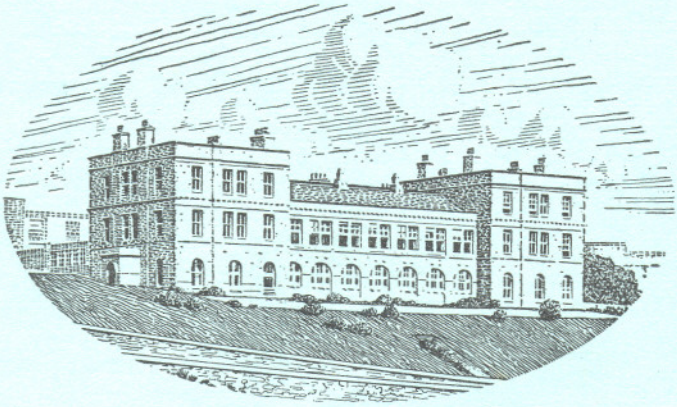
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME XXIX, No. 2

(*issued September* 1950)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1950

Price Thirty Shillings net

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POPULATION-DISPERSION IN *TELLINA TENUIS* DA COSTA

By N. A. Holme, B.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–8)

CONTENTS

INTRODUCTION

Although many investigations have been made of soil populations, both in terrestrial and aquatic environments, little is yet known of the distribution of individuals in relation to one another. A study of distribution in the horizontal plane lends itself either to a statistical treatment of samples from adjacent areas, or, where possible, to plotting of individuals *in situ*.

Salt & Hollick (1946) have studied the micro-distribution of wireworms by statistical treatment of eighty-one similar soil samples taken from a square yard of pasture. The wireworms were shown to be non-randomly distributed, there being a tendency for individuals to be aggregated.

In this paper an account is given of a population of the mollusc *Tellina tenuis* da Costa in which distribution is shown to be non-random, tending towards an even distribution. Investigations have been made both by statistical treatment of samples and by plotting of individuals.

Although there is some evidence that populations of this mollusc on other shores are not so distributed, the results from this area seem to be of sufficient general interest to be placed on record.

I am most indebted to Mr G. M. Spooner for assistance with the statistical calculations.

Tellina tenuis

Tellina is a small, thin-shelled, lamellibranch, which reaches a length of about 16 mm. in the Exe estuary. When excavated at low tide the animals are found at depths ranging from 2 to 4 in., smaller sizes usually being nearer the surface. Nearly all the animals are found lying on their sides, in a quiescent state, with neither siphons nor foot protruded.

At high tide, however, the animal probably assumes an upright position with siphons protruded, as shown in Fig. 1. The inhalent siphon is very extensile and ranges over the surface of the sand, drawing in material lying on

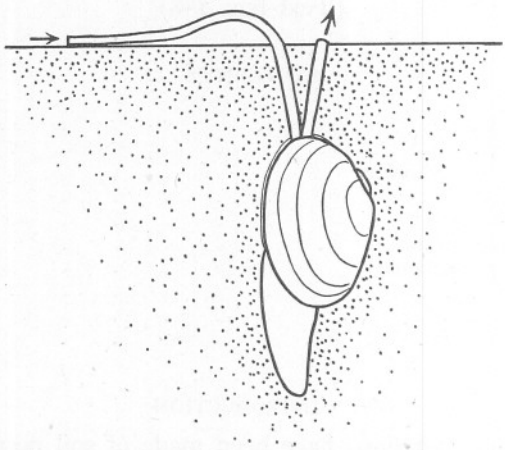

Fig. 1. Position of *Tellina tenuis* in the sand at high tide. After Yonge (1949).

or just above the surface. The shorter exhalent siphon does not project above the surface of the sand (see Yonge, 1949). Prof. C. M. Yonge, F.R.S., informs me that *Tellina* probably makes vertical migrations in the sand, coming nearer the surface at high tide.

Description of the Habitat

The habitat, which has been described by the writer (Holme, 1949), is a sheltered sandy beach within the mouth of the Exe estuary. From about half tide downwards the soil consists of fine clean sand, which slopes down to a small stream known as Salthouse Lake. A bed of clay occurs at a depth of about 2 ft. below the surface, and the sand is consequently not very well drained.

