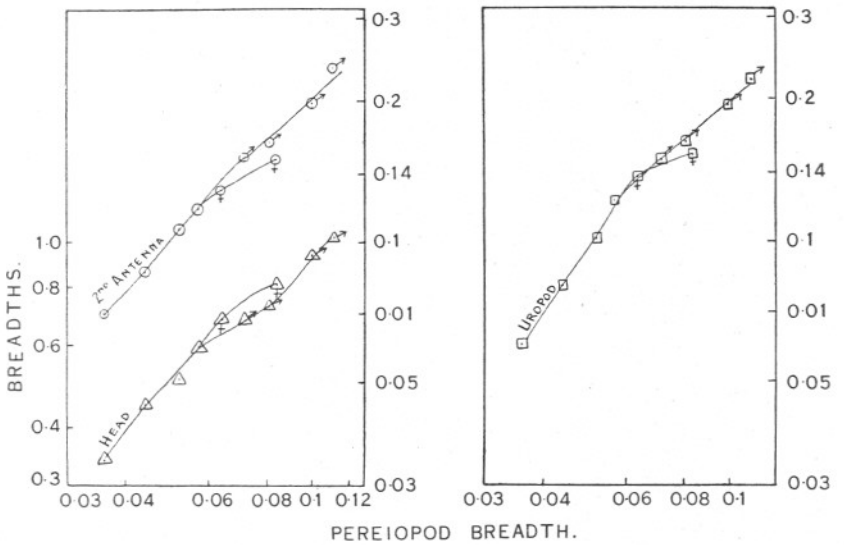


FIG. 18. The mean depth of head, and breadths of second antenna (first large joint), and uropod (last two joints), plotted against the breadth of the first pereiopod propodite, on a double logarithmic grid.

in the female, on account of the presence of the secondary sexual character of brood-pouches on this segment. As regards head-length, the female has a higher comparative growth-rate than the male (Table IV), with respect to the pereiopod, although both are negatively heterogonic. On account of the great growth of the fifth segment in females, the growth-rate of the head relative to fifth segment-length is higher in males.

It appears that the head is comparatively little affected by onset of sexual maturity, unlike the male appendages or the female fifth segment which undergo acceleration of growth, but, as might be expected, its growth is more like that of the fifth segment than that of the appendages.

(iii) The distribution of positive and negative heterogony to opposite

sexes in the case of the uropod and fifth segment (Fig. 16) illustrates and confirms the foregoing conclusions (1, 2, and 3).

4. (i) When breadth is compared with breadth, the relative rate of growth in breadth (Fig. 18) is highest in the indeterminates, the breadths of the various appendages being here decidedly positively heterogonic with respect to the pereiopod breadth. The females appear to become gradually lower in rate, whereas the males tend to show a variable drop in rate at first, and a later partial recovery.

(ii) When appendage-length is compared with appendage-breadth, the relative rate of growth in length is higher than that in breadth (Fig. 17); this is particularly observable in the case of the male uropod (which shows extreme positive heterogony of length as compared to other organs). In this case the length growth-rate is accelerated in the male at maturity, differing in this respect from the first pereiopod and second antenna, where the males' curve simply continues that of the indeterminates and females.

(iii) From (i) and (ii) above it can be seen that the various appendages tend to become relatively longer and narrower with growth, and that this alteration in proportions appears to be most conspicuous in those organs which show most marked positive heterogonic growth in length relative to other parts.

The results here given agree in substance with those obtained by Professor Kunkel; in particular an inspection of his Figs. 1 and 2 reveal curves for first antenna, and first and second gnathopods, coinciding in general form with mine for second antenna and uropod, respectively, in Fig. 14. He also finds that a change of proportions occurs with growth in the appendages he measured, and that this change is a relative elongation and narrowing of the part concerned—a result in complete agreement with my conclusions.

The work upon *Gammarus chevreuxi* detailed above was begun in the biological laboratory of Stowe School, continued at the Department of Zoology in Birmingham University, and finished during a visit to the Zoological Department, King's College, London.

It is a great pleasure to record my gratitude to Professor J. S. Huxley, who was responsible for the inception of the work, for its direction while in progress, and for the preliminary introduction; and also for the help I received in some of the laborious statistical work at the hands of a friend.

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Notes on the Biology of *Tellina tenuis* da Costa.

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With 5 Figures in the Text.

CONTENTS.

I. Introduction and Methods employed.

The study of the rate of growth of the invertebrate population of the sea and of the amount and time of deposition of the broods on the sea-bottom is of importance both for investigations on the economy of the sea and in relation to fishery problems. It is not usual, however, to obtain at one time sufficient numbers of a particular species as are necessary for studies on such questions as the rate of growth of the individual, or of the number of year groups composing the population. When, therefore, a quantitative digging in Kames Bay on the Cumbrae, on the Firth of Clyde, revealed sufficiently large numbers of *Tellina tenuis* living in the sand, an opportunity suggested itself for attempting such studies. A general

survey of the various bays in the Cumbrae was made, but Kames Bay was selected for intensive study, both on account of its accessibility and its richness in *Tellina tenuis*. A number of stations was fixed in the bay above and below low-water mark of spring tides, and these were examined on six different occasions from the last week of September, 1926, to the first week of October, 1927, so that the samples cover a complete year in the life of the species, and enable the growth of at least one year group to be traced accurately. At the same time parallel observations were made in other areas in the neighbourhood.

The method of sampling differed according as the stations lay in the intertidal zone or below low-water mark. In the first case a square with sides of half a metre was marked out on the sand and then dug out to a depth of about 15 cm. with a spade, experiment having shown that digging to this depth would capture all the *Tellina tenuis* on the ground. When dug out the sample was placed on a sieve of perforated zinc with circular holes 2 mm. in diameter and washed.

Below low-water mark a Robertson bucket dredge was used to collect the samples, and sufficient sand or mud collected to fill a 20 cm. cube. This, also, was washed on the 2 mm. sieve. Examinations for young broods were carried out with a sieve having holes 1 mm. in diameter.

The ratio of the quantity of sand in a $\frac{1}{4}$ sq. m. dug to a depth of 15 cm. to that of a 20 cm. cube is about 4·7 to 1·0. Where the two methods of digging and of dredging with the bucket dredge were tested, one against the other at the same station, the catches were in about the theoretical proportions, but the dredge, owing to its skimming action, contained a relatively higher proportion of small individuals. On this account the results got by the two methods, expressed as percentages of the total catch, are discussed separately. The measurement of *Tellina tenuis* used in the tables is that of the greatest antero-posterior length in mm. taken to the mm. above, i.e. all specimens between 7·1 and 8 mm. are included in the 8 mm. column.

II. List of Stations.

The stations in Kames Bay at which *Tellina tenuis* was secured are as follows :—

Stn. 1 High-water mark, neap tides.
,, 1a 20 yards below Stn. 1.
,, 2 40 ,, ,, ,,
,, 3 80 ,, ,, ,,
,, 4 120 ,, ,, ,,
,, 5 160 ,, ,, ,, low-water mark, spring tides.
,, 6 Approx. 2 fms. at high water, neap tides.
,, 7 ,, 3 ,, ,, ,, ,, ,,
,, 8 ,, 5 ,, ,, ,, ,, ,,

The bottom at all these stations consists of fine clean sand, practically all passing through a 1 mm. sieve, with a trace of mud only at Stn. 8.

In addition the following bays in the Cumbrae and neighbourhood were worked for samples of *Tellina tenuis* on one or more occasions.

1. Garrison Bay. A small sandy bay to the west of Kames Bay, one station at L.W.M.
2. Fintry Bay. A large sandy bay on the west of the Cumbrae, stations at mid-tide and L.W.M.
3. White Bay. A small sandy bay on the north of the Cumbrae, stations at mid-tide and L.W.M.
4. Balloch Bay. A large muddy bay on the east side of the Cumbrae, three lines of stations at H.W.M., mid-tide, and L.W.M.
5. Castle Bay. A small sandy bay on the Little Cumbrae, one station at L.W.M.
6. Hunterston Sands. A line of stations up the Hunterston Sands on the Ayrshire coast opposite Keppel. Stations at L.W.M. and at 100, 300, and 750 yards up from it. This last station being about three-quarters way up the beach.

III. Range and Density of *Tellina tenuis*.

Tellina tenuis is the dominant form in certain sandy bays in the Cumbrae and its neighbourhood. It ranges from a little below H.W.M. to a depth of 3–4 fm., with its maximum concentration in the region of L.W.M. spring tide.

The density in certain of the bays is very high, and the following list of some of the densities per $\frac{1}{4}$ sq. m. found during the investigations will give an idea of the abundance of this species.

TABLE 1.

Table showing the maximum density, per $\frac{1}{4}$ sq. m., of *Tellina tenuis* in certain bays in the Cumbrae and neighbourhood.

Kames Bay.	On one occasion	1897
,, ,,	Usual at L.W.M.	760–1000
White Bay		242
Balloch Bay		218
Castle Bay, Little Cumbrae		312
Hunterston Sands		765
Garrison Bay		265

These high numbers contrast markedly with those which I have found in the sands along the south shore of the Firth of Forth, where the best hauls, made at North Berwick and Cramond, gave only 15 and 8 *Tellina tenuis*, respectively, per $\frac{1}{4}$ sq. m.

IV. Intensive Study of *Tellina tenuis* in Kames Bay.

(a) *Density at each intertidal Station.*

In Kames Bay the density of *Tellina tenuis* decreases from L.W.M. to H.W.M. in a regular manner. In September, 1926, for example, the density per $\frac{1}{4}$ sq. m. at each station above L.W.M. was as follows :—

TABLE 2.

Stn.	1	1a	2	3	4	5
No. of *Tellina tenuis*	0	14	132	205	473	822

In all subsequent observations a similar result was obtained, except that the numbers of *Tellina tenuis* at Stns. 4 and 5 were usually rather closer.

(b) *Distribution according to Size.*

The distribution according to size is also very remarkable, and the uniformity of the physical conditions in the area may be, in part, the cause. The bay is long and narrow, the slope is gentle, and the bottom consists of fine sand with a high and uniform water content. An estimate of the water content was made by Mr. Elmhirst, and the percentage loss of weight when a sample of wet sand from each station was dried is as follows :—

TABLE 3.

	Wind drifted sand above H.W.M.	Stn. 1	Stn. 2	Stn. 3	Stn. 4	Stn. 5
% loss	17·4	19·9	20	20	20	20

The texture of the sand is very uniform and, unlike the sand of most of the other bays examined in the neighbourhood, is not mixed with large quantities of broken shells. The distribution of size-frequencies at the various stations in Kames Bay may represent the normal one when the area exposed during ebb tide is sufficiently entensive and uniform in slope to permit of zoning. In most bays the short slope, or sand banks, or constitution of the bottom, or a combination of all these factors may make it difficult to trace the levels as clearly as in Kames Bay, or may obliterate the zoning normal in other areas.

During these investigations some fifteen to sixteen thousand individuals, mostly from Kames Bay, were measured, and in Table 7 (p.701) the percentage of the catch at each mm. size is set out for the various stations. From this table it is evident that the larger individuals occur in the upper reaches of the bay, while the smaller sizes predominate at lower levels. The differences in density and size-frequency at the various stations are perhaps more clearly shown in Figure 1, where the actual collections of *Tellina*

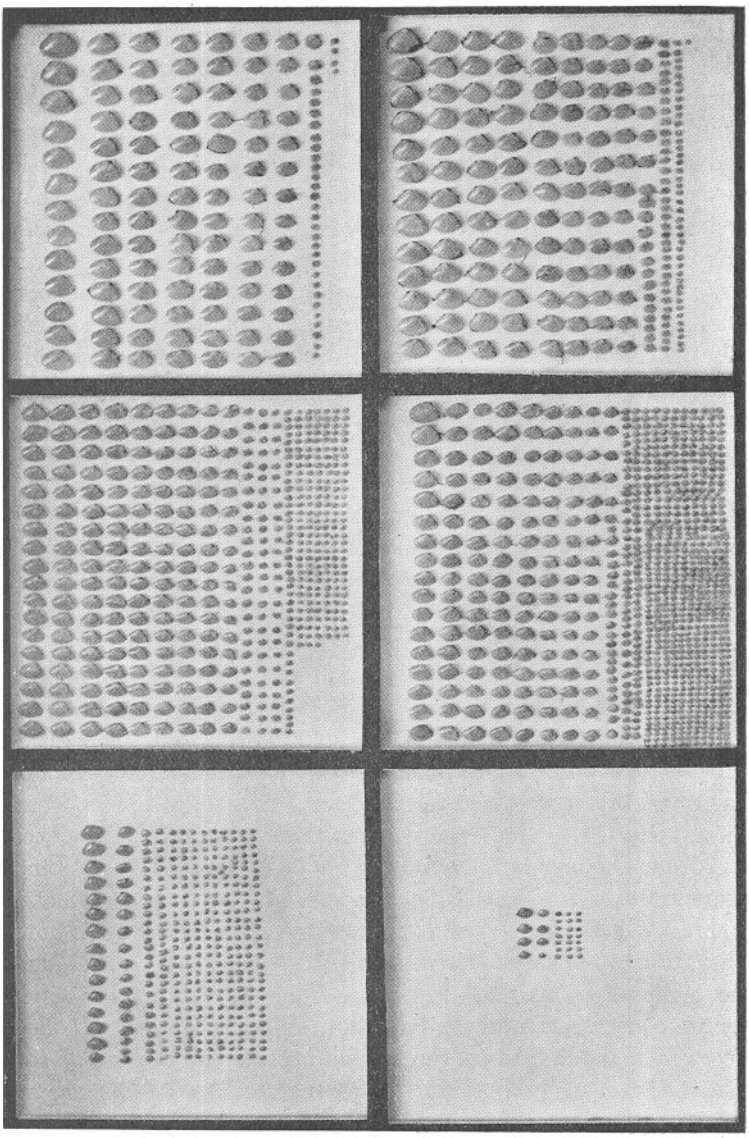

FIG. 1.—Photograph showing the actual numbers of *Tellina tenuis* taken in September, 1926.

