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

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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.

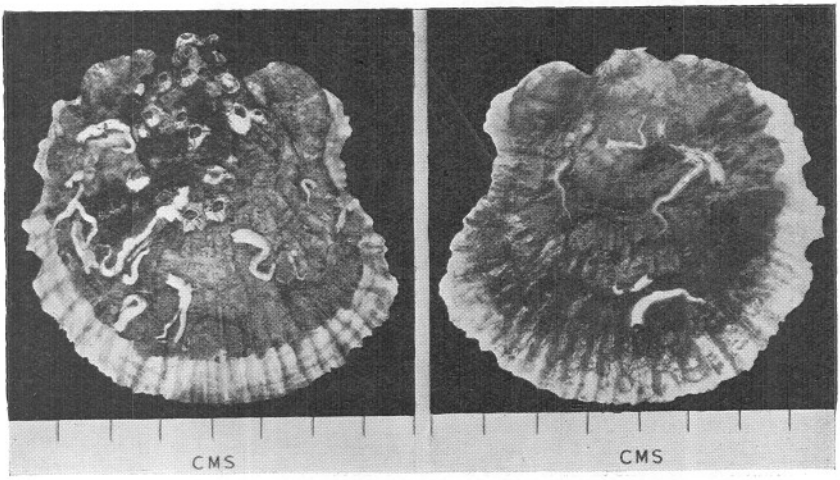


FIG. 1.—Photo[1] of right and left valves of *O. edulis* from Turnaware Bar at extreme low-water mark, November 10, 1927, showing the nature and size of the increase in shell-area effected since October 5, 1927 (from photos by Mr. A. J. Smith). The white rim which shows more effectively in the left-hand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

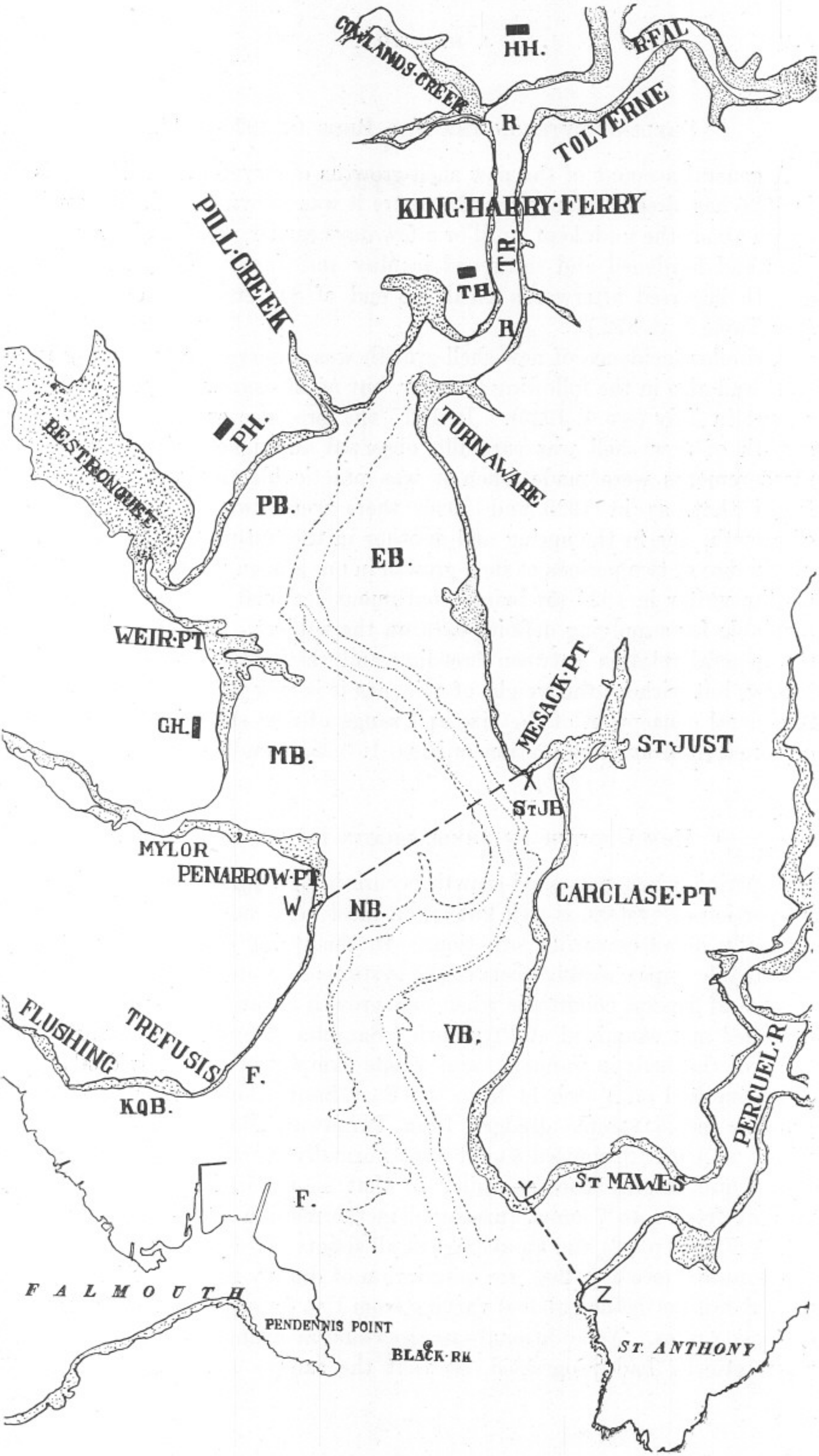
	Truro beds.	Depth in fms.		Falmouth beds.	Depth in fms.
M.B.	Mylor Bank	$\frac{1}{4}$ to $1\frac{1}{4}$	N.B.	Falmouth North Bank	$\frac{3}{4}$ to $1\frac{3}{4}$
E.B.	East Bank	$\frac{1}{4}$ to $1\frac{1}{4}$	ST.J.B.	St. Just beds	$1\frac{1}{4}$ to $1\frac{3}{4}$
P.B.	Parson's Bank	$\frac{1}{4}$ to $\frac{3}{4}$	V.B.	Vilt Bank or St. Mawes beds	$\frac{3}{4}$ to 2
Turnaware Bar		0 to $1\frac{1}{4}$			
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 ; P.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.