In the lower half of the beach *T. tenuis* and *Arenicola marina* are dominant members of the fauna. *Cardium edule* and *Macoma balthica* occur in small numbers in this region.

The stations referred to are on a traverse from high- to low-water marks.

Stations were at 100 ft. intervals up the beach, heights above M.L.W.S.T. being: Station H, 2 ft.; Station G, 4 ft. (L.W.N.T.); Station F, 6 ft. (half-tide mark); Station E, $7\frac{1}{2}$ ft.

Other stations, indicated in Roman numerals, are at a little above half-tide mark, on a traverse ranging from sand to mud.

Population Counts

On a number of occasions counts have been made of populations of *Tellina* in adjacent areas on the beach. Each time a square metal frame was driven into the sand and the soil inside it excavated to a depth which appeared to include all the fauna. The soil was sieved through a 1 mm. mesh. In 1947, areas of $\frac{1}{4}$ m.^{2} were excavated, but later investigations have been on $\frac{1}{10}$ m.^{2} areas.

If individuals are distributed at random, the counts from separate samples should vary according to a Poisson distribution.

Salt & Hollick (1946) have made use of the 'coefficient of dispersion' when dealing with parallel samples of wireworm populations. It follows directly from the fact that the σ^2 of the Poisson distribution tends to equal the mean in value that the expression

$$\frac{\Sigma(x-\bar{x})^2}{\bar{x}(n-1)}$$

leads to unity when individuals are randomly distributed, to less than unity when they are evenly distributed, and to more than unity when they are aggregated. The significance of the divergence is tested by the formula

$$2\sqrt{\frac{2n}{(n-1)^2}}.$$

Where n, the number of samples, is less than 10, the latter expression is greater than unity, so that samples numbering less than 10 cannot be tested for an even distribution.

July and August 1947 (see Holme, 1949)

Pairs of samples, such as D+3 or D−3 were about 4 ft. $4\frac{1}{2}$ in. apart (6 ft. to their outside edges), and the collections around Station I were within 11 ft. of one another.

Numbers per $\frac{1}{4}$ m.^{2} were:

I−3B	5	E II−3	19	D−3	3	G−3	47
I−3A	4	II+3	22	D+3	3	G+3	47
I+3	7						
I+8	7	III−3	1	F−3	45	H−3	42
		III+3	0	F+3	46	H+3	45
						H+15	48

The results show a general uniformity in density at any one station; also a very even population at Stations F, G and H, which range from low tide up to half-tide mark. The 'coefficient of dispersion' of the 7 samples from these three stations is 0·085. There are too few samples, however, to show a significant result.

20 *October* 1948

Twelve areas of $\frac{1}{10}$ m.^{2} were excavated within a radius of $4\frac{1}{2}$ ft. from Station G. Numbers of *Tellina* in each square were respectively: 27, 25, 24, 28, 26, 26, 32, 31, 32, 24, 29 and 29.

The 'coefficient of dispersion' is 0·307, but this lies within the limits of significance: $1 \pm 0{\cdot}89$.

18 *November* 1948

Four adjacent samples of $\frac{1}{10}$ m.^{2} were excavated at a position 30 ft. north-east of Station F.

Numbers of *Tellina* were 15, 15, 14 and 17 respectively. The 'coefficient of dispersion' is 0·13.

The above sets of readings taken together suggested that the distribution of *Tellina* is non-random, and this is confirmed by results shown below.

Plots of Individuals

Natural Populations

Further information has been obtained by plotting the position of each shell in $\frac{1}{10}$ m.^{2} squares. The frame was driven into the sand, and the soil outside it was then scraped away carefully, a little at a time. As each shell was uncovered its position was plotted, by measuring the perpendicular distance from the 'centre' of the shell to two adjacent edges of the square. It was nearly always possible to locate each shell without disturbing it. The length of each shell, and its approximate depth below the surface, was also noted. Excavation of a square usually took over an hour, and was only practicable in the better drained parts of the beach.