Stns. 2, 3, 4, 5 on $\frac{1}{4}$ sq. metre.
Stns. 6, 7 in a 20-cm. cube.

tenuis made in September, 1926, at Stns. 2, 3, 4, and 5 in a $\frac{1}{4}$ sq. m. of sand dug to a depth of 15 cm., and at Stns. 6 and 7 in a 20-cm. cube of sand collected by a bucket dredge, are shown. At Stn. 6, for example, few individuals over 7 mm. were taken, while at Stn. 2 the majority of the specimens were from 13 to 15 mm. in length.

Gemmill (**9**) found that in *Mytilus edulis* and *Patella vulgata* the individuals at higher levels were of smaller size than those at low levels, while the reverse is found for *Tellina tenuis*. He suggests that the differences of size at high and low levels are due to Patella and Mytilus feeding only when covered by the tide, and that therefore individuals from higher levels will have less time for feeding. The differences between Mytilus and Patella and Tellina are probably due to the fact that both Mytilus and Patella when the tide recedes are exposed to the air and must suspend most of their activities.

Segerstråle (**10**), working on *Macoma baltica* in a fjord at the Tvärminne Zool. Station, found only large specimens in the deepest parts of the fjord, but inshore both large and small ones were present. He suggests that this distribution of sizes may be due to migration. From the few investigations I have made on *Macoma baltica* it seems probable that along the Scottish coast the size distribution is similar to that of *Tellina tenuis*.

Table 7 (p. 701) also shows that the character of the hauls in Kames Bay above and below L.W.M. is quite different at all seasons. Below L.W.M. the population is composed only of individuals whose rate of growth and general size is apparently small. Stn. 8 may be considered, for all practical purposes, as marking the seaward limit of the species. The numbers taken at this station are small and range in size from 3 to 5 mm. At Stn. 7 the numbers are higher than at Stn. 8, but at all seasons about 90% of the population was found to be under 7 mm. At Stn. 6 the numbers are still higher, the population contains larger specimens, but even here few individuals over 7 mm. are met with. At Stn. 5, however, the character of the catch changes, and the change is even more marked in the higher stations. At Stn. 5 the numbers per sq. m. reach the maximum concentration in the bay, and, from the method of collection, it is certain that all sizes on the ground are represented in the sample. At Stn. 4 the density approximates to that at Stn. 5, but the rate of growth is slightly increased. At Stns. 3 and 2 the density falls off rapidly, but the rate of growth increases considerably.

(c) *Rate of Growth.*

We may begin the study of the rate of growth of *Tellina tenuis* in Kames Bay at the stations above L.W.M., where growth, assuming that the

population is more or less stationary, is fairly rapid, and deal later with the results from the stations below L.W.M. where growth is slower.

As may be seen from the figures for Stn. 5 (Table 7), the group of individuals at 3 to 4 mm. in length formed about 80% of the population

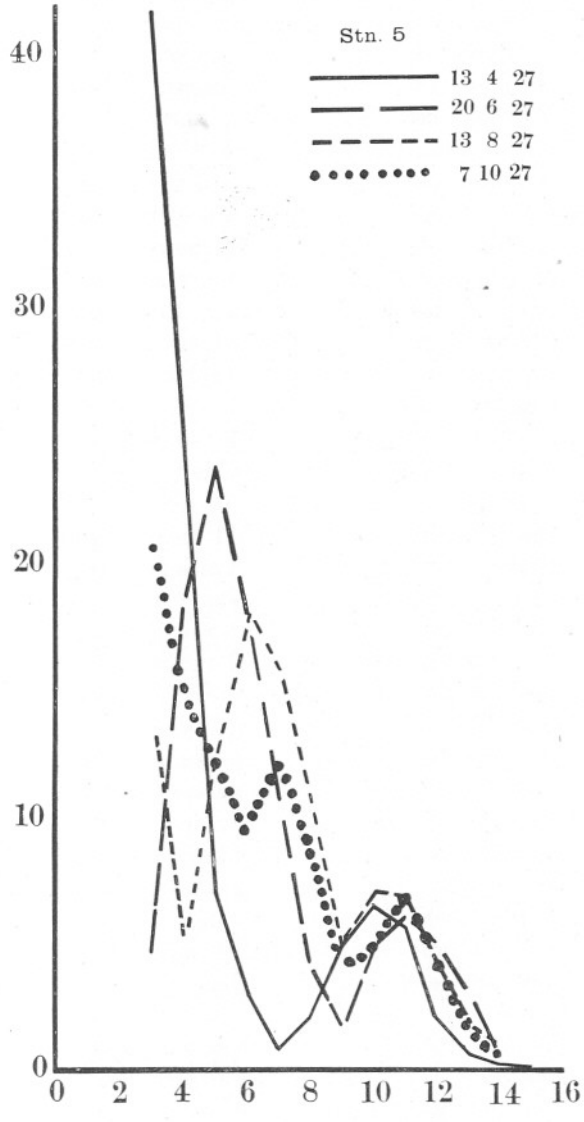

FIG. 2.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 5 in April, June, August, and October, 1927.

in September, 1926, and there is a hint of a second group at 8–9 mm. From September to April there is little growth, but from April onwards growth is fairly rapid (Fig. 2). By June the mode at 3 mm. in April has shifted to 5 mm., and that at 10 mm. in April to 11 mm. By August the mode at 5 mm. in June has shifted to 6 mm., while that at 11 mm. remains about the same figure. There is in addition a third mode in the August curve marking the presence of the 1927 spat which had recently made its appearance on the ground. In August, 1927, when growth may be considered to have ceased for the year, there are three modes on the curve, at 3 mm., 7 mm., and 11 mm., which might reasonably be taken as representing three year-groups, provided there is not more than one spatting season per annum. A comparison of the curve for September, 1926, with that of October, 1927 (Fig. 4), shows that this can hardly be the case, for it is evident that there is one year-group entirely missing. In the size-frequency curve for September, 1926, there is one mode at 3 mm., as in October, 1927, but there is none at 7 mm., as in October, 1927. Now we have actually traced the growth of two groups during the year from 3 mm. and 9 mm. in September, 1926, to 7 mm. and 11 mm. in October, 1927. In other words, the smaller sized group has grown 4 mm. in length during the year, and the larger one 2 mm. To assume that in 1926 growth was much more rapid than in 1927 does not seem the best way out of the difficulty, for that would mean a growth-rate in 1926 practically double that of 1927. It seems much more reasonable to assume that the year-group at 7 mm. in the October, 1927, curve is unrepresented on the September, 1926, curve, and that the group at 11 mm. on the October, 1927, curve is poorly represented on the September, 1926, curve. The growth-rate being much higher at the upper stations, the absence, or poor representation, of these two groups becomes much more marked.

If, then, we accept the idea that one year-group is unrepresented in the curve for October, 1927, at Stn. 5, we may say that at L.W.M. in Kames Bay in October, 1927, there were four year-groups represented in the population, namely, the spat of 1927 (0+group), mostly 3 to 4 mm. in length; the 1926 spat (1+group) ranged round 7 mm.; the missing 1925 spat (2+group), which would have ranged round 9 mm.; and lastly the 1924 spat (3+group) ranged round 11 mm. There may, of course, be a few representatives of older groups, but, if present, they form a very insignificant part of the population.

These figures indicate that since 1924 there have been alternate good and bad years of spat fall. For example, the 0+group in the autumn of 1927 is only about a third part that of the autumn of 1926, which is a very well-marked group, while the 0+group of 1924 is almost absent. Boysen Jensen (**2**) notes a similar occurrence in Danish waters where he has found that the spat of *Syndosmya alba* appears about every second year.

The growth-rate of *Tellina tenuis* at Stn. 4 is similar to that at Stn. 5 (Table 7). There is the same high density, the same year-groups can be traced, but growth is a little more rapid. On the curves for October, 1927, for example, the modes are at 7·5 mm., 10 mm., and 12 mm. for

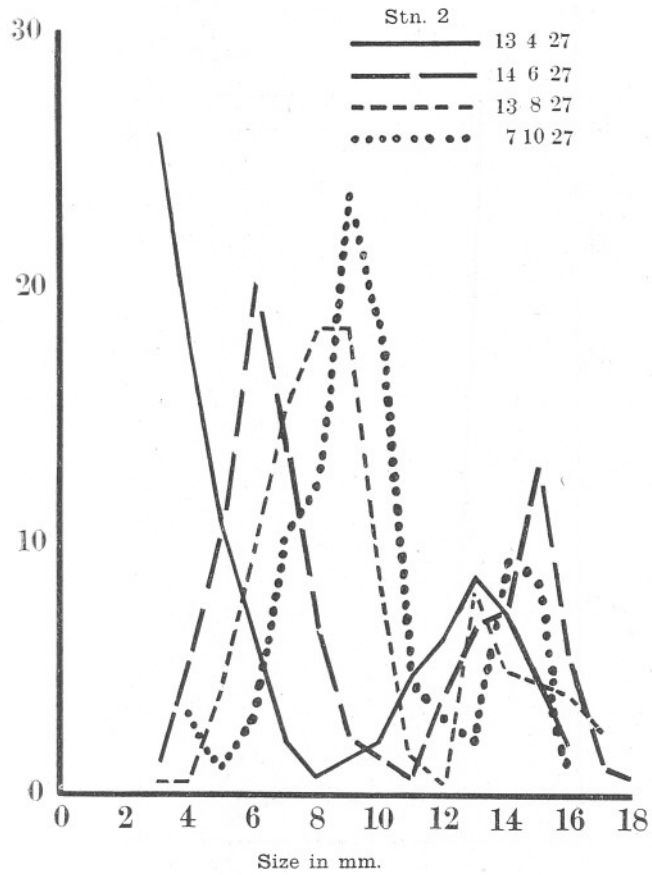

FIG. 3.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 2 in April, June, August, and October, 1927.

Stn. 4, as compared with 7 mm., 9 mm., and 11 mm. at Stn. 5. As before the absence of the 1925 spat (2+group) is clearly marked.

There are noticeably few of the 1927 spat retained by the 2 mm. sieve at Stn. 4, while they are present in numbers at Stn. 5, and this contrasts with the conditions found in the previous year, where, in September, 1926, they were numerous both at Stns. 4 and 5 (Table 7). The difference

this year may be due to a retardation of the growth of the spat by the generally unfavourable conditions of 1927.

The size-frequency tables for Stns. 3 and 2 differ considerably from those of the lower stations. The individuals are, on the whole, considerably

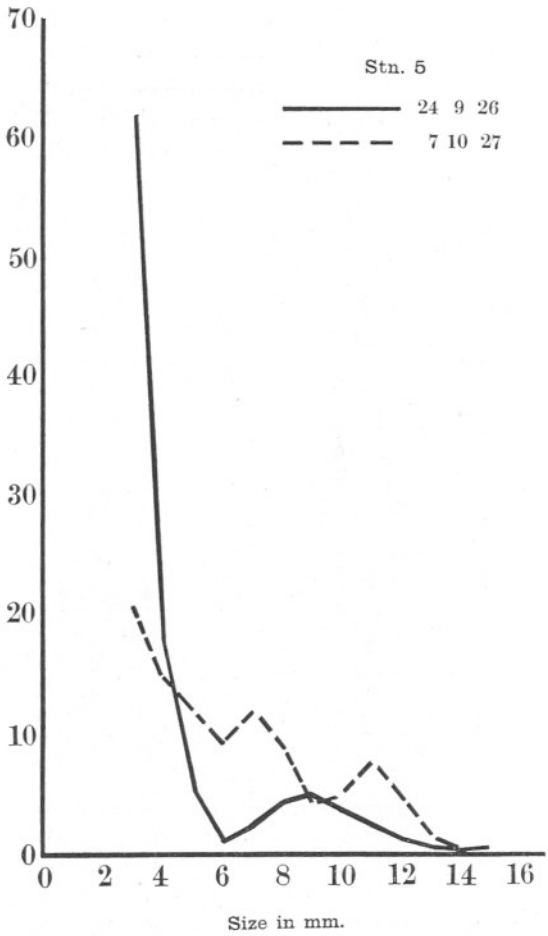

FIG. 4.—Graph showing the percentage (ordinate) of the catch at each mm. at Stn. 5 in September, 1926, and October, 1927.

larger, the rate of growth is more rapid, and the curves indicate a rather less compact group round the mean. For the latter peculiarity a reason may be suggested from an inspection of the figures for Stns. 3 and 2 in Table 7. The spat, as will be shown later, is probably deposited over a period and the earlier falls seem to be below L.W.M., but sooner or later

some is deposited in the intertidal area as well. The earlier spat has still a short period of growth before winter sets in, e.g. in autumn there is a mode in the curves for Stns. 3 and 2 at 5 mm., but during the winter large numbers of smaller individuals make their appearance at these stations, as is shown in Table 7 where the percentage of individuals at 3 mm. in length

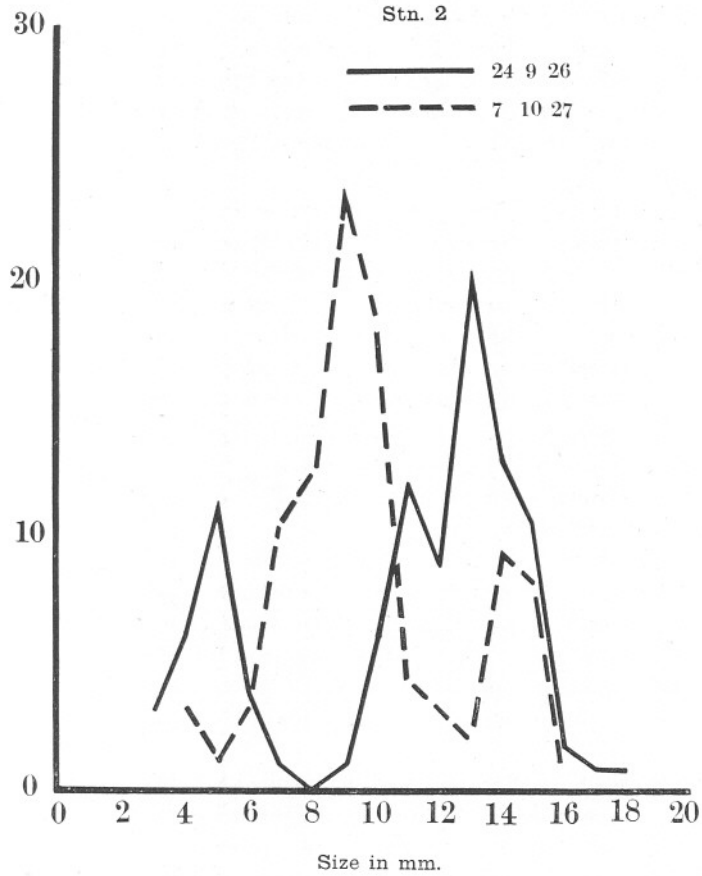

FIG. 5.—Graph showing the percentage (ordinate) of the catch at each mm. for Stn. 2 in September, 1926, and October, 1927

rises from 10% in September, 1926, to 13% in January, 1927, and to nearly 30% in April, 1927, at Stn. 3. At Stn. 2 a similar rise occurs. When, therefore, growth starts again in spring there are the rather larger individuals which have reached a size of 5 mm. in the autumn, and the smaller ones at 3 and 4 mm., and these two sets of individuals, growing at about the same rate, give the appearance of a double group whose

limits lie close together. This increase of small individuals at Stns. 3 and 2 may be due either to a prolonged spat fall, or to a gradual movement of the animals themselves, or to a slight continuance of growth during the winter months. Until the history of the earlier stages of *Tellina tenuis* is worked out this must be left an open question.