COWLANDS·CREEK
HH.
R·FAL
R
TOLVERNE
KING·HARRY·FERRY
PILL·CREEK
TR.
TH.
R
RESTRONGUET
PH.
TURNAWARE
PB.
EB.
WEIR·PT
MESACK·PT
GH.
MB.
ST·JUST
X
ST·JB
MYLOR
PENARROW·PT
W
NB.
CARCLASE·PT
FLUSHING
TREFUSIS
VB.
F.
KQB.
PERCUEL·R
Y
ST MAWES
F.
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

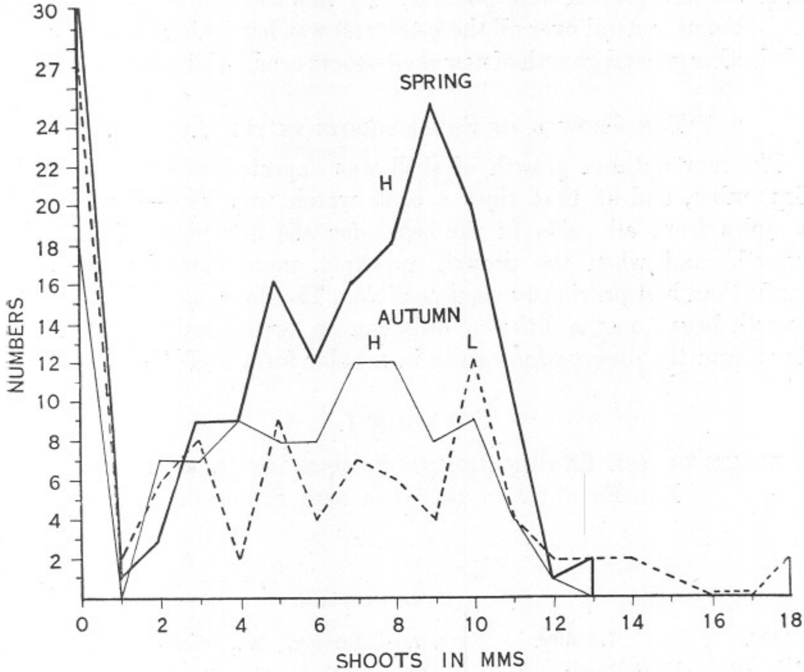


FIG. 3.—Graphs[1] showing the range and frequency of shell-shoots in samples of *O. edulis* from the same situation, namely, low-water springs at Turnaware Bar, Upper Fal Estuary, in the spring, May 18 (H), and autumn, November 10 (H and L), of the same year, 1927.