Although the shells occupy a depth range in the soil of about 2 in., their horizontal distribution only has been plotted. No clear correlation has been found between the horizontal spacing of individuals and the depths at which they occur. As it seems possible that the observed distribution is related to the activities of the siphons on the surface of the soil, the omission of any reference to depth seems permissible. In one square the orientation of each shell was noted, but here again there seemed to be little correlation with spacing of the animals. Plots of positions in this square are shown in Fig. 2, and in other squares in which the orientation was not noted in Figs. 4 and 6.

Although the spatial arrangement of individuals appears at first sight to be haphazard, there is, however, a suggestion of a general spacing out of the shells. A measure of this can be made by subdividing the large square into thirty-six

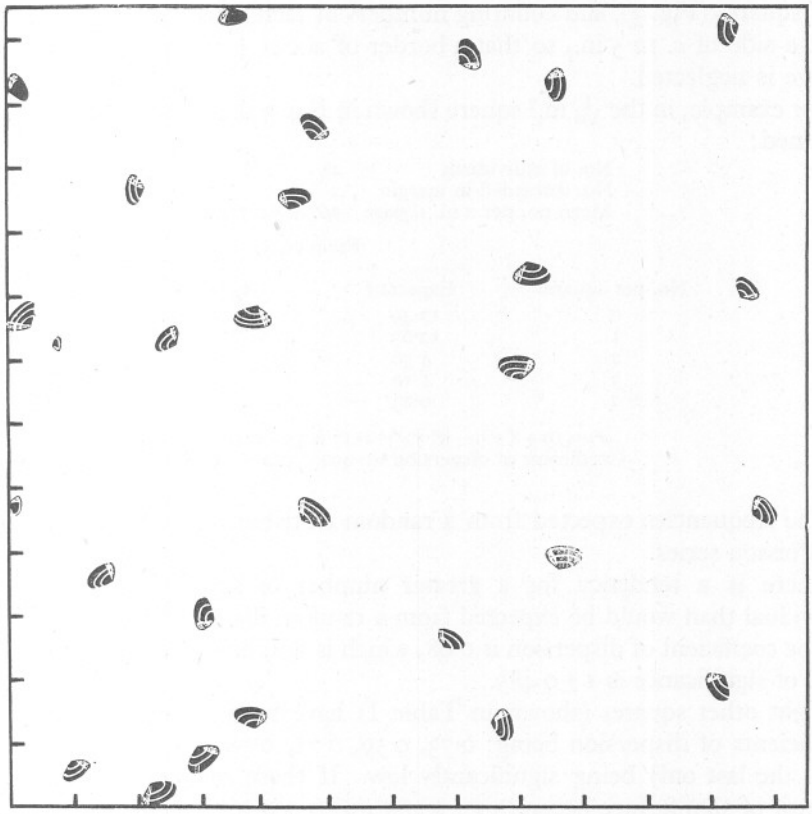

Fig. 2. Plot of positions of *Tellina* in a $\frac{1}{10}$ m.^{2} square (Station F, 11. vii. 49), density 280 per m.^{2} The sides of the square are divided into inches. The shells are drawn approximately to scale, and their orientation is shown by their shaded posterior end. The size and orientation of two shells (top right), shown without rings, is not known.

1	1	1	2	1	1
3	1	0	2	0	0
0	0	1	0	1	1
1	1	0	1	0	1
0	1	0	0	1	1
1	0	1	0	1	0

2

Fig. 3. Distribution of *Tellina* in the square shown in Fig. 2. This has been subdivided into thirty-six squares of side 2 in., the number of animals occurring in each square being indicated.

2 in. squares (Fig. 3), and counting numbers in each square. The $\frac{1}{10}$ m.^{2} areas have a side of *c.* 12·5 in., so that a border of about $\frac{1}{2}$ in. on two sides of the square is neglected.