Returning now to the figures for Stns. 3 and 2 (Table 7), it is seen that the density is markedly less at Stn. 3 than at Stn. 4, and rather less at Stn. 2 than at Stn. 3. The individual growth is larger than at Stn. 5 (compare Figs. 3 and 4), but four-year groups can be traced as at Stn. 5. The absence of the 2+group (1925 spat) is again evident if we compare the curves for September, 1926, with those of October, 1927, for Stn. 2 (Fig. 5).

Stn. 1a marks for all practical purposes the upper limit of the species. The individuals here are smaller, and the density less, than at Stn. 2. The number of specimens taken in the samples has varied considerably, so no attempt is made to discuss the rate of growth at this level.

Turning now to the stations below L.W.M. we find that at Stn. 6 growth is slow and the modes lie close together. In this case it might have been better to have measured the specimens to the nearest half mm. in order to separate the year groups. In October, 1927, (Table 7) the 0+group and 1+group are quite well marked at 3 mm. and 6 mm. respectively, while the 3+group might lie at 9–10 mm. The missing 2+group would probably lie about 8 mm.

With regard to Stn. 7 it is not possible, in the present state of our knowledge of the species, to give an accurate figure for the rate of growth of the individuals at this level nor a satisfactory reason for their permanent dwarf size. This station lies near the seaward limit of its range and conditions probably begin to prove adverse, but, on the other hand, at the landward limit individuals, if few, are of considerable size.

Davis (**3**) and Ford (**6**) have given the results of their studies on the rate of growth of certain allied species of lamellibranchs from deep water, but in the present state of our knowledge it is not possible to draw comparisons between the rate of growth in Scottish waters and that in the Southern areas.

To summarise the remarks made on the rate of growth of *Tellina tenuis* in Kames Bay, we may say that the *Tellina tenuis* population is almost entirely composed of four-year groups, one of which is not well represented. At each station from 3 fm. to near H.W.M. the rate of growth is slightly different, being progressively more rapid as we proceed shorewards. Appended is a table showing the modes for each year-group at Stations 6 to 2 for the October, 1927, curves.

TABLE 4.

Station.	Year groups. 0+	1+	2+ (missing)	3+
6	3 mm.	6 mm.	8 mm.	9·5 mm.
5	3 mm.	7 mm.	9 mm.	11 mm.
4		7·5 mm.	10 mm.	12 mm.
3	4 mm.	8·5 mm.	11 mm.	14 mm.
2	4 mm.	9·5 mm.	11·5 mm.	14·5 mm.

V. Comparison of the Rate of Growth of *Tellina tenuis* in Kames Bay with that of the other bays in the neighbourhood.

In Table 8 (p. 702) are given the size-frequencies at each mm., in percentage of the total, of *Tellina tenuis* for some of the other bays in the Cumbrae and its neighbourhood. As these collections were made for the purposes of the general survey no attempt is made to trace out the year-groups till repeated observations, like those in Kames Bay, have been made, but the figures as they stand are interesting and suggestive. Growth is evidently more rapid in areas such as the Hunterston sands, White Bay, Garrison Bay, and Castle Bay, than in the corresponding levels in Kames Bay. The modes on the curves for these bays correspond rather to those of the curves for Stn. 2 in Kames Bay than to those of Stn. 5 as their position at, or near, L.W.M. would lead us to expect. Ford (**7**) has found similar results for *Syndosmya alba* in Bigbury Bay and, he states that "the average size of the mollusc is greater when the numbers are fewer." The numbers in these other cases, with the exception of one haul on the Hunterston sands, correspond to those of Stns. 3 and 2 in Kames Bay, so it may be that the progressive changes in the rate of growth at the various stations in Kames Bay are determined not only by the actual position on the beach but also by the density of population, i.e. by the amount of food available for each individual.

The figures also suggest that in these other bays rather older year-groups are present than in Kames Bay, and that some of the individuals may be five, six, or even more years of age. In all these areas, however, the 1926 brood predominates as in Kames Bay.

Ford (**8**) has found a similar result in the case of *Spisula elliptica*, and he states that "the 1922 stock was the predominant element throughout, and even at the beginning of the summer growth in 1924 it formed over nine-tenths of the weight of the whole stock."

VI. Comparison of the Distribution of *Tellina tenuis* and *Tellina fabula* in Kames Bay.

In Kames Bay both *T. tenuis* and *T. fabula* occur plentifully, but the relative frequency and area of distribution of the two species do not

correspond. In the adjoining table the numbers of each species in the collections made during September, 1926, at Stns. 1 to 8 are given, along with those from stations in deeper water as far as the limit of the species.

TABLE 5.

TABLE SHOWING THE NUMBERS OF *T. TENUIS* AND *T. FABULA* AT VARIOUS STATIONS IN KAMES BAY.

	Contained in ¼ sq. m.				Contained in 20-cm. cube.					
Station	2	3	4	5	6	7	8	7 fm.	10 fm.	14 fm.
No. *T. tenuis*	132	205	473	822	327	29	—	—	—	—
No. *T. fabula*	—	—	3	3	26	101	144	134	10	—

Thus *T. tenuis* is abundant between tide marks and just below L.W.M., but dies away at greater depths, while *T. fabula* is sparingly distributed between tide marks but becomes abundant in depths of 4–6 fm., and dies away in turn about 11 fm. The growth-rate of *Tellina fabula*, for comparison with that of *Tellina tenuis*, has not yet been fully worked out, but it is probably of the same order as that of *Tellina tenuis* at Stn. 6.

VII. STATE OF THE REPRODUCTIVE ORGANS.

Active spermatozoa were first noticed in a few individuals from between tide marks at the end of May when the ova were flat and compressed by crowding in the gonad. In July mature ova were found rounded off, while in August some specimens, both male and female, appeared more or less spent. No actual spawning was noticed.

In June small specimens of 7 mm. length were found to have maturing gonads, showing the incidence of maturity in the 1+year group.

VIII. SPAT FALL.

The state of the reproductive organs was taken to indicate that no young brood would appear on the bottom before about June, but, to make certain, sampling with a 1 mm. sieve was conducted at, and above, L.W.M., a position shown by later studies to be rather an unfortunate one. Better results might have been obtained had the samples been taken below L.W.M.

No specimens of *Tellina tenuis*, passing the 2 mm. sieve but retained by the 1 mm. sieve, were found during the winter or spring months. In August, 1927, the whole 20-c.c. cube of sand dredged at Stns. 6, 7, and 8 was sieved through the two sieves as well as samples from Stns. 4 and 5. The same observations were repeated in October, 1927, and, in addition, samples were taken from Stns. 3 and 2. The results are set out in the adjoining table.

TABLE 6.

TABLE SHOWING THE NUMBERS OF *TELLINA TENUIS* PASSING THE 2-MM. SIEVE BUT RETAINED BY THE 1-MM. SIEVE.

	Numbers in 20-cm. cube			Numbers in $\frac{1}{4}$ sq. m. calculated from the small samples.				
Stn.	8	7	6	5	4	3	2	1a
Aug., 1927	18	290	11	85	10	—	—	—
Oct., 1927	28	167	85	102	105	126	20	20

These results indicate that the spat is deposited during the summer months in large numbers a little way below low-water mark, but by autumn it is also to be found spread in large numbers up to the half-tide mark, and in noticeably diminished numbers in the higher levels. Deposition probably lasts for a period of 2 to 3 months, but this point has still to be cleared up.

IX. FOOD.

During the winter months the food consists almost entirely of debris, thalloid and filamentous algæ predominating, with some detritus from the land. Diatoms play a small part while, amongst other less important material, sponge spicules, starch grains, and sulphur bacteria occur, the latter probably derived from decaying algæ.

During the spring diatom increase the food consists entirely of diatoms, while during the early summer months the food is again mixed, but diatoms still predominate. Davis (**4**) has found similar results in the case of *Spisula subtruncata*; an examination of the stomach contents showed that these bore a great similarity to the detritus on the bank. These results are also in accord with the general conclusions of Blegvad (**1**).

X. MORTALITY.

No special study of the mortality has yet been made, but at all seasons a few dead valves, mostly attached by the ligament, are to be found in the samples. Only once, in June, 1927, at about half-tide, when many dead shells were seen mingled with the little heaps of debris and seaweed on the shore, was a special collection of the dead material made. Three hundred and thirty-eight valves of *Tellina tenuis*, ranging in size from 3 mm. to 12 mm., still attached by the ligament, were found, and in no case were these bored by *Natica*. In addition to these empty valves there were 56 specimens, ranging from 3 mm. to 13 mm., with the body still inside. In some the flesh was quite fresh, but in others it was black and decaying. This suggests that the mortality is due to "natural causes,"

and not to the action of *Natica*, such as Davis (**5**) has found in the case of *Spisula*, or of fishes, which frequently cause heavy mortality in the bivalve population.

XI. Conclusion.

These results can only be regarded as preliminary, and there are many points in the life-history of *Tellina tenuis* still to be made out. This work was begun as part of a much larger scheme of investigation on the Clyde fauna, especially in regard to the age and renewal of certain groups of bottom-dwelling organisms, and to the numbers and season of appearance of the young broods. The attempt to work out the rate of growth and number of year-groups in the *Tellina tenuis* population by measurement and not by the study of annual rings is an initial step in the attempt to estimate the age of the bivalve population in Scottish waters. There is a great deal of uncertainty as to what the rings to be seen on the shells of certain species really indicate, and in other species these rings are not readily distinguishable. Hence it was felt that with such an abundance of *Tellina tenuis* available the study of the annual increment by measurement was possible. The results show that this is so, although confirmatory work is necessary to settle in how far the annual increment varies from season to season. Larger collections are necessary to secure adequate numbers of the older year-groups. The variation in the rate of growth from bay to bay is also important.

The search for the first appearances of the broods of various bivalves on the bottom is also being continued, certain areas being periodically examined with a fine sieve. In this way it should be possible to determine when and where spat is actually deposited. An attempt will also be made during the summer to trace the distribution of the larval stages of *Tellina tenuis* and of the sizes of less than 1 mm. The early stages of this bivalve are probably pelagic, and, as bivalves of small size are taken in large numbers in the tow-net collections in the area, the identification of at least some of them should be possible.

XII. Acknowledgments.

To Mr. Elmhirst, the Superintendent of the Marine Station at Millport, I am indebted for the information in paragraphs VII and IX, and for the figures of the water-content of the sand in Kames Bay. I am also indebted to him for the facilities which I have enjoyed at the Marine Station; without his help in collecting the samples this work could not have been undertaken.

I have also to thank Dr. Ritchie of the Royal Scottish Museum for kindly reading the manuscript of this paper.

XIII. SUMMARY.

1. The present paper deals with the results of investigations into certain phases in the life-history of the bivalve mollusc *Tellina tenuis* carried out during the autumn of 1926 and 1927.

2. Collections in the intertidal zone and below L.W.M., were made in a number of bays in the Cumbrae and neighbourhood, Kames Bay, Millport, being selected for intensive study.

3. In Kames Bay *Tellina tenuis* ranges from a little below H.W.M. to depths of about 4 fm. The maximum concentration of about 1000 per $\frac{1}{4}$ sq. m. is found at L.W.M. springs and the numbers decrease to zero at H.W.M. and 4 fm.

4. In Kames Bay the density of *Tellina tenuis* falls in a progressive manner from L.W.M. to H.W.M.

5. The size-frequency distribution shows a regular gradation from the lower to the higher levels. At L.W.M. and below individuals of small size predominate, while at H.W.M. they are proportionately few.

6. At higher levels growth is more rapid than at the lower levels.

7. The size-frequency curves and density of *Tellina tenuis* in the other bays at L.W.M. correspond with those of half-tide in Kames Bay.

8. The rate of growth may therefore be influenced by the density of population as well as by the habitat.

9. In all areas the 1926 brood predominates.

10. The *Tellina tenuis* population in Kames Bay seems to be composed of four year-groups, one of which is almost unrepresented. Collections from neighbouring bays indicate that older groups may be present.

11. The amount of young brood on the bottom seems to vary considerably from year to year, being large and small in alternate years.

12. The two closely related species, *T. tenuis* and *T. fabula*, are both plentiful in Kames Bay, but their range is not coincident.

13. Ripe sperms were found from May onwards and ova were rounding off in June.

14. Young *Tellina tenuis*, passing the 2-mm. sieve but retained by the 1-mm. sieve, were found in Kames Bay in August, chiefly below L.W.M., but in October plentifully distributed up to half-tide and in lesser numbers higher up the shore.

15. The food usually consists of vegetable detritus, but during the spring increase diatoms appear almost exclusively in the gut.

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TABLE 7.