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.

1926.	Locality.	Totals examined. Normal.	Totals examined. Dumpy.	Total with new shell-shoots. Normal. No.	Normal. Range of shoots in mms.	Normal. Average of shoots in mms.	Dumpy. 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.	Range of shoots in mms.	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 $61{\cdot}5 \times 60{\cdot}3$ mm. and after growth on November 10th $66{\cdot}6 \times 65{\cdot}8$ 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

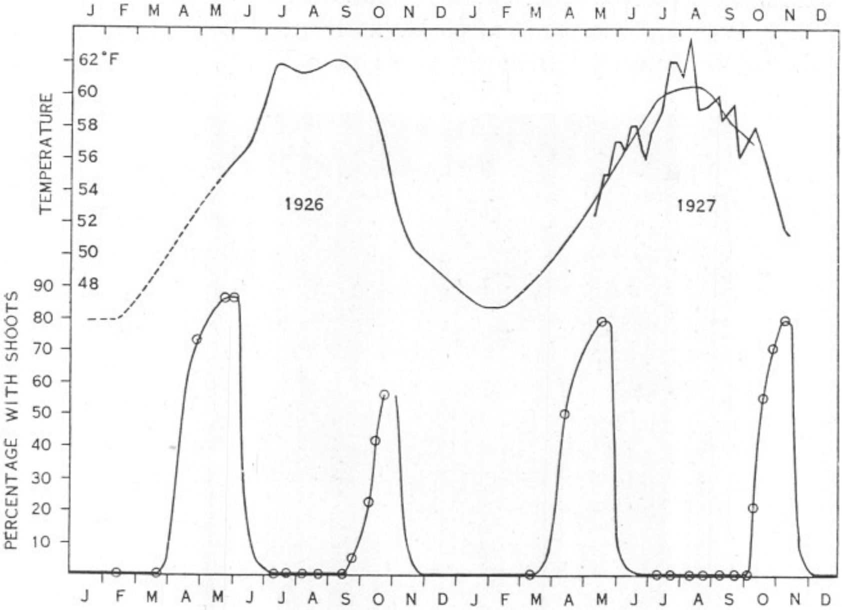


FIG. 4.—Mean percentage of *O. edulis* growing new shell-shoots at Turnaware Bar in 1926 and 1927, with correlated temperature variation at the East Bank station.
The oysters ranged in size mainly from 2¼ to 3 inches, and were of an age estimated at 3 to 5, and rarely 6 years, old, with a mean age of 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,

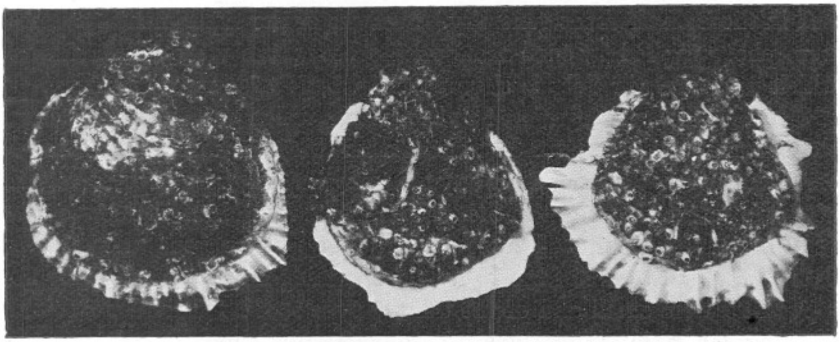


FIG. 6.—Photo of three individuals of *O. edulis*, showing a heavy autumn shell-growth at West Mersea, River Blackwater, October 22, 1923. These individuals were proved to be ripe female individuals in July, 1923, and put into the sea on August 2. × ca. ⅔. (From a photo by Mr. A. J. Smith.)