For example, in the $\frac{1}{10}$ m.^{2} square shown in Fig. 3 the following results were obtained:

No. of individuals	28
No. discarded in margin	2
Mean no. per 2 in. square	$26/36 = 0{\cdot}722$

	Frequency	
No. per square	Expected	Observed (f)
0	17·49	14
1	12·63	19
2	4·56	2
3	1·10	1
>3	0·23	0

$\sigma^2 = (19+8+9-18{\cdot}\dot{7})/35 = 17{\cdot}\dot{2}/35 = 0{\cdot}492$
Coefficient of dispersion $= 0{\cdot}492/0{\cdot}722 = 0{\cdot}68$

The frequencies expected from a random distribution are calculated from the Poisson series.

There is a tendency for a greater number of squares to contain one individual than would be expected from a random distribution.

The coefficient of dispersion is 0·68, which is not, however, significant. The level of significance is $1 \pm 0{\cdot}485$.

Eight other squares (shown in Table I) have been treated similarly, the coefficients of dispersion being: 0·73, 0·59, 0·78, 0·78, 0·82, 0·74, 0·87 and 0·51, the last only being significantly low. If these readings are combined the test of significance becomes $1 \pm 0{\cdot}485/\sqrt{9} = 1 \pm 0{\cdot}16$. The mean of the nine readings is 0·72, so taken together the results show a significant degree of uniform dispersion in the population.

A further, and more revealing, method of showing the spreading tendency of the shells is obtained by plotting the distance of each individual from its nearest neighbour. Inevitably a number of shells are found closer to the edge than to their nearest neighbour within the square, and this tends to leave a fairly substantial residue of shells in which the minimum distance is unknown. Since it is intended to show that individuals do not occur close together, this procedure would leave an element of doubt in the results. This has been overcome by marking a marginal strip round the sample area, of width 1 in., in which the shells are to be neglected, except in their capacity as neighbours. That is, the shells lying in the margin do not contribute a 'minimum distance' reading: they are, however, available when 'minimum distances' for shells in the inner square are being measured (Fig. 4).

The only distances still in doubt are those of shells in the inner square which are nearer to the outer edge than to any other shell. These must, however, be at least 1 in. from their nearest neighbour.

The results of the minimum-distance measurements for the nine squares are shown in Table I. It will be seen that there is a tendency for individuals seldom to occur closer than 1 in. apart, and none was found closer than 0·6 in.

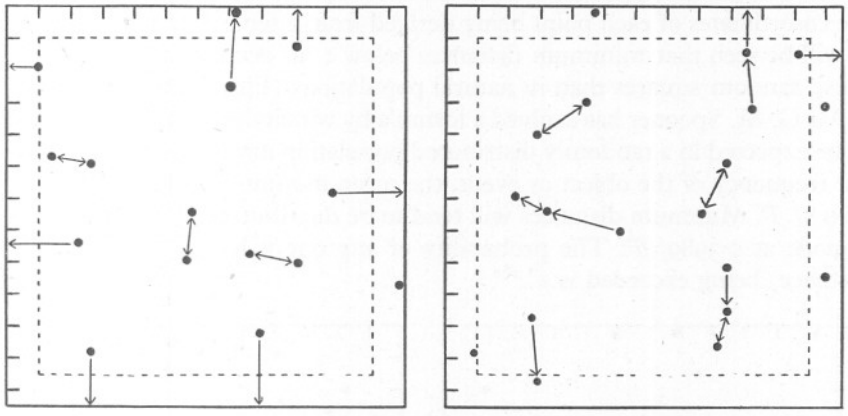

Fig. 4. Plot of positions in two $\frac{1}{10}$ m.^{2} squares, showing the method of measuring minimum distances. A, 30 ft. north-east of station F, 18. xi. 48, density 150 per m.^{2} B, Station F, 3. xi. 48, density 190 per m.^{2}.