TABLE SHOWING THE PERCENTAGE OF THE TOTAL CATCH OF *TELLINA TENUIS* AT EACH SIZE-FREQUENCY IN MM. AT STATIONS 2 TO 7 IN KAMES BAY.

STN. 2.

	mm.																Total specimens.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
24.9.26	3·0	6·0	11·3	3·8	0·8	–	0·8	6·0	12·1	9·0	20·4	12·9	10·5	1·6	0·8	0·8	132
20.1.27	12·0	23·5	13·7	1·1	3·3	0·6	1·7	3·3	9·3	8·7	10·9	7·6	4·4	–	0·6	–	183
13.4.27	26·0	18·0	10·7	6·6	2·0	0·7	1·3	2·0	4·6	6·0	8·6	7·3	4·6	2·0	–	–	151
14.6.27	1·2	5·4	10·7	20·2	13·7	6·6	2·4	1·8	0·6	3·6	6·6	7·1	13·1	5·4	1·2	0·6	168
13.8.27	0·5	0·5	4·0	9·3	15·2	18·2	18·2	8·4	1·5	0·5	7·9	4·9	4·4	3·9	2·5	–	203
7.10.27	–	3·1	1·0	3·1	10·3	12·4	23·6	18·5	4·2	3·1	2·0	9·3	8·3	1·0	–	–	97

STN. 3.

																	Total specimens.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
24.9.26	10·2	14·7	15·1	3·4	1·4	2·0	3·4	5·8	9·2	7·8	8·8	11·2	4·4	1·4	1·0	–	205
20.1.27	13·6	15·5	13·1	4·1	0·4	1·8	4·1	7·8	7·4	11·8	13·6	6·0	0·4	0·9	–	–	221
13.4.27	28·7	20·4	11·9	3·9	1·3	1·0	1·6	2·0	5·0	6·6	8·6	7·6	1·0	–	0·3	–	303
14.6.27	4·4	20·0	20·3	14·4	13·4	5·6	1·9	1·9	1·2	3·8	6·3	3·8	3·1	0·6	–	–	321
13.8.27	3·2	4·4	7·6	10·5	16·3	16·6	13·7	5·3	1·2	3·7	5·6	6·6	4·4	0·5	0·8	–	411
7.10.27	5·1	8·4	5·7	8·1	10·6	15·5	12·6	10·9	2·2	1·9	5·1	5·1	5·7	1·3	1·3	–	310

STN. 4.

																	Total specimens.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
24.9.26	36·3	19·9	7·6	1·2	0·9	3·0	7·8	8·7	8·2	5·5	0·9	–	–	–	–	–	473
20.1.27	35·0	20·3	8·1	2·9	1·4	2·7	6·3	6·3	7·9	7·4	1·9	–	–	–	–	–	632
13.4.27	36·1	20·5	10·5	4·4	0·9	0·9	3·4	4·3	5·7	5·5	6·6	1·6	–	–	–	–	560
14.6.27	5·4	20·1	25·3	17·1	11·0	3·8	1·0	4·4	4·0	3·6	2·4	1·5	0·4	–	–	–	742
13.8.27	1·7	3·7	10·7	19·3	20·5	18·8	10·3	3·3	2·3	2·8	3·2	1·9	1·4	0·1	–	–	835
7.10.27	2·0	3·5	6·9	14·1	16·8	18·7	13·3	5·2	3·5	6·9	5·4	2·2	1·4	–	–	–	594

STN. 5.

																	Total specimens.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
24.9.26	61·8	17·9	2·5	0·6	1·7	3·9	4·6	3·1	2·2	1·0	0·4	–	0·3	–	–	–	822
7.2.27	49·7	20·2	5·0	1·8	1·9	3·5	5·7	5·3	4·3	2·1	0·3	0·1	–	–	–	–	905
13.4.27	41·5	25·1	7·0	2·9	0·9	2·2	4·9	6·5	5·6	2·2	0·7	0·2	0·1	–	–	–	998
20.6.27	4·6	18·1	23·7	17·9	10·8	4·2	1·6	4·9	6·1	4·9	2·9	0·4	–	–	–	–	736
13.8.27	13·1	5·3	12·3	17·9	15·7	10·4	4·8	6·9	6·7	4·1	1·9	0·9	–	–	–	–	862
7.10.27	20·7	14·9	12·0	9·3	11·9	8·7	4·1	4·7	7·7	4·5	1·3	0·3	–	–	–	–	764

STN. 6.

																	Total specimens.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
6.10.26	69·2	19·4	1·8	1·8	1·8	1·8	3·1	0·3	0·5	–	–	–	–	–	–	–	325
17.4.27*	63·4	25·1	8·0	0·9	1·1	0·3	0·9	–	–	0·3	–	–	–	–	–	–	355
13.8.27	38·6	15·8	13·4	17·0	11·8	1·1	1·0	0·8	–	–	–	–	–	–	–	–	254
8.10.27	27·3	13·4	14·9	24·2	10·8	5·2	1·5	2·6	–	–	–	–	–	–	–	–	194

* In January, 1927, a cube of 20 c.c. only gave 3 specimens of 3 mm. in length, but owing to the stormy weather when the haul was made it cannot be considered as a true sample.

STN. 7.

																	Total specimens.
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
6.10.26	65·5	7·0	3·5	17·3	7·0	–	–	–	–	–	–	–	–	–	–	–	29
20.1.27	35·7	40·5	10·7	6·0	–	–	1·2	1·2	4·0	1·2	–	–	–	–	–	–	84
17.4.27	70·9	20·2	5·0	1·0	–	1·5	1·5	–	–	–	–	–	–	–	–	–	203
13.8.27	42·1	25·4	10·5	11·4	5·2	2·7	1·8	0·9	–	–	–	–	–	–	–	–	114
8.10.27	53·9	26·6	9·1	7·0	2·1	0·7	0·7	–	–	–	–	–	–	–	–	–	143

TABLE 8.

TABLE SHOWING THE PERCENTAGE OF THE TOTAL CATCH OF *TELLINA TENUIS* AT EACH MM. AT CERTAIN STATIONS IN THE FAIRLIE SANDS, WHITE BAY, GARRISON BAY, AND CASTLE BAY, LITTLE CUMBRAE.

	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	24	Total specimens.
Fairlie Sands L.W.M., 15.6.27	0·9	8·8	20·6	22·9	15·3	9·8	2·7	0·9	0·3	0·6	1·8	2·4	3·0	3·6	3·0	1·5	1·5	0·3	0·3	–	339
,, ,, ,,	2·9	5·7	10·3	19·8	23·7	21·7	7·7	2·1	0·8	1·0	0·9	0·9	1·1	0·5	0·3	0·1	0·3	–	–	–	765
White Bay, L.W.M., 14.4.27	–	–	1·6	11·1	14·3	6·4	–	–	1·6	6·4	9·5	12·7	15·7	1·6	–	7·9	1·6	6·3	3·2	1·6	242
,, ,, 8.10.27	5·4	28·5	26·0	11·1	5·8	5·0	3·3	2·9	0·8	0·4	0·8	1·6	0·4	1·6	4·1	0·4	–	0·8	0·8	–	218
Garrison Bay, L.W.M., 16.6.27	0·8	4·6	5·4	15·9	19·6	13·2	7·6	3·8	2·3	3·0	4·6	3·8	6·0	6·0	1·9	1·5	0·4	–	–	–	265
Castle Bay, Little Cumbrae, L.W.M., 18.6.27	3·8	13·4	20·2	29·1	15·7	8·0	1·4	0·7	0·4	0·4	0·7	0·7	0·7	0·9	1·8	2·1	0·7	–	–	–	312

Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

Structure of Pearls.

By C. Amirthalingam.

Nature, Vol. CXIX, 1927, *pp.* 854–855.

It is pointed out that in some pearls from *Ostrea edulis* a layer identical to the brown horny layer found on the *inner* surface of the shell of oysters occurs. Microscopic examination of sections of this layer showed a brown matrix in which rhombic crystals were embedded and it could not be stained with water-blue. It would appear that this brown layer is more related to the periostracum, on account of its horny nature and unstainable properties, than to the organic matrix of the prismatic or nacreous layers. It is known that under favourable conditions the secretions—lime salts and albuminous fluid which hardens to form the conchyolin—are so regulated that nacreous layers are formed, and that the brown layer on the inner surface of the oyster shells is probably secreted at the end of the autumn period of growth. Hence the occurrence of concentric layers of horny periostracum-like substance in pearl generally and in the shells of oysters and other molluscs may be due to a disturbance in rhythmic action of the secreting epithelia whereby only the first part of the phase of shell-formation is completed with the oncoming of winter or at the end of a shell-growing period.

C. A.

The Soluble Silicate Content of Soils.

By W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1927, **18**, 433–436.

The method of Diénert and Wandenbulcke serves for the estimation of silicate in soil extracts. Values from 18 to 124 parts per million of SiO_2 were obtained from a one to five water extract of air-dry soil. Higher values were given by alkaline than by acid soils, but there was no close parallel between soluble silicate and either pH value or electrical conductivity.

W. R. G. A.

The Control of the Beat of the Fan Segments in *Chætopterus variopedatus*.

By N. J. Berrill.

Nature, *Vol. CXIX*, 1927, *pp.* 564–565.

Experiments isolating the fan segments and extirpating segmental ganglia were recorded, showing that the rhythmical beat of each segment is controlled by the ganglia of that segment, and that the control of a lateral half segment is by the ganglionic lobe of the same side. Further, that there is a secondary nervous control co-ordinating the rhythm of the two halves of each segment and also the consecutive beat of the three segments involved.

N. J. B.

Echinochrome.

By R. K. Cannan.

Biochem. Journ., 1927, *Vol. XXI*, *p.* 184.

In the course of a survey of the biological field for organic oxidation-reduction systems which develop reversible potentials at an inert electrode, the alleged respiratory pigment Echinochrome has been examined. The pigment was separated from the eggs, perivisceral fluid and test of *Arbacia punctulata*. The pigment does not form a dissociable compound with oxygen but is, rather, the oxidant of an electromotively active reversible oxidation-reduction system. The electrode potentials of the system have been measured over the pH range 2·2 to 9·76. The normal electrode potential at 30°C. is +·1995. The alleged respiratory function of echinochrome is discussed.

R. K. C.

On the Feeding Mechanism of *Nebalia bipes*.

By H. Graham Cannon.

Trans. Roy. Soc. Edin., *Vol. LV*, 1927, *pp.* 355–369

Nebalia is a mud-living form feeding on food particles filtered from a food stream produced by its foliaceous trunk limbs. The food stream enters anteriorly and makes its exit at the posterior end of the carapace. The current is produced by the oscillatory movements of the trunk limbs. The anterior limbs are the main inhalent pumps, the posterior being exhalent as well as inhalent. The exopodites and epipodites act as valves allowing water to pass out posteriorly and preventing water passing forwards. The trunk limb endopodites are armed along their

inner edges with four rows of setæ. The first and third rows are hooked and those of successive limbs interlock, forming a continuous filter wall on either side of the median chamber between the limbs. The fourth form a row of comb setæ combing the food off the filter walls, and the second a row of brush setæ sweeping the food upwards towards the mid-ventral food groove. The proximal setæ of the first row are stout and are not hooked, and form a gnathobasic series pushing the collected food towards the mouth. On the eighth trunk limb the fourth-row setæ are absent, and the third rows interlock, forming a wall preventing the entrance of water into the filter chamber posteriorly. On the first trunk limb the first-row setæ are not hooked, but two groups towards the base of the limb are very stout and function in pushing large food particles directly on to the mouth-parts. The proximal endites of the maxillules and maxillæ both point between the bifid lower lip towards the mouth. The distal endites bite together in the transverse plane. The mouth-parts, both structurally and in their method of functioning, closely resemble those of a Mysid. From a comparison with Paranebalia it is suggested that Nebalia evolved from a Mysid, or some other primitive Malacostracan possessing a feeding mechanism similar to that of Hemimysis, that took to mud-living habits. The foliaceous limbs are in no way primitive, but evolved from typical biramous Malacostracan limbs in connection with the new method of filter feeding.

H. G. C.

On the Feeding Mechanism of a Mysid Crustacean, ***Hemimysis Lamornæ*****.**

By H. Graham Cannon and Miss S. M. Manton.

Trans. Roy. Soc. Edin., *Vol. LV*, 1927, *pp.* 219–253.

H. Lamornæ exhibits two types of feeding, one on large food masses and the other on minute particles filtered from a water current. In the filter mechanism the maxilla acts as a suction pump and a true filter. The comb of setæ on the proximal endite forms the filter plate. The filtered food is pushed on the mouth between the bases of the paragnaths by the long setæ of the maxillulary proximal endites and the comb of setæ on the proximal endites of the first trunk limbs. It is pushed directly on to the spine-rows of the mandibles. The food stream along the ventral food groove is produced by the swimming activities of the trunk limbs. Each exopodite rotates so that its tip describes an ellipse. By this rotary action a food-bearing stream is sucked down each cone of rotation and passes in between the limb bases to the ventral food grove. Large food masses are held by the trunk limb endopodites and mandibular palps and bitten into by the incisor processes of the mandibles and the distal

endites of the maxillules. The mandibles are asymmetrically arranged so that food bitten off by the incisor processes is automatically passed on to the *laciniæ mobiles* and then to the molar processes. Storch's description of the feeding process of a Daphnid and his views on the evolution of the feeding mechanism of Crustacea and Tribolites are criticised. Simple biramous swimming paddle limbs, such as occur posteriorly in *Lepidocaris* are suggested as being the primitive limb rather than a filtering "phyllopodium" as considered by Storch. From primitive articulates possessing biramous limbs there evolved, on the one hand, the Branchiopoda, and the other Cructacea, in which the limbs projected ventrally from the body in two parallel series, and on the other, Marella and the Trilobites, in which the limbs projected laterally. In the Branchiopoda the endopodite became a foliaceous swimming organ, while in the Malacostraca the expodite became the swimming part, but it became whip-like and not foliaceous. In both cases the swimming activities produced an orally directed food stream. In Marella and the Trilobites the foliaceous exopodite became the swimming branch of the limb. In the Trilobites the pleural shield developed to enhance the food-collecting activities of the exopodites. In both Trilobites and Crustacea the presence of a large labrum assists in sucking food into the mouth region.