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

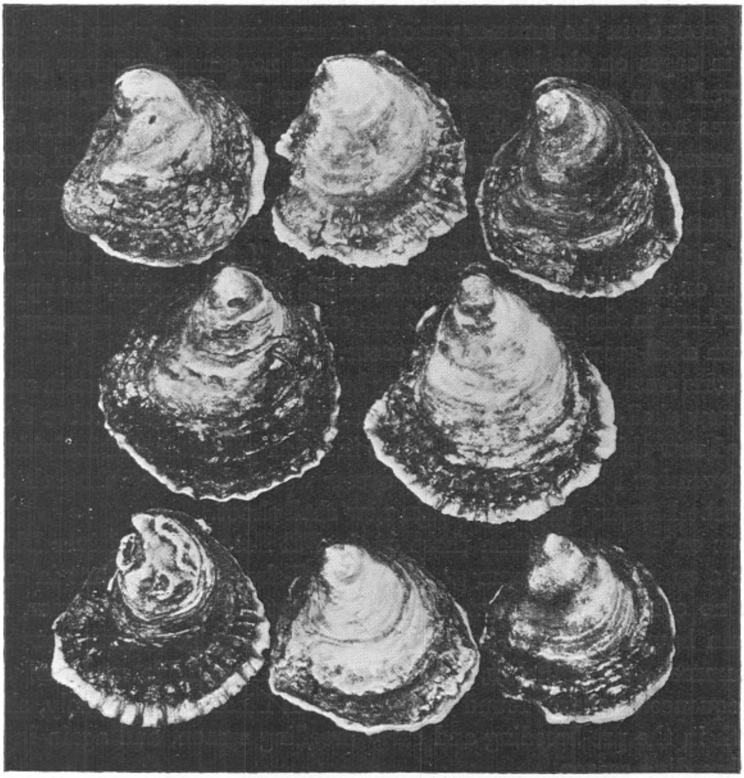


FIG. 7.—Photo of *O. edulis*, showing good autumn shell-growth in the River Yealm from August 30 to October 1, 1923. × ca. $\frac{2}{3}$. (From a photo by Mr. A. J. Smith.)

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 ($\frac{1}{2}$–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

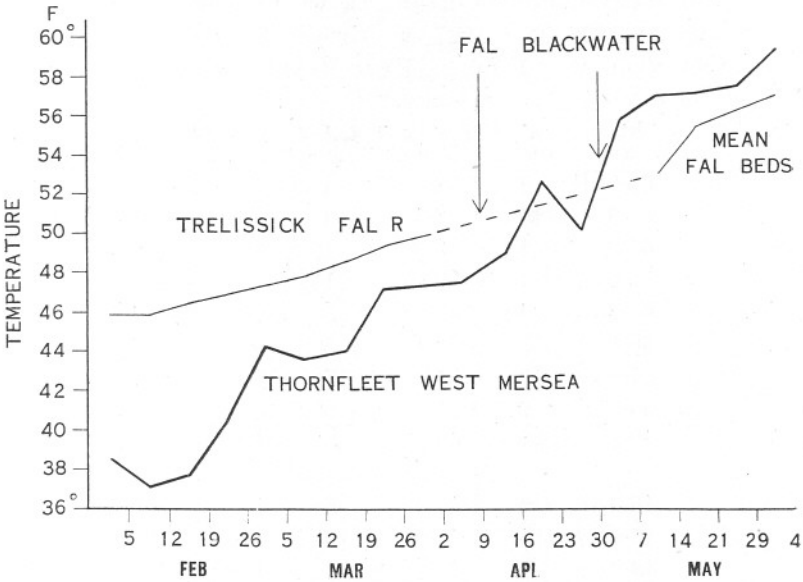


Fig. 8.—Comparison of the surface sea-temperature—from weekly means—on the Thornfleet beds, River Blackwater ; and the upper part of the Fal Estuary, from observations at Trelissick Reach in February and March, and the main Banks on the beds in May. The dotted part of the Fal graph covers a period when 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