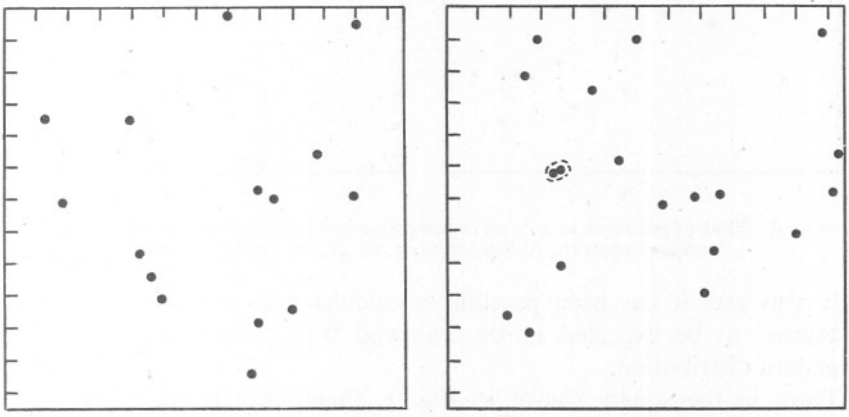

Fig. 5. Randomly distributed points in two $\frac{1}{10}$ m.^{2} squares, for comparison with Fig. 4. Points less than 0·6 in. apart are enclosed by dashes. A, density 150 per m.^{2} B, density 190 per m.^{2}

from its neighbour. That this lower minimum distance is not due to the space occupied by the shell itself is shown by subsequent results (p. 278) in which individuals occurred as close together as 0·1 in. Since the shells occupy a zone of 2 in. depth there seems to be no *a priori* reason why two should not occupy the same position in the horizontal plane, one above the other.

In interpreting the results it should be noted that where two shells are close to one another, the distance between them is often recorded twice, once in respect of each shell.

For comparison, plots have been made of points within 'random squares', the co-ordinates of each point being derived from a table of random numbers. It will be seen that minimum distances below 1 in. occur more frequently in these random squares than in natural populations (Figs. 5 and 6B; Table I).

Mr G. M. Spooner has evolved a formula by which the 'minimum distances' to be expected in a randomly distributed population may be derived. Given P, the frequency of the object or event, the mean minimum distance is shown to be $0{\cdot}5/\sqrt{P}$. Minimum distances will tend to be distributed asymmetrically with a mode at $0{\cdot}3989/\sqrt{P}$. The probability of any one value of x (the minimum distance) being exceeded is $\epsilon^{-x^2\pi P}$.

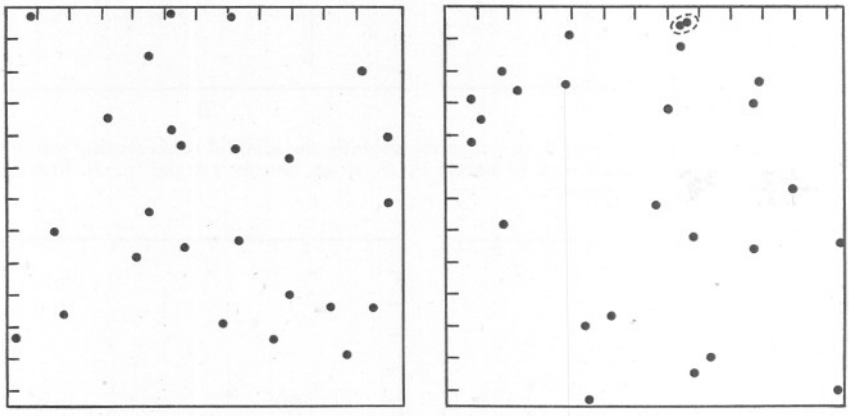

Fig. 6. Plots of positions in a $\frac{1}{10}$ m.^{2} square of density 250 per m.^{2}, compared with a 'random square'. A, Station G, 3. xi. 48. B, random square.

In this way it has been possible to calculate the number of 'minimum distances' to be expected under 0·95 and 0·55 in. respectively, assuming a random distribution.

Thus, in the square shown in Fig. 2, there were twenty-eight animals ($P = 1/5{\cdot}54$ in.^{2}), seventeen of which were within the 1 in. border. The probability of minimum distances exceeding 0·55 in. is calculated to be 0·8422, and $1 - 0{\cdot}8422 = 0{\cdot}1578$ are therefore expected below 0·55 in. Since seventeen animals occur, the number of minimum distances to be expected below 0·55 in. is $17 \times 0{\cdot}1578 = 2{\cdot}68$. In the same way a minimum distance of less than 0·95 in. has an expected frequency of 6·82.