H. G. C.

Myothermic Observations on the Dogfish.

By A. V. Hill.

Journ. Physiol., Vol. LXII, 1926, *p.* 156.

Heat production was studied in the muscles of the lower jaw of the dogfish and the relations found between heat, tension, length and duration of stimulus were similar to those obtaining in muscles from other animals. The great rapidity of response of these muscles entails a rapid increase of heat production with duration of tetanus, and results in a rapid onset of fatigue.

A. V. H.

Fatigue, Retention of Action Current and Recovery in Crustacean Nerve.

By A. Levin.

Journ. Physiol., Vol. LXIII, 1927, *p.* 113.

The excised limb nerves of crustaceans, which are non-medullated, survive well and form a suitable object for electro-physiological investigation. They are rapidly fatigued by tetanic stimulation, as shown by the

nearly total disappearance of the electric response, and they recover if left at rest for sufficient time. This fatigue goes hand in hand with an increase in the negativity of the nerve, additional to the negativity of the action current and of a more persistent nature. Each single impulse, by itself of very short duration, leaves behind it a state of negativity (" retention of action current "), wearing off in a few seconds; this negativity accumulates if the stimuli follow each other frequently enough and it then takes a longer time to wear off. The greater the amount of the " retention " present at any moment, the greater the reduction in size of the electric response. The disappearance of " retention " is a sign of complete recovery.

This experimental fatigue is a combination of local and conduction fatigue. It is considerably greater near the stimulating electrode, but the whole nerve also is fatigued as the result of conducted impulses.

This " retention " of action current is widely encountered in all kinds of excitable tissues and is probably connected with the processes of restitution.

A. V. H.

The Viscous-Elastic Properties of Muscle.

By A. Levin and J. Wyman.

Proc. Roy. Soc., London, B. Vol. CI, 1927, *p.* 218.

The viscous-elastic properties of muscles were studied by means of an improved form of myograph which enables very accurate tension-length curves to be obtained for stretches or releases, carried out at any desired constant speed on various types of muscles, smooth and striated. In all these muscles the same general phenomena were found, in connection with the relation between work done and speed of shortening, though some muscles were more suitable for the investigation than others. The quick-moving jaw muscles of the dogfish, however, showed precisely the same characteristics, on a different time scale, as the slow-moving body muscles of Holothuria.

The results are discussed theoretically, and it is shown that they can be deduced from the conception that a muscle is a viscous-elastic system containing (*a*) a purely elastic element, and (*b*) a damped elastic element, these being in series with one another; and the bearing of the results upon theories of muscular contraction is considered.

A. V. H.

A Study of the Fertilisation Membrane in the Echinoderms.

By A. D. Hobson.

Proc. Roy. Soc., Edin., Vol. XLVII, Part I (*No.* 7), *p.* 94, 1927.

Removal of the zona pellucida of the eggs of *Echinus esculentus* by centrifuging or by means of acid sea-water does not prevent the formation of the fertilisation membrane. Insemination of eggs of *Asterias rubens* in which the nuclear membrane is just beginning to disappear (i.e. at the very beginning of maturation) causes partial activation with formation of Seifriz's "protoplasmic papillæ." Artificial parthenogenesis of the eggs of *Asterias rubens* can be induced by means of isotonic $CaCl_2$, KCl, NaCl, and $MgCl_2$. This indicates that a decrease of surface tension is unnecessary for the formation of the fertilisation membrane. The relation between the pH of the medium and the degree of extrusion of the fertilisation membrane in *Echinus miliaris* has been examined. It is concluded from these results that the osmotic pressure due to the presence of a protein between the membrane and the egg surface is responsible for the extrusion of the membrane. The influence of the salt concentration of the medium supports this view and indicates that the fertilisation membrane is, from the moment of its formation, completely permeable to salts. The origin of the fertilisation membrane is discussed, but in the absence of critical evidence a definite conclusion cannot be reached.

A. D. H.

Contribution to the Study of *Gromia oviformis* Dujardin.

By Margaret W. Jepps, M.A.

Quart. Journ. Micr. Sci., Vol. LXX (*No.* 280), *p.* 701, 1926.

1. *Gromia oviformis* Dujardin is a common British Marine Rhizopod, which frequently reaches a diameter of 2 mm.

2. There appear to be two distinct forms of *Gromia oviformis;* a smaller oval variety is provisionally distinguished from the type as the *dubia* form.

3. The apparently homogeneous pseudochitinous shell has a complex microscopic structure, of which some description is given.

4. The protoplasm, which fills the shell, is crowded with stercomata, xanthosomes, and a heterogeneous collection of ingested debris, all of which take a part in giving its colour to the animal.

5. There are numerous nuclei scattered throughout the protoplasm. Some of them are always undergoing a simple kind of division, which, however, involves some rearrangement of the chromatin.

6. A process of sporulation has been seen, occasionally in nature, and frequently in aquarium specimens; repeated divisions of the nuclei results in the formation of very numerous uniflagellate swarm spores, 2–3μ in diameter. These swim out of the shell. Their further development has not so far been observed.

M. W. J.

A Note on Hæmerythrin.

By G. F. Marrian.

Brit. Journ. Exp. Biol., Vol. IV, 1927, *p.* 357.

A brief study of the dissociation curves of oxyhæmerythrin was made, using the colorimetric method of Pantin and Hogben. At pH 7·0 dissociation curves were plotted at temperatures of 0–15–25 and 35° C. From a consideration of these curves, the heat of dissociation of oxyhæmerythrin was calculated to be 10,350 calories per gramme-molecule of oxygen. Variation of pH between 6·0–10·0 appeared to have little effect on the shape of the dissociation curve.

The stability of oxyhæmerythrin is greatest at pH 8·0–9·0.

A yellow compound which appeared to be analogous to methæmoglobin was obtained by the action of K_3FeCy_6 or H_2O_2 on oxyhæmerythrin. This change occurred spontaneously with some rapidity at pH 3·0–4·0. By reduction of "methæmerythrin" with sodium hydrosulphite at pH 9·0 and subsequent re-oxidation by atmospheric oxygen, oxyhæmerythrin was re-obtained.

Spectroscopic examination showed that oxyhæmerythrin had a weak absorption band at about 5000 Å, which was only visible over a limited range of dilution. "Methæmerythrin" showed a more distinct band at about 4000 Å, which was visible over a greater range of dilution.

Several unsuccessful attempts were made to demonstrate the presence of Anson and Mirsky's hæm in the molecule. No hæmochromagen spectrum was visible after reduction of the pigment in alkaline solution. No coloured extract was obtained by the Schultz separation.

The addition of concentrated sulphuric acid to a solution of oxyhæmerythrin produced a deep purple or reddish brown solution with a marked green fluorescence that had a strong superficial resemblance to acid hæmatoporphyrin. A well-defined absorption band at about 5400 Å was observed in such solutions. After neutralisation no spectrum typical of alkaline hæmatoporphyrin was observed.

Like hæmocyanin, hæmerythrin was shown not to cause blueing of guaiacum in the presence of hydrogen peroxide.

G. F. M.

The Vertical Distribution of Plankton in the Sea.

By F. S. Russell.

Biol. Rev. and Biol. Proc. Cambridge Phil. Soc., Vol. II (*No.* 3), *pp.* 213–262. 1927.

This is a summary review of our present knowledge of the vertical distribution of plankton in the sea. The possible factors controlling the distribution of the plankton plants and animals are first discussed. Information on variation with depth of such physical factors as light intensity and colour, temperature, viscosity and density, current and wind effects, and pressure are given ; salinity, oxygen and CO_2 content, hydrogen ion concentration, and the presence of dissolved nutrient salts are also dealt with. Finally, observations on the swimming speeds of some plankton animals and the sinking speeds of both animals and plants are cited. The vertical distribution of the phytoplankton in the sea is outlined, together with the various changes that are brought about in it by internal and external causes. The vertical distribution of the animal plankton as shown by the results of field collections is dealt with at some length, illustrations being given of the regional, seasonal and daily changes that may occur therein, and also of ontogenetic changes and other alterations that may be due to spawning habits or to hydrographical conditions. The next section gives some of the principal results obtained by experimental work and their bearing on the behaviour of the animals in nature as shown by field observations. Lastly, a discussion of the subject is given in which light is regarded as the most important controlling factor. The paper ends with a bibliography of 168 titles. F. S. R.

New Mutations in *Gammarus Chevreuxi* Sexton.

By E. W. Sexton and A. R. Clark.

Nature, Vol. 117, *pp.* 194–195. *Feb.* 6, 1926.

Describes several recent mutations in three distinct new stocks of Gammarus from the wild ; in all three, red-eyes appeared recessive to black-eye. Two of the stocks are of special interest. In the first, two distinct kinds of red-eyes occurred, a bright red, and a very dark, almost blackish red, the exceptional feature being that the dark-red always *lightens* as the animal grows older, but even though it may lighten so much as to become bright-red, the animal always functions as a dark-red. The second stock produced the most striking mutation which has yet appeared in Gammarus—a change in the *body*-colour. Instead of the normal pale-green body, dark green gonads, and eggs, the body in this mutation, the gonads, eggs, and, in some cases, the eyes, were pure white. The first White female of this type was mated with a Red male of the same brood which carried white and gave all white-eyed offspring, some of which remained white through life (" Permanent Whites "),

whilst some developed colour as they grew (the "Changeling Whites"), until at maturity they were indistinguishable from normal red-eyed animals. Changeling by Changeling gave reds and whites; Permanent Whites mated together gave all white-eyed young, but the reciprocal crosses of the Permanent Whites mated with Reds or Changelings of their own stock gave remarkable results. White female by any Red or Changeling male, young always white-eyed *at birth*; White male by homozygous Red female, young always red-eyed; by heterozygous Red, or by Changeling female, reds and whites were produced. E. W. S.

Inheritance in *Gammarus Chevreuxi* Sexton.

By E. W. Sexton and C. F. A. Pantin.

Nature, Vol. 119, *pp.* 119–120. 1927.

The white body mutation described in the previous note is discussed with special reference to the Changeling Whites, i.e. those animals which, arising from a mating of Pure White female by Red male, are hatched with white body and white eyes, but develop green body- and gonad-colour and red eye-colour as they grow. It is shown that Changelings occur only where Reds would be expected; that they always have a white-body mother; always behave genetically as Reds—but are always heterozygous for white body. The following hypothesis is suggested. Normal individuals possess a gene for body colour which corresponds to the white-body mutant gene. Individuals homozygous for white-body factor cannot lay down body-pigment or red eye-pigment, consequently white-body females lay eggs with no pigment. The developing embryo has therefore no pigment, even if the fertilising sperm carries the colour factor. A White individual results which changes to Red as life proceeds, since the colour factor from the sperm is able later to make good the deficit of pigment. E. W. S.

A revised Classification of the Tetraphyllidean Cestoda, with Descriptions of some Phyllobothriidæ from Plymouth.

By W. N. F. Woodland.

Proc. Zool. Soc., London, 1927, *pp.* 519–548.

Twelve species of Phyllobothriidæ are described, including three new species, and one new genus—*Scyphophyllidium*—is proposed. The characters of the family Phyllobothriidæ are re-defined, together with those of the families Proteocephalidæ and Tetrarhynchidæ, and all three families are included in the Order Tetraphyllidea, which is also re-defined. The Tetrarhynchidæ are thus deposed from ordinal rank, and Braun's family Lecanicephalidæ and Southwell's Order Heterophyllidea are shown to be purely artificial groupings. W. N. F. W.

On *Dinobothrium septaria* van Beneden 1889, and *Parabothrium bulbiferum* Nybelin 1922.

By W. N. F. Woodland.

Journ. Parasitology, Vol. XIII, 1927, *pp.* 231–248.

The scolices and mature and gravid proglottids of *Dinobothrium septaria* (a Phyllobothriid) and *Parabothrium bulbiferum* (a Bothriocephalid) are described in detail and some conclusions drawn respecting the affinities of the Tetrabothriidæ and the value of the scolex as a classificatory character.

W. N. F. W.

Formation of Calcareous Tubes Round the Siphons of Teredo.

By C. M. Yonge.

Nature, Vol. CXIX, 1927, *pp.* 11–12.

Calcareous tubes form round the siphons of *Teredo norvegica* after animals are left in still (e.g. tank) water for some months; there is a great deposit of fæcal matter, largely wood, around the openings, and the siphons retain communication with the surrounding water by means of these calcareous tubes. The longest were some $\frac{2}{5}$ inch. This condition of affairs is normal in the giant shipworm, *Kuphus arenarius*, which lives embedded in mud in mangrove swamps in the Pacific, and is in constant danger of being silted up.

C. M. Y.

The Absence of a Cellulase in Limnoria.

C. M. Yonge.

Nature, Vol. CXIX, 1927, *pp.* 855.

A series of experiments, using the ground-up bodies of great numbers of *Limnoria lignorum* and incubating the extract for 2–4 weeks with sawdust at 32° C, failed to show any indication of the digestion of wood. Starch was quickly digested by the same extract. Although wood fragments are always found in the gut, there is apparently no enzyme capable of digesting cellulose, such as is present in Teredo. There is no evidence of symbionts, such as are found in Termites. Since Limnoria has been found boring into the insulation of submarine cables, wood is not necessary to it as in the case of Teredo. The view is put forward that Limnoria (and also *Chelura terebrans*, for which the same results were obtained) bore into wood for *protection only*, and not, as in the case of Teredo, for nutrition as well.

C. M. Y.

Marine Biological Association of the United Kingdom.

Report of the Council, 1927.

The Council and Officers.

The Council has to record with deep regret the death of Sir Arthur Shipley, G.B.E., F.R.S., Master of Christ's College, Cambridge, who served the Association as Chairman of Council for a period of over twenty years, with conspicuous ability and success, and always had its interests at heart.

The usual four quarterly meetings of the Council were held in London, at which the average attendance was twelve. The meetings were held in the Rooms of the Royal Society.

The Council carried out a revision of the Articles of Association, which was duly confirmed by two Special General Meetings of the Association, the first of which was held in the Rooms of the Royal Society and the second in those of the Linnean Society. The thanks of the Association are tendered to these two Societies for their courtesy in providing hospitality.