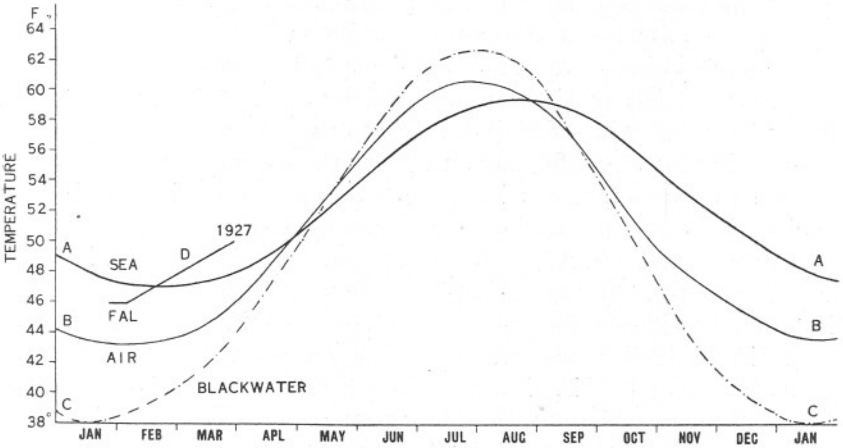


FIG. 9.—Comparison of mean air (from monthly means for a period of thirty-five years) over the Fal Estuary (B) and the River Blackwater (C) and mean surface sea-temperature (A) one mile off the entrance to Fal Estuary for a period of thirty-six years (1872–85, 1894–1915), with observations of sea-temperature (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. 1 f.[2]	East Bank. Depth, ½ to 1 f. bottom.		River. Depth, 8 to 8½ f. Bottom.		River. 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.	Category. 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	–	–	–	–	–	–	–	–	–	–	–	–

No.	Description	North Shore. Blackwater, Sept. 17, 1927. Wt.	Vol.	Age.	No.	North Shore. Blackwater, Oct. 4, 1927. Wt.	Vol.	Age.	No.
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 ($35{\cdot}2^{\circ}/_{\circ\circ}$), 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

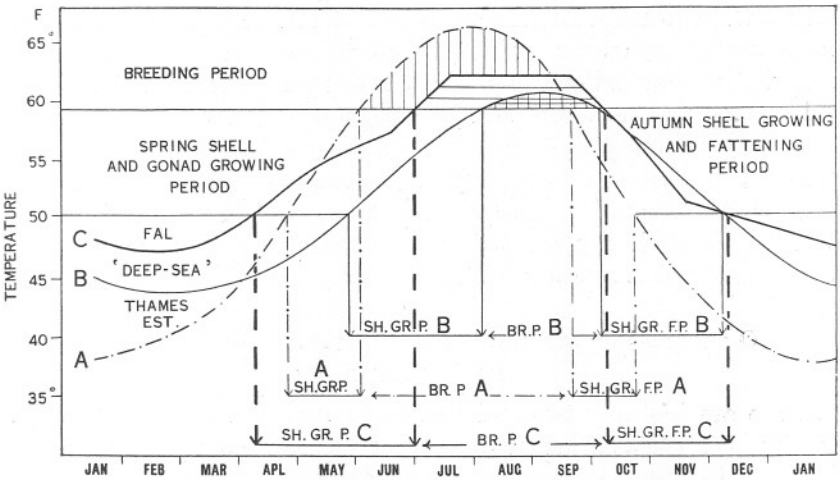


FIG. 10.—Diagrammatic representation of the varying periods of functional activities of *O. edulis* in three different types of environment controlled by rate and range of temperature variation.

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 Lightship, 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 idal 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 superabundant 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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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.

REFERENCES.

1. Orton, J. H. Report on a Survey of the Fal Estuary Oyster Beds (Nov., 1924) with Notes on the Biology of the Oyster (*O. edulis*). Falmouth, 1926.

2. Orton, J. H., and Amirthalingam, C. Notes on Shell Depositions in Oysters. Journ. Mar. Biol. Assoc., XIV, 4, 1927.

3. Orton, J. H. Observations on the Fal Estuary Oyster Beds during 1926, including a Study in Over-fishing. Journ. Mar. Biol. Assoc., XIV, 4, 1927.

4. Do. On Lunar Periodicity in Spawning of normally grown Falmouth Oysters (*O. edulis*) in 1925, with a comparison of the spawning capacity of normally grown and dumpy Oysters. Journ. Mar. Biol. Assoc., XIV, 1, 1926.