Comparisons of expected and actual minimum distances are given in Table II. There is seen to be a tendency for minimum distances below about 1 in. to be eliminated by the spacing out of individuals.

Table I. Minimum Distances between Individuals in Natural Populations, Compared with those in the 'Random Squares' Shown in Figs. 5A, 5B and 6B.

The column marked 'others at least 1·0' refers to those shells in the inner square which are nearer the outside edge than to their nearest neighbour inside the square. The column marked 'Discarded, in border' refers to those in the outer border, whose minimum distances are not measured. Note that relatively more distances below 1·0 in. occur in the random squares.

			Minimum distance, in inches																		
Position	Date	Density ($\frac{1}{10}$ m.^{2})	>2·0	2·0	1·9	1·8	1·7	1·6	1·5	1·4	1·3	1·2	1·1	1·0	Others at least 1·0	0·9	0·8	0·7	0·6	0·5	<0·5	Discarded, in border
G	3. xi. 48	25	1	—	—	1	4	2	4	2	—	—	—	—	3	—	—	—	2	—	—	6
F	3. xi. 48	19	2	—	2	4	—	1	—	—	—	2	2	—	1	—	—	—	—	—	—	5
30′ N.E. of F (i)	18. xi. 48	15	3	—	—	—	—	—	4	—	—	2	—	—	4	—	—	—	—	—	—	2
30′ N.E. of F (ii)	18. xi. 48	15	4	—	—	—	—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	7
30′ N.E. of F (iii)	18. xi. 48	14	4	1	—	2	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	3
30′ N.E. of F (iv)	18. xi. 48	17	3	—	1	—	—	2	—	—	—	—	2	—	5	—	—	—	—	—	—	4
F	11. vii. 49	28	2	—	—	1	—	2	1	2	—	2	—	1	6	—	—	—	—	—	—	11
6′ S. of F	11. vii. 49	21	3	—	—	2	—	—	—	—	3	—	—	—	2	—	2	1	2	—	—	6
G+75	11. vii. 49	19	4	—	1	2	2	—	2	—	—	—	1	—	3	—	—	—	—	—	—	4
Total		173	26	1	4	12	6	9	11	4	3	6	5	1	30	—	2	1	4	—	—	48
Random (Fig. 5A)	—	15	1	—	—	1	—	—	—	—	—	2	—	—	4	—	3	—	2	—	—	2
Random (Fig. 5B)	—	19	2	—	—	1	—	—	—	—	2	1	1	—	3	2	2	—	—	—	2	3
Random (Fig. 6B)	—	25	—	1	1	—	—	—	3	—	—	—	—	—	2	2	2	6	—	—	—	8

Table II. Table of Expected and Observed Minimum Distances for the Squares Shown in Table I.

		1·00 in. or over		0·95–0·60 in.		0·55 in. or under	
Density	In border	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.
25	6	12·03	17	4·27	2	2·70	—
19	5	9·78	14	2·63	—	1·59	—
15	2	9·79	13	2·03	—	1·18	—
15	7	6·03	8	1·24	—	0·73	—
14	3	8·52	11	1·58	—	0·90	—
17	4	9·43	13	2·24	—	1·33	—
28	11	10·18	17	4·14	—	2·68	—
21	6	10·21	10	2·98	5	1·81	—
19	4	10·48	15	2·82	—	1·70	—
	Total	86·45	118	23·93	7	14.62	0

Artificial populations

If the population density is increased the chances of randomly distributed individuals coming to lie close together becomes greater. Two experiments have been made in which individuals were concentrated within a metal circle from which they could not escape. After a period of several weeks a $\frac{1}{10}$ m.^{2} area within the circle was excavated and positions of the shells plotted.

Experiment I

The metal circle was made from a strip of sheet steel 6 ft. long and 6 in. wide, which was bent into a circle of diameter *c.* 22 in., and the ends joined. The circle was pushed into the sand until its top was level with the surface.