In March a Committee of four members of the Council visited and inspected the Plymouth Laboratory and the work upon which the Staff and visitors were engaged.

The Plymouth Laboratory.

The new building, which was completed in 1926, has been in full use during the year, and has proved in every way satisfactory. The provisions made for the special needs of physiological and biochemical research are adequate, and the separate working rooms have been much appreciated by visiting physiologists and zoologists who have occupied them. The central heating is proving adequate in winter for the whole range of buildings.

The engines and pumps circulating water have been in constant service and have not needed any replacement; the animals in the aquarium are maintained in healthy condition, and a number of consignments of animals acclimatised to aquarium conditions have been sent to the Aquarium of the Zoological Society of London.

The stone building rented at Fisher's Nose continues to be used for storage, and the buildings at Pier Cellars, Cawsand Bay, have been of service in connection with Dr. W. R. G. Atkins' investigations on the penetration of light into the sea and in connection with experiments on

the lunar periodicity in the spawning of molluscs, which have been made by Mr. C. Amirthalingam.

The Ship and Motor-boat.

The steam drifter *Salpa* has worked continuously and the cost of maintenance is still light for a vessel of this type.

The 25-ft. motor-boat has been in daily use, and its two 3-h.p. paraffin engines have been maintained in satisfactory working order at slight expense.

The Staff.

Mr. C. F. A. Pantin was given leave of absence for some weeks in the early part of the year to conduct a course of lectures and practical work on Comparative Physiology at University College, London.

Dr. C. M. Yonge, who for three years has been a temporary Assistant Naturalist at the Laboratory, left at the end of September. He has been appointed Balfour Student by the University of Cambridge and also leader of a proposed expedition to the Great Barrier Reef of Australia, which is being organised by a Joint Committee of the British Association.

Mr. O. D. Hunt, who was acting during the early part of the year as Lecturer in the Natural History Department of the University of Glasgow, did not resume his post as Assistant Naturalist at the Laboratory in October, as he had received an important commercial appointment in connection with the prevention of the growth of organisms on the bottoms of ships.

Mr. R. Palmer has received an appointment on the staff of the Zoological Laboratory at University College, London.

Occupation of Tables.

The following investigators have occupied tables at the Plymouth Laboratory during the year :—

C. Amirthalingam, London (Rhythmic spawning in *Pecten opercularis*).
Miss D. Atkins, London (Pinnotheres and Loxosoma).
L. E. Bayliss, London (Studies on the catch muscle in Pecten).
Miss L. Beanland, Aberystwyth (Community species).
N. J. Berrill, London (Regeneration).
Miss Anna Bidder, Cambridge (Yolk absorption in Cephalopods).
E. Boyland, Manchester (Chemical changes in Muscles).
Prof. H. Graham Cannon, Sheffield (Feeding Mechanisms of Malacostraca).
Dr. S. F. Cook, Harvard (Respiratory pigments).
E. J. H. Corner, Cambridge (Marine Algæ).
Dr. H. Dryerre, Edinburgh (Factors affecting the cardiac inhibitory fibres of the vagus in Dogfish heart).
V. C. Wynne Edwards, Oxford (Life-history of Jassa).

Mr. and Mrs. Philip Eggleton, London (Comparative study of muscles of marine animals).
Dr. T. J. Evans, Guy's Hospital (Scyphistoma of Cyanea).
Miss G. H. Faulkner, London (Filograna).
Dr. Gottfried Fraenkel, Göttingen (On the Righting Reflex of Starfish).
Miss Sylvia Garstang, London (Neural gland of Ascidians).
Prof. E. S. Goodrich, F.R.S., Oxford (Anatomy of Fish).
Dr. Pixell-Goodrich, Oxford (Testing stains for Protozoa).
J. Gray, Cambridge (The effect of electrolytes on the contractile tissues of Pecten).
Dr. B. Gutowski, Warsaw (Movements of bile duct).
Prof. Dr. Sabro Hatta, Sapporo, Japan (Vertebrate Embryology).
C. C. Hentschel, London (Gregarines).
Prov. A. V. Hill, F.R.S., London (Nervous activity).
A. D. Hobson, Edinburgh (1, Artificial Parthenogenesis in *Thalassema Neptuni*. 2, Effect of Electrolytes on muscle of gut of *Dytiscus marginalis*).
Torsten Hŏjer, Stockholm (Methylene blue colouring of the nervous system of *Carcinus mœnas*).
Dr. Eric Holmes, Cambridge (Metabolism of nervous system of Maia).
F. R. Horne, Gresham's School, Holt (Colouration of Anthea and Actinia).
Prof. R. Izumi, Hirosaki, Japan (Collecting fish eggs).
Dr. Carlo Jucci, Naples (Physiology of ciliary movement in Anemones).
P. Kirtisinghe, London (Fishes).
Miss F. M. C. Leak, Sheffield (Studies in the Maxillary Segment of the Crustacea).
Dr. A. Levin (the late), Leningrad (Action Current in Crustacean Nerves).
J. R. Lumby, Lowestoft (Phosphate estimation).
Miss S. M. Manton, Cambridge (Crustacean feeding habits).
Prof. O. Meyerhof, Berlin (General Physiology).
Miss E. A. T. Nicol, Cambridge (Physiology of digestion in Polychætes).
Dr. Yô K. Okada, Tokio (Autolytus).
M. N. Phadake, Cambridge (Cytology of Echinus eggs).
Mrs. Kathleen F. Pinhey, Montreal (Hæmocyanin. Tyrosinase in Crustacea).
Dr. H. H. Poole, Dublin (Light penetration into the sea).
Dr. S. G. M. Ramanujam, Madras (General).
George Rayner, Leeds (Development of swim bladder of Clupeoids).
Miss E. M. Rees, London (Algæ).
J. A. Robertson, Birmingham (Disintegration in Polycelis in relation to gaseous content of water).
Miss Sharpington, London (Algæ).
Dr. T. A. Stephenson, London (Bionomics and Histology of Anemones).
G. A. Steven, Edinburgh (General).
B. W. Tucker, Oxford (Effects of Parasitisation of Gyge on Gebia).
Prof. D. M. S. Watson, F.R.S., London (Gas content and mechanism of swim bladder of Fishes).
G. P. Wells, London (Physiology of Invertebrate Muscle).
D. P. Wilson, Manchester (Polychæte larvæ).
Dr. J. M. Yoffey, Manchester (Comparative vertebrate histology and physiology).

The usual Easter Vacation Course in Marine Zoology was conducted by Dr. J. H. Orton, and was attended by forty-two students from Oxford, Cambridge, London, Edinburgh, Manchester, Sheffield, Portsmouth, Southampton, Eton, and Rothamsted.

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 fourteen students.

Dr. E. W. Shann brought one boy from Rugby, Mr. J. M. Branfoot a class of seven from Oundle, Mr. D. M. Reid a class of two from Harrow, Mr. A. S. Gillespie a class of three from Monkton Combe School (Bath), and M. F. R. Horne a class of four from Gresham's School, Holt, during the Easter Vacation.

During Whitsuntide Mr. W. H. Leigh-Sharpe brought a class of nine from Chelsea Polytechnic.

A joint meeting of the Challenger Society and representatives from Marine Laboratories was held at the Plymouth Laboratory on May 6th–7th.

General Work at the Plymouth Laboratory.

Mr. Ford has again devoted his attention to the study of the herring and its fisheries in the English Channel and off the South-east of Ireland. The first four papers of a proposed series describing the results of his work are now being printed for publication in the *Journal*. Probably the most interesting part of this year's work has been the study of the growth of " whitbait " herrings found in the rivers Tamar and Lynher. On May 26th, 1927, several thousands of young clupeoids, including tiny herrings, were caught by means of a small-meshed Saltash tuck-seine in the Tamar about 3–4 miles above Saltash Bridge. The haul, fortunately, had been taken just soon enough to obtain a fair number of herrings still in the process of metamorphosis, although the majority were completely metamorphosed and fully scaled. Since then, samples, roughly fortnightly, have been taken, both from the Tamar and Lynher, with the result that a good general picture of the increase in average size from month to month has been obtained. An account of this work forms Part 4 of the papers mentioned above, and in it the question of the interpretation of the data is given. The results are of value, confirming as they do the lengths at which the first winter-ring is formed, calculated from measurements of adult scales. Both the adult scales and the direct measurement of the young fishes caught in the two rivers agree in demonstrating that the length at the end of the first year varies over a wide range, and that on an average this length is in the region of 12–13 cm. The examination of the stomach contents of the fishes caught has shown that mysids are by far the most common item of food.

The study of the Plymouth fishery during the winter of 1926–27 confirmed the expectation expressed in last year's Report to the effect that the 1920 year-class would remain in evidence in the catches, although probably less markedly than during the two previous seasons. The younger classes of 1922 and 1923, more particularly the latter, were also well represented, so that it may be expected that they will also make themselves apparent in the season 1927–28.

Dr. Orton's work on sex-change and on the correlation of spawning and shell-growth of the oyster (*O. edulis*) to environmental conditions has been continued for another summer during the past year, and the general results previously obtained have been confirmed and extended. Several thousand oysters have been examined in samples dredged on the same day from beds on the west coast and on the east coast of England. At the same time local variations on each set of beds have been studied. In this way valuable comparative results have been obtained. Special attention has been given to all the seasonal cyclical changes which occur in the oyster, and it has been found that this attitude is essential to an understanding of the primary functions of the organism, namely, growth, reproduction and the accumulation of reserve food products, i.e. fattening, and is also essential to an understanding of the interrelations of these functions. Work on the Fal has shown clearly that there is an early spring period of shell-growth (increase in shell area) (March–April) preceding the summer breeding period, which, in turn, is followed by a distinct post-spawning period of shell-growth and fattening. This sequence has now been followed in a significant amount of material over a period of two complete cycles, and local variations have been studied.

On the Fal have been obtained records which show—contrary to general expectation—that the rate of change of temperature over the main beds is relatively slow, and that the yearly range of temperature is also relatively small. These facts appear to be of fundamental importance in maintaining the main cyclical series on the Fal, namely, spring shell-growth, breeding, and autumn shell-growth, and indicate a fundamental difference of metabolism at least in the summer and other periods. Gonad proliferation occurs at a variable rate in the spring and in the autumn, and rapidly in the summer, and an accumulation of reserves, fattening, occurs during and after the shell-growing period on the Fal in the autumn.

On the River Blackwater, where there is a rapid rise in temperature in the spring, a spring period of growth of shell material occurs, but this period may overlap the beginning of the breeding period. A late summer or autumn growth of shell also occurs on these beds after the main breeding period and apparently before the main fattening period. A similar spring and autumn growth of shell has been observed in other estuarine beds,

especially the River Yealm. It would appear, therefore, that the oyster will ultimately become a valuable subject for the study of differential metabolic processes apparently controlled by different temperature levels. The data obtained on shell-growth are being prepared for publication with a critical examination of possible causative factors.

Spawning records were made during 1927 from samples of oysters dredged simultaneously on west and east coast beds, and the fact established that significant spawning occurred on the east coast beds at the beginning of June at a temperature of about 59°–60° F. On the west coast beds, owing to the cold weather, temperatures fluctuated from 57°–59° F. during June, and a certain amount of indecisive spawning occurred in that month on the warmer portions of the beds, but significant spawning, comparable to that observed on the east coast beds, did not begin until the second week in July when a general rise in temperature to about 59°–60° F. occurred. During the summer significant incomplete and abortive spawning occurred on the Fal beds coincident with the occurrence of low temperatures (i.e. 57°–58° F.) due to the tidal influx of Channel water of low temperature, which in turn is explained by the relative coldness of the summer. This latter observation proves that in a cold summer there will occur in the Fal Estuary beds a heavy loss of eggs and potential oyster larvæ. An account of the observations on spawning in 1926 and 1927 will be prepared for publication in the future.

Dr. Orton has discussed means for preserving the Fal Estuary oyster beds in a report to the Truro Corporation Oyster Committee, and has presented reports on oyster beds to other Oyster Companies. He has also carried out experiments with the rough whelk-tingle, *Murex erinaceus*, and recorded observations which demonstrate the considerable negative economic value of this oyster pest.

During 1926 and 1927 the various phases of the development of the gonad have been studied, and Dr. Orton now recognises more than twenty partly definite and partly arbitrary stages which will be described and figured. By analysing representative samples of about one hundred oysters with regard to these gonad phases, it will be shown that it is possible to compare with a fair degree of accuracy any population of oysters with any other at a given time.

Dr. Lebour's work on the larval crabs of the Plymouth district has resulted in the successful rearing of three species from egg to crab, two of these, *Inachus Dorsettensis* and *Portunus puber*, having reached the seventh young crab stage in about three months, the third, *Xantho incisus*, only reaching the first young stage. All of these were reared in plunger jars on oyster larvæ until they reached the megalopa stage, when they were fed, as before, on pieces of mussel. All the young crabs were also fed on mussel. Amongst other larvæ eaten by the zoeae Echinus larvæ

from artificial fertilisations were successfully used but no crab was reared through the whole of its life-history on these.

A paper is finished and is now being printed for the *Journal*, dealing with larval Ebalia and Pinnotheres. Zoeae of the rare *Pinnotheres veterum* were found in the plankton and changed into megalopæ in the Laboratory, whilst *P. pisum* was hatched from the egg. A very close resemblance is found between the larvæ of Ebalia and Pinnotheres.

Of the thirty-seven crabs known from the Plymouth district twenty-three have now been hatched from the egg, and many of them reared through several larval stages. Of the remaining fourteen all but three can be recognised in one or more stages from the plankton. Those reared from Zoea to crab include Gonoplax, Thia, and Pirimela, and the knowledge gained throws much light on their relationships. A general account of the crab larvæ is nearly ready for publication.

Dr. Lebour has also continued her studies of the planktonic diatoms for the purpose of a book which is intended to be a companion volume to the *Dinoflagellates of Northern Seas*. It is hoped that before long this will be completed.