5. Do. The Conditions for Calcareous Metabolism in Oysters and other Marine Animals. Nature, Vol. 116, p. 13, 1925.

6. Do. Observations and Experiments on Sex-Change in the European Oyster (*O. edulis*). Part I. The Change from Female to Male. Journ. Mar. Biol. Assoc., XIV, 4, 1927.

7. — The Book of Normals. Meteorological Office, Air Ministry (M.O. 236, Section I), 1919.

8. Fox, W. L., and Phillips, J. B. Report of the Observatory Committee of the Royal Cornwall Polytechnic Society with Meteorological Tables for the year 1915. Falmouth, 1916.

9. Mill, H. R. On the Temperature of the Water in the Firth of Forth. Proc. Roy. Soc. Edin., Vol. XIII, 1884–86, p. 347.

10. Dickson, H. N. The Mean Temperature of the Surface Waters of the Sea round the British Coasts, and its Relation to the Mean Temperature of the Air. Quart. Journ. Roy. Met. Soc., Vol. XXV, No. 112, Oct., 1899.

11. Hansen, Helland, and Nansen, F. Temperatur-Schwankungen des Nordatlantischen Ozeans und in der Atmosphäre. Videnskaps-selskapets Skrifter, I. Mat-naturv. Klasse, 1916, No. 9. Kristiania, 1917.

12. Orton, J. H. Sea-temperature Breeding and Distribution in Marine Animals. Journ. Mar. Biol. Assoc., XII, 2, 1920.

13. Do. An Account of Investigation into the Cause or Causes of the unusual Mortality among Oysters in English Oyster Beds during 1920 and 1921. Fish. Invest., II, Vol. VI, No. 3. Part I. Report, 1923, London.

13a. Do. Do. Vol. VI, No. 4, Part II. Appendices, 1924.

14. Lebour, M. V. The Microplankton of Plymouth Sound from the Region beyond the Breakwater. Journ. Mar. Biol. Assoc., XI, 2, 1917.

15. Savage, R. E. The Food of the Oyster. Fishery Investigations, II, Vol. VIII, 1, 1925. London.

16. NELSON, T. C. On the Feeding Habits of Oysters. Proc. Soc. Exp. Biol. and Med., XXI, 1923, pp. 90–91. New York.

17. RUSSELL, E. S. Report on Seasonal Variation in the Chemical Composition of Oysters. Fish. Invest. London, II, Vol. VI, 1, 1923.

18. ORTON, J. H. The so-called Baccy Juice in the Waters over the Thames Oyster Beds. Nature, Vol. 111, p. 773, 1923.

19. MARSHALL, S. M., and ORR, A. P. The Relation of the Plankton to some Chemical and Physical Factors in the Clyde Sea Area. Journ. Mar. Biol. Assoc., XIV, 4, 1927.

20. — Book of Normals. Meterological Office, London. M.O. 214a, 1915.

21. KNUDSEN, M. Conseil. Inter. pour l'Exploration de la Mer. Supplement to the Bulletin, 1906–07.

22. ORTON, J. H. On Incomplete Spawning and the Problem of Fertilisation in *O. edulis*. Nature, Vol. 120, p. 403, 1927.

23. Do. The Mode of Feeding of the Jelly-fish *Aurelia aurita* on the smaller Organisms in the Plankton. Nature, Vol. 110, p. 178, 1922.

24. YONGE, C. M. Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis*. Journ. Mar. Biol. Assoc., XIV, 2, 1926.

25. ATKINS, W. R. G. A Quantitative Consideration of some Factors concerned in Plant Growth in Water. Journal du Conseil, Vol. I, 3, 1926.

26. HARVEY, H. W. Nitrate in the Sea. Journ. Mar. Biol. Assoc., XV, 1, 1928.

27. ATKINS, W. R. G. The Phosphate Content of Sea-water in Relation to the growth of the Algal Plankton. Part III. Journ. Mar. Biol. Assoc., XIV, 2, 1926.

28. GARDINER, J. STANLEY. Summary Report (only) on a conjoint meeting on Oyster Research. Fish Trades Gazette. Vol. 38, No. 1942, August 7, 1920, p. 53.

29. ATKINS, W. R. G. The Hydrogen-Ion Concentration of Seawater in its relation to Photosynthetic Changes. Part II. Journ. Mar. Bio. Assoc., XIII, 1, 1923.