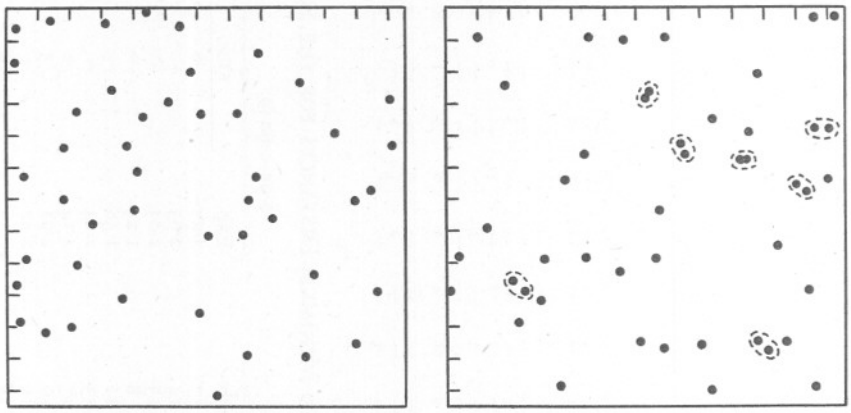

Fig. 7. A, plot of positions in a $\frac{1}{10}$ m.^{2} square of artificially high density (Exp. I), 30. iii. 49, density 460 per m.^{2} The animals have dispersed from a point just outside the top left-hand corner. B, random square of the same density.

The position chosen was 15 ft. north-east of Station F, where there is a fairly well drained sand supporting a small natural population of *Tellina*. About 100 specimens of *Tellina*, of various sizes, were sieved from sand near low-water mark and placed in a small pit near the edge of the enclosed area. They were then covered over with sand and left for 8 weeks, when a $\frac{1}{10}$ m.^{2} square was excavated. Forty-six shells were found, their positions being shown in Fig. 7A.

The pit in which the shells were originally placed is just outside the square, at the top left-hand corner in the figure, and it will be seen that the population density is higher towards this corner. Examination of the area where the shells had been introduced revealed quite a number which had not yet spread out.

Dividing the large square into thirty-six smaller squares, a coefficient of dispersion of 0·43 is obtained, which is significantly different from unity.

Plots of minimum distances gave the following results:

	Artificial population	Random square
Density	46	46
No. in outer margin	14	11
No. 1 in. or more from edge	2	2
Minimum distances (in.):		
<0·5	—	14
0·5	—	—
0·6	2	1
0·7	—	3
0·8	2	—
0·9	5	1
1·0	3	3
1·1	3	—
1·2	5	6
1·3	2	1
1·4	1	—
1·5	—	1
1·6	3	—
1·7	1	1
1·8	1	1
1·9	—	1
2·0	2	—
>2·0	—	—

These results may be summarized thus:

	Density	In border	1 in. or over	0·95–0·6 in.	<0·55 in.
Artifical population	46	14	23	9	0
Random square	46	11	16	5	14
Expected (from formula)	46	[14]	15·23	9·73	7·04

Spacing-out is shown by the absence of individuals below 0·55 in. rather than in reduced numbers between 0·95 and 0·6.

The results of this experiment show that individuals can spread out and take up their characteristic arrangement in the adult stage, and in a fairly short space of time.

After excavation, most of the shells were returned to the circle, and covered over. A $\frac{1}{10}$ m.^{2} square was again excavated $3\frac{1}{2}$ months later, only twenty-eight specimens being taken.

'Minimum distance' measurements were as follows:

Density		28	
No. in outer margin		7	
No. 1 in. or more from edge		1	
Minimum distances:			
in.		in.	
<0·5	2	1·3	2
0·5	—	1·4	—
0·6	—	1·5	1
0·7	2	1·6	1
0·8	—	1·7	6
0·9	2	1·8	—
1·0	1	1·9	—
1·1	2	2·0	—
1·2	1	>2·0	—

This square is the only one so far in which individuals have been found less than 0·5 in. apart. The general arrangement is otherwise as in natural populations.