Hydrographic stations between Plymouth and Ushant have been worked as in previous years, the results of the observations being communicated to the International Council, the French Fishery Department, and the Ministry of Agriculture and Fisheries. The continuous record of these data since April, 1921, is frequently referred to in connection with various investigations. Determination of nitrates in the water of the English Channel has also been continued by Mr. H. W. Harvey, and, in addition, preliminary experiments on the variation in velocity of wind-impelled currents have been made, as a result of which experiments on a larger scale are projected by the Ministry of Agriculture and Fisheries in the North Sea.

Mr. Russell has been occupied for most of the year in working up the collections he made in 1926 with the ring-trawl to study the vertical distribution of young fishes and other plankton animals. The material has been treated in the usual manner, excepting that on this occasion one hundred Calanus from each sample were measured and the sex determined and the same number of Sagitta measured. It is hoped that thus some light will be thrown on the behaviour of the two sexes of Calanus, and on the depth and seasonal distribution of Sagitta with regard to age.

All the post-larval fishes have been sorted and measured. We now have continuous records of young fish between the months of April and August for three years, and a further year's material has been obtained this year (1927) in weekly samples caught by means of oblique hauls with the ring-trawl. It should now be possible to draw up a table showing the seasonal distribution of the pelagic young stages of our common

food fishes and of their growth. It is hoped that these results will form a basis on which to check the results of unusual hydrographical conditions on the spawning of fishes in future years.

During the course of the research on the diurnal changes in the vertical distribution of plankton it has become evident that certain species live in the daytime very close to the bottom. A stramin net has been improvised which, when attached to the frame of an Agassiz trawl, will fish a few inches above the bottom without catching bottom deposits or animals living thereon that may have been disturbed by the passage of the net over the bottom. Results of considerable interest have already been obtained with this net.

Mr. Russell has published in *Biological Reviews* a paper summarising our knowledge of the vertical distribution of plankton in the sea—both phyto- and zoo-plankton—together with an account of experimental work that has a direct bearing on the behaviour of marine plankton animals. An exhibit illustrating this research was shown at the Soirée of the Royal Society in May.

The investigations which Mrs. E. W. Sexton has been carrying on for a number of years on the Mendelian inheritance of eye-colour in the Amphipod *Gammarus chevreuxi* have made considerable progress, and several papers describing results are well advanced. In co-operation with M. C. F. A. Pantin an explanation has been attempted of the behaviour in inheritance of the mutation known as "changeling," in which the eye and the body of the just hatched young shows no coloured pigment, but such pigment appears at a later stage in development. The facts may be adequately explained by supposing that in the normal coloured egg there is a precursor substance which is necessary for pigment formation. When this precursor substance is absent from the egg the young are hatched without pigment, and only become coloured after they have fed and grown.

Mr. H. O. Bull has completed for publication in the *Journal* an account of an investigation carried out from January, 1926, to June, 1927, on the relationship existing between the state of maturity and the chemical composition of the liver and muscular tissue of the whiting. Mr. Bull has also been studying the formation of conditioned "responses" in fishes. By this means it has been shown that *Blennius gattorugine* is sensitive to temperature changes of only 0·5° C., momentarily induced in the surrounding water, and to changes in salinity of four parts per thousand also acting for a few seconds only. Responses to olfactory and gustatory stimuli are also being investigated. Two species of Wrasse have been used for the formation of conditioned responses, using lights of different wave-lengths, intensities, and positions, as the signalling stimuli, and a motor response, involving entry into an opaque bottle for food, as

the reaction they were trained to perform. The method is being used also for investigating colour discrimination and responses to auditory stimuli.

During the year Mr. D. P. Wilson has been attempting to rear the larvæ of some common Polychætes, so that they can be identified in plankton samples. A very common post-larval Terebellid, the genus and species of which were previously unknown, has been reared to stages at which it was possible to recognise it as the young of *Loimia medusa*. The comparatively well-known post-larvæ of *Lanice conchilega* have similarly been reared to early bottom stages. Artificial fertilisations of *Sabellaria spinulosa* and *S. alveolata* have been made, and after several attempts the larvæ were reared to stages just prior to metamorphosis, but so far only specimens picked out from the plankton have undergone that change. The early larvæ of these two species cannot at present be distinguished from one another, but the later stages are easily separated. Investigations have also been made into the life-histories of *Polydora ciliata* and *P. hoplura*, two Polychætes which bore into rocks and oyster shells. In both cases the larvæ are retained for a time in sacs attached to the wall of the burrow alongside the parent, but while in the former species they are released comparatively early in development and have a fairly long planktonic life, in the latter they are retained to a late stage and are ready to settle down soon after liberation. One other Polychæte, *Nereis pelagica*, has been reared from the egg to a juvenile stage of about fifty segments.

Department of General Physiology.

The new laboratories have been fairly well occupied, but only full during the Easter and Summer vacations. They are well supplied with chemical apparatus and reagents, and a more adequate supply of physical apparatus is being got together gradually as funds permit since the individual items are costly. We are indebted to the physical Laboratory, Trinity College, Dublin, and to Prof. J. Joly for the loan of apparatus which is still in use by Dr. H. H. Poole and Dr. Atkins in the prosecution of their work on light penetration in the sea. The photometer cases were machined in the University workshop, and the Physical and Botanical Laboratories lent much of the apparatus used in the overhaul and re-standardisation of the photo-electric photometers, for which the new laboratories of the Royal Dublin Society provided facilities. Dr. Atkins worked there with Dr. Poole for a month at Easter, but was unable to continue the work till completed. Much still remains to be done as regards standardisation of new apparatus and the more extended use at sea of that now available. Measurements of the illumination have now been made down to 65 metres at Station E1.

This work is a natural corollary of that upon the minor constituents of sea-water, which is being continued. The acres of the ocean have depth as well as area, but the effective depth is limited by the supply of light energy required in photosynthesis. The minor constituents at present known to be essential and to exist in limiting amounts, may not be a complete list. Work on others is contemplated when opportunity occurs. The same applies to the continuation of Dr. Atkins' work on net preservation, but it is difficult to carry on the observations and tensile tests on the numerous treated nets at the same time as the work on illumination and on the minor constituents of sea-water. The preservatives already studied include cutch, the Dutch method, the use of copper oleate, a mixed fatty acid copper soap, and a naphthenic acid copper soap together with methods for incorporating resin, tar, or anti-fouling paint as binders. Certain treated nets have now been under test for "rotting" for over twenty-six months without loss in strength. The action of sunlight and general weathering of fabrics due to rain and wind is also receiving attention.

Mr. Pantin has made progress with his work on amœboid movement. Investigation of the action of non-electrolytes has been extended. By diluting isotonic mixtures of sodium chloride and calcium chloride with isotonic glycerol it is shown that it is the ratio of Calcium to Alkali metal ion that is important and not the absolute Calcium concentration. Urea has a peculiar action on amœba in relation to the presence of Calcium and work is shortly to be undertaken on this.

The effect of absence of Oxygen on amœboid movement has been extensively studied. As mentioned last year movement continues in the absence of Oxygen, but ultimately stops. It is found, however, that the sensitivity of amœba to traces of toxic substances is enormously enhanced in the absence of oxygen. Concentrations of these substances which are without effect on the amœba in the presence of oxygen inhibit movement in five to six hours when it is absent.

In pure de-oxygenated sea-water amœba can maintain activity for thirty to sixty hours before inhibition occurs. As in muscle and cilia, the inhibition is reversible.

Published Memoirs.

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

AMIRTHALINGAM, C. *Structure of Pearls.* "Nature," Vol. CXIX, 1927, pp. 854–855.

ATKINS, W. R. G. *Preservation of Fishing Nets.* Nos. 1–4. The Fishing News, 1927, No. 715, p. 31; No. 717, p. 57; No. 719, p. 8; No. 721, p. 39.

ATKINS, W. R. G. *The Methods of using Copper Soaps to Preserve Fishing Nets.* Journ. de Conseil, Vol. II, 1927, pp. 144–150.

ATKINS, W. R. G. *The Soluble Silicate Content of Soils.* Scient. Proc. Roy. Dublin Soc., Vol. XVIII (N.S.), 1927, pp. 433–436.

ATKINS, W. R. G., AND WILSON, E. G. *The Colorimetric Estimation of Minute Amounts of Compounds of Silicon, of Phosphorus and of Arsenic.* Biochem. Journ., Vol. XX, 1926, pp. 1223–1228.

ATKINS, W. R. G. *Histological Applications of Measurements of Acidity or Alkalinity and of Oxidation or Reduction.* Lee, Microtomists' Vade Mecum, Chap. 28, pp. 359–375. New ed. revised by J. B. Gatenby. In the press.

BAYLISS, L. E. *A Conductivity Method for the Determination of Carbon Dioxide.* Biochem. Journ., Vol. XXI, 1927, pp. 662–664.

BERRILL, N. J. *The Control of the Beat of the Fan Segments in Chœtopterus variopedatus.* "Nature," Vol. CXIX, 1927, pp. 564–565.

CANNAN, R. K. *Echinochrome.* Biochem. Journ., Vol. XXI, 1927, pp. 184–189.

CANNON, H. G. *On the Feeding Mechanism of Nebalia bipes.* Trans. Roy. Soc., Edin., Vol. LV, 1927, pp. 335–369.

CANNON, H. G., AND MANTON, S. M. *On the Feeding Mechanism of a Mysid Crustacean, Hemimysis Lamornœ.* Trans. Roy. Soc., Edin., Vol. LV, 1927, pp. 219–253.

HARVEY, H. W. *Fundamental Problems relating to River Pollution.* "Nature," Vol. CXIX, 1927, pp. 463–464.

HARVEY, H. W. *Stream and Drift Currents and Effect of Wind.* Marine Observer, Vol. IV, 1927, pp. 181–183.

HILL, A. V. *Myothermic Observations on the Dogfish.* Journ. Physiol., Vol. LXII, 1926, pp. 156–159.

HOBSON, A. D. *A Study of the Fertilisation Membrane in the Echinoderms.* Proc. Roy. Soc., Edin., Vol. XLVII, 1927, pp. 94–117.

JEPPS, M. W. *Contribution to the Study of Gromia oviformis.* Dujardin. Quart. Journ. Micr. Sci., Vol. LXX, 1926, pp. 701–720.

LEBOUR, M. V. *Life History of the Edible Crab.* Fishing News, Vol. XV, 1927, No. 742, pp. 32–36.

LEBOUR, M. V. *Researches on Rearing a Crab.* Discovery, Vol. VIII, 1927, No. 94, pp. 311–313.

LEVIN, A., AND WYMAN, J. *Viscous Elastic Properties of Muscle.* Proc. Roy. Soc., Ser. B, Vol. CI, pp. 218–243.

MARRIAN, G. F. *A Note on Hœmerythrin.* Brit. Journ. Exp. Biol. Vol. IV, 1927, pp. 357–364.

ORTON, J. H. *On Incomplete Spawning and the Problem of Fertilisation in O. edulis.* "Nature," Vol. CXX, 1927, pp. 403–404.

ORTON, J. H. *The Habits and Economic Importance of the Rough Whelk-Tingle* (Murex erinaceus). "Nature," Vol. CXX, 1927, pp. 653–654.

RUSSELL, F. S. *The Vertical Distribution of Plankton in the Sea.* Biol. Reviews and Biol. Proc. Camb. Phil. Soc., Vol. II, 1927, pp. 213–262.

SEXTON, E. W., AND PANTIN, C. F. A. *Inheritance in Gammarus chevreuxi* Sexton. "Nature," Vol. CXIX, 1927, pp. 119–120.

STEDMAN, ELLEN, AND STEDMAN, EDGAR. *Hœmocyanin. Part IV. The Dependence of the Shape of the Oxygen Dissociation Curve on the State of Ionisation of the Protein.* Biochem. Journ., Vol. XXI, 1927, pp. 533–543.

WOODLAND, W. N. F. *A Revised Classification of the Tetraphyllidean Cestoda, with Descriptions of some Phyllobothriidæ from Plymouth.* Proc. Zool. Soc. Lond., 1927, pp. 519–548.

WOODLAND, W. N. F. *On Dinobothrium septaris* Van Beneden, 1889, *and Parabothrium bulbiferum* Nybelin, 1922. Journ. Parasitology, Vol. XIII, 1927, pp. 231–248.

YONGE, C. M. *Formation of Calcareous Tubes round the Siphons of Teredo.* "Nature," Vol. CXIX, 1927, pp. 11–12.

YONGE, C. M. *Food from the Sea. I. The Shellfish Industry.* Review of Reviews, 1927, No. 445, pp. 137–141.

YONGE, C. M. *The Absence of a Cellulase in Limnoria.* "Nature," Vol. CXIX, 1927, p. 855.

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, and the Council are specially grateful to Dr. G. P. Bidder for a full set of the Reports of the *Valdivia* Expedition.

Finance.

The Council wish to express their thanks to the Development Commissioners for their continued support of the work of the Association. They have to thank, also, for generous grants, the Fishmongers' Company (£600), the British Association (£35), the Ray Lankester Trustees (£20) and the Universities of Oxford, Cambridge, Bristol, Birmingham, Leeds and London.

Thanks are due to Mr. E. T. Browne for an additional donation of £200 to the building Fund.

Vice-Presidents, Officers and Council.

The following is the list of gentlemen proposed by the Council for election for the year 1928–29 :—

President.

Sir E. RAY LANKESTER, K.C.B., LL.D., F.R.S.

Vice-Presidents.

The Duke of BEDFORD, K.G.
The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of BALFOUR, K.G., F.R.S.
Viscount ASTOR.
Lord MONTAGU OF BEAULIEU.
Lord ST. LEVAN, C.B., C.V.O.
The Right Hon. Sir ARTHUR GRIFFITH BOSCAWEN.
The Right Hon. Sir AUSTEN CHAMBERLAIN, K.G., M.P.
Sir W. B. HARDY, F.R.S.
The Right Hon. Sir ARTHUR STEEL-MAITLAND, Bart., M.P.
GEORGE EVANS, ESQ.
Sir NICHOLAS WATERHOUSE, K.B.E.
Prof. W. C. MCINTOSH, F.R.S.
G. A. BOULENGER, Esq., F.R.S.
J. O. BORLEY, Esq., O.B.E.

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Elected Members

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Col. Sir Henry F. Bowles, Bart.
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Prof. J. C. Drummond, D.Sc.
Prof. H. Munro Fox.
Prof. J. Stanley Gardiner, F.R.S.
Prof. A. C. Hardy.
Prof. S. J. Hickson, D.Sc., F.R.S.
Prof. A. V. Hill, Sc.D., F.R.S.
E. S. Russell, Esq., D.Sc.
J. M. Tabor, Esq.
Prof. W. M. Tattersall.

Chairman of Council.

Prof. E. W. MacBride, D.Sc., F.R.S.

Hon. Treasurer.

George Evans, Esq., 1 Wood Street, London, E.C.2.

Secretary.

E. J. Allen, Esq., D.Sc., F.R.S., The Laboratory, Citadel Hill, Plymouth.

The following Governors are also members of the Council:—

G. P. Bidder, Esq., Sc.D.
E. T. Browne, Esq.
George Evans, Esq.
H. G. Maurice, Esq., C.B. (Ministry of Agriculture and Fisheries).
Nigel O. Walker, Esq. (Prime Warden of the Fishmongers' Company).
W. T. Brand, Esq. (Fishmongers' Company).
Lothian D. Nicholson, Esq. (Fishmongers' Company).
Prof. G. C. Bourne, D.Sc., F.R.S. (Oxford University).
J. Gray, Esq. (Cambridge University).
P. Chalmers Mitchell, Esq., C.B.E., D.Sc., F.R.S.(British Association).
Prof. E. W. MacBride, D.Sc., F.R.S. (Zoological Society).
Sir Sidney Harmer, K.B.E., F.R.S. (Royal Society).

THE MARINE BIOLOGICAL ASSOCIATION

Dr. *Statement of Receipts and Payments for the*

GENERAL

	£ s. d.	£ s. d.
To Balance from 31st March, 1927 :—		
Cash in hand	75 1 2	
Cash at Bank	68 18 8	143 19 10
,, Grants :—		
Ministry of Agriculture and Fisheries Grant from Development Fund	11,250 14 10	
Fishmongers' Company	600 0 0	
British Association	35 0 0	
Royal Society Gore Fund	30 0 0	11,915 14 10
,, Subscriptions		166 14 0
,, Composition Fee (Founder)		100 0 0
,, Donations		41 1 0
,, Sale of Specimens (*less* Purchases)		661 8 7
,, ,, Fish (*less* Expenses)		49 14 1
,, ,, Nets, Gear, and Hydrographical Apparatus		617 3 0
,, Table Rent (including Cambridge University, £52 10s. ; Oxford University, £52 10s. ; London University, £52 10s. ; Bristol University, £25 ; Trustees of the Ray Lankester Fund, £20 ; Birmingham University, £10 10s.)		323 10 0
,, Tank Room Receipts		429 12 1
,, Interest on Investments :—		
4% War Stock	3 2 8	
4% New Zealand Stock	13 2 10	
Deposit Account	21 12 4	37 17 10
,, Royalties on Films		2 7
,, Sale of Dr. M. V. Lebour's Book		6 5 0
		£14,493 2 10

The Association's Bankers hold on its behalf :—
£51 National Savings Certificates.
£78 9s. 4d. 4% War Stock, 1929–42 (Deed Stock).
£410 14s. 8d. New Zealand 4%, 1943–63.

BUILDING

	£ s. d.
To Balance at Bank 31st March, 1927	137 8 6
,, Donations	206 6 0
	£343 14 6

Year 1st April, 1927, to 31st March, 1928. Cr.

FUND.

By Salaries :—	£	s.	d.	£	s.	d.
Director	1,112	10	0			
Physiologist	910	0	0			
Naturalists	3,275	18	0			
Hydrographer	558	6	8	5,856	14	8
,, Laboratory Wages (including National Insurance)				1,871	7	10
,, Annual Upkeep of Library				553	2	2
,, Scientific Publications :—						
Journal, Vol. XIV, No. 3 (part), No. 4, and Vol. XV, No. 1	888	19	8			
Less Sales	64	12	1			
	824	7	7			
Less Grant from Royal Society	30	0	0	794	7	7
,, Annual Upkeep of Laboratories and Tank Rooms :—						
Buildings and Machinery	221	18	7			
Electricity, Gas, Coal, and Water	289	12	4			
Chemicals and Apparatus	545	0	9			
Rates, Taxes, and Insurance	104	3	8			
Travelling	134	6	7			
,, "Challenger" Society Meetings	13	12	0			
Stationery, Postages, Telephone, Carriage, and Sundries	382	10	9	1,691	4	8
,, Annual Maintenance and Hire of Boats :—						
Wages (including Diet Allowance, National Insurance, and Casual Labour)	1,570	16	4			
Coal and Water	570	15	9			
Maintenance and Repairs, with Nets, Gear, and Apparatus	1,044	15	2			
Boat Hire and Collecting Expeditions	34	17	4			
Insurance	326	3	4	3,547	7	11
,, Interest on Bank Loans					14	10
,, Balance, 31st March, 1928 :—						
Cash in hand	21	12	1			
Cash at Bank	156	11	1	178	3	2
				£14,493	2	10

FUND.

By Expenditure on Buildings and Equipment	£	s.	d.
	343	14	6
	£343	14	6

Examined and found correct,

(Signed) N. E. WATERHOUSE, *Auditor.*
L. D. NICHOLSON } *Members of*
D. M. S. WATSON } *Council.*

3 *Frederick's Place,*
Old Jewry, London, E.C. 2.
24*th April*, 1928.

List of Annual Subscriptions

Paid during the Year, 1st April, 1927, to 31st March, 1928.

	£	*s.*	*d.*
Dr. W. M. Aders	1	1	0
E. J. Allen, Esq., D.SC., F.R.S.	1	1	0
C. Amirthalingam, Esq. (1927 and 1928)	2	2	0
Prof. J. H. Ashworth, D.SC., F.R.S.	1	1	0
The Right Hon. Lord Askwith, K.C.B., D.C.L.	1	1	0
W. J. Bazeley, Esq.	1	1	0
Dr. Bělehrādek	1	1	0
N. J. Berrill, Esq.	1	1	0
Mrs. M. G. Bidder	1	1	0
Birkbeck College	1	1	0
Mrs. H. Moss Blundell	1	1	0
L. A. Borradaile, Esq., SC.D.	1	1	0
Colonel Sir Henry Bowles, Bart.	1	1	0
Dr. A. Bowman	1	1	0
Sir J. Rose Bradford, K.C.M.G., M.D., D.SC., F.R.S.	1	1	0
J. M. Branfoot, Esq.	1	1	0
Brighton Public Library	1	1	0
H. H. Brindley, Esq.	1	1	0
R. H. Burne, Esq.	1	1	0
R. R. Butler, Esq.	1	1	0
L. W. Byrne, Esq.	1	1	0
Dr. W. T. Calman, F.R.S. (1926 and 1927)	2	2	0
Prof. H. Graham Cannon, D.SC.	1	1	0
Prof. C. Chilton	1	1	0
Dr. A. H. Church, F.R.S.	1	1	0
Dr. J. Clark	1	1	0
J. F. Coonan, Esq.	1	1	0
L. R. Crawshay, Esq.	1	1	0
Prof. O. V. Darbishire	1	1	0
G. Despott, Esq.	1	1	0
Director of Agriculture and Fisheries, Travancore	1	1	0
F. A. Dixey, Esq., F.R.S.	1	1	0
C. C. Dobell, Esq., F.R.S.	1	1	0
H. V. Dobson, Esq., J.P.	1	1	0
Prof. J. C. Drummond, D.SC.	1	1	0
Carried forward	38	17	0

	£	s.	d.
Brought forward	38	17	0
F. Martin Duncan, Esq. (1925–1927)	3	3	0
Prof. J. S. Dunkerly, D.SC., PH.D.	1	1	0
Howard Dunn, Esq.	1	1	0
P. Eggleton, Esq.	1	1	0
George Evans, Esq.	1	1	0
G. P. Farran, Esq.	1	1	0
G. Herbert Fowler, Esq., PH.D. (1926 and 1927)	2	2	0
Dr. E. L. Fox	1	1	0
Prof. H. M. Fox,	1	1	0
Miss E. A. Fraser, D.SC.	1	1	0
Prof. J. S. Gardiner, F.R.S. (1927 and 1928)	2	2	0
Samuel Gardner, Esq.	1	1	0
Prof. E. S. Goodrich, F.R.S.	1	1	0
A. P. Graham, Esq.	1	1	0
J. R. Groome, Esq.	1	1	0
Dr. H. P. Hacker (1927 and 1928)	2	2	0
W. Hall, Esq.	1	1	0
A. C. Hardy, Esq.	1	1	0
John C. Hemmeter, Esq., PHIL.D., M.D., LL.D.	1	1	0
C. C. Hentschel, Esq.	1	1	0
C. F. Hickling, Esq. (1927 and 1928)	2	2	0
Prof. S. J. Hickson, D.SC., F.R.S.	1	1	0
Prof. A. V. Hill, F.R.S.	1	1	0
Prof. J. P. Hill, F.R.S.	1	1	0
W. T. Hillier, Esq., M.R.C.S.	1	1	0
A. D. Hobson, Esq.	1	1	0
Frank R. Horne, Esq.	1	1	0
Capt. G. C. L. Howell	1	1	0
O. D. Hunt, Esq.	1	1	0
Prof. Julian S. Huxley	1	1	0
J. J. Judge, Esq.	1	1	0
P. Kirtisinghe, Esq.	1	1	0
The Hon. Lionel Lindsay	1	1	0
A. G. Lowndes, Esq.	1	1	0
J. R. Lumby, Esq.	1	1	0
Prof. E. W. MacBride, D.SC., F.R.S.	1	1	0
Stanislaus Makovski, Esq.	1	1	0
G. I. Mann, Esq.	1	1	0
D. J. Matthews, Esq.	1	1	0
Capt. W. N. McClean	1	1	0
Carried forward	87	3	0

	£	s.	d.
Brought forward	87	3	0
J. H. Midgley, Esq.	1	1	0
W. S. Millard, Esq.	1	1	0
C. C. Morley, Esq.	1	1	0
National Museum of Wales	1	1	0
H. G. Newth, Esq.	1	1	0
Chas. Oldham, Esq.	1	1	0
G. Ord, Esq.	1	1	0
J. H. Orton, Esq., D.SC. (1920–1927)	8	8	0
G. W. Paget, Esq.	1	1	0
The Hon. John H. Parker (1927 and 1928)	2	2	0
Enrique Pascual, Esq., O.B.E. (1925–1929)	5	0	0
Pawlyn Brothers	1	1	0
T. A. Pawlyn, Esq.	1	1	0
F. T. K. Pentelow, Esq.	1	1	0
Plymouth Corporation (Museum Committee)	1	1	0
Plymouth Education Authority	1	1	0
Plymouth Proprietary Library	1	1	0
Port of Plymouth Incorporated Chamber of Commerce	1	1	0
William Procter, Esq.	1	1	0
W. P. Pycraft, Esq.	1	1	0
Charles H. Rudge, Esq.	1	1	0
E. S. Russell, Esq., D.SC. (1926 and 1927)	2	2	0
The Right Hon. Lord St. Levan, C.B., C.V.O.	1	1	0
J. T. Saunders, Esq.	1	1	0
R. E. Savage, Esq.	1	1	0
F. W. Schiller, Esq. (1925–1927)	3	3	0
Edgar Schuster, Esq., D.SC.	1	1	0
W. L. Sclater, Esq.	1	1	0
Lieut.-Col. R. B. Seymour Sewell, I.M.S.	1	1	0
Miss Lilian Sheldon	1	1	0
B. Webster Smith, Esq.	1	1	0
Thos. and Wm. Smith, Ltd.	1	1	0
Lieut.-Commander R. Spry, R.N. (1927 and 1928)	2	2	0
States Committee for Fisheries, Guernsey	1	1	0
A. C. Stephen, Esq.	1	1	0
E. J. Stream, Esq., M.A.	1	1	0
H. H. Sturch, Esq.	1	1	0
Eric J. Tabor, Esq.	1	1	0
Harold E. Tabor, Esq.	1	1	0
J. M. Tabor, Esq.	1	1	0
Carried forward	145	14	0

	£	s.	d.
Brought forward	145	14	0
S. Takeda, Esq.	1	1	0
Prof. W. M. Tattersall	1	1	0
Harold Thompson, Esq.	1	1	0
Sir Herbert Thompson, Bart.	1	1	0
Sir John Thornycroft, F.R.S.	1	1	0
Torquay Natural History Society	1	1	0
Alan H. Ware, Esq.	1	1	0
Sir Nicholas Waterhouse, K.B.E. (1924–1927)	4	4	0
A. W. Waters, Esq.	1	1	0
Prof. D. M. S. Watson, F.R.S.	1	1	0
Mrs. F. J. Weldon	1	1	0
W. A. Willes, Esq.	1	1	0
D. P. Wilson, Esq. (1927 and 1928)	2	2	0
Ronald Winckworth, Esq.	1	1	0
W. B. Woodrow, Esq.	1	1	0
C. M. Yonge, Esq., PH.D.	1	1	0
Total	£166	14	0

List of Donations to the Building Extension Fund

For the Year 1st April, 1927, to 31st March, 1928.

	£	s.	d.
E. T. Browne, Esq.	200	0	0
C. F. A. Pantin, Esq.	5	5	0
George Ord, Esq.	1	1	0
Total	£206	6	0

	£	s.	d.
Year 1924–25	1,823	12	6
Year 1925–26	1,787	5	0
Year 1926–27	251	15	6
Year 1927–28	206	6	0
Total	£4,063	19	0

THE BRITISH JOURNAL OF EXPERIMENTAL BIOLOGY

Edited by J. GRAY

WITH THE ASSISTANCE OF

F. A. E. CREW	J. B. S. HALDANE	C. F. A. PANTIN
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CONTENTS

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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 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.

CONTENTS OF NEW SERIES, Vol. XV., No 2.

NOTICE.

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

TERMS OF MEMBERSHIP.

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

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

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