Experiment II

About 200 specimens of *Tellina* were placed within a smaller circle, diameter 17 in., close to the previous position. The specimens were scattered over the surface of the sand and covered over. An attempt was made to excavate $4\frac{1}{2}$ weeks later, but this had to be abandoned owing to rain, which started to fill the hole. Only eleven specimens had been removed and these were replaced in the circle.

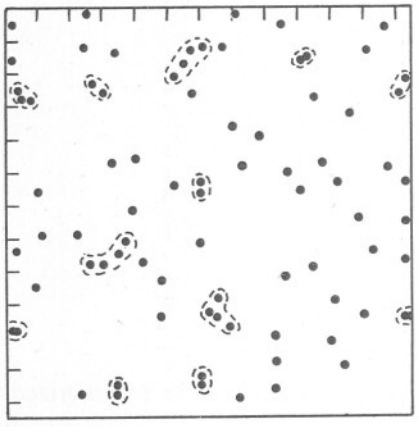

Fig. 8. Plot of positions in a $\frac{1}{10}$ m.^{2} square of artificially high density (Exp. II), 13. vi. 49, density 810 per m.^{2} Note that in thirty-one cases animals occur closer than 0·6 in. apart.

Eight weeks from the start of the experiment, a $\frac{1}{10}$ m.^{2} square was successfully plotted (Fig. 8). The density was eighty-one and when the square was subdivided into thirty-six 2 in. squares, seventy-four were contained within them. The coefficient of dispersion is 0·54, which is just within the limits of significance.

Measurements of minimum distance, however, show that the characteristic spacing found at lower densities had not been assumed:

Density		81	
No. in outer margin		25	
No. 1 in. or more from edge		1	
Minimum distances:			
in.		in.	
<0·5	20	1·0	6
0·5	1	1·1	3
0·6	2	1·2	0
0·7	2	1·3	2
0·8	9	1·4	0
0·9	9	1·5	1

The formula gives 21·93 individuals below 0·55 in., and 21·36 between 0·95 in. and 0·6 in., which is very close to that attained by the animals in this experiment.

Thus in this square the animals are spread rather evenly, judged by information obtained by subdividing the large square; but are distributed at random as shown by minimum-distance measurements. The even distribution is probably explained by the animals being spread out at the start of the experiment, and is of little consequence.

The absence of any tendency to spread out from one another is remarkable, and shows that the 'minimum distance' shown in previous results does not limit the density in an upward direction. Observations on dense natural populations are needed to confirm this break-down of the 'minimum distance' at higher densities, but in view of the constancy of results on previous occasions the results of the last experiment cannot be disregarded.

The occurrence of animals as close together as 0·1 in. shows that the minimum distance is not controlled by the size of the shell itself, but may be the result of some aspect of the animal's behaviour.

Discussion

Aggregation in a population can be quite easily shown by statistical treatment of a very few samples. If any two are widely divergent, aggregation can be shown to occur. On the other hand, an even distribution can only be shown by a much larger number of samples, and any small errors in technique will tend to make the figures approach random.

The results obtained with *Tellina* show that a significant degree of 'over-dispersion' or evenness of the population does occur. This over-dispersion applies to individuals occurring in any one small area, and also to populations extending from low tide up to half-tide mark on the beach in question.

One aspect of this distribution is shown by measuring the distance of each animal to its nearest neighbour. In natural populations it is shown that fewer than would be expected occur less than 1 in. apart, and none occur less than 0·6 in. apart. Where populations on the shore were artificially increased the same type of spacing was shown at a higher density (460 per m.^{2}), but not at a density of 810 per m.^{2} As the density increases the chances of randomly distributed individuals lying close to one another is increased, so that at a density of 460 per m.^{2} a result significantly different from random has been obtained.

It is possible that at moderate densities each individual occupies a territory delineated by the activities of the inhalent siphon on the soil surface, but that at higher densities the spacing breaks down owing to the confusion resulting from a number of siphons meeting one another on the surface. Thus the 'territory', if there be one, would seem not to limit density. This is supported by observations of Stephen (1928–30), who found populations as high as 7588 per m.^{2} in Kames Bay. Examination of Stephen's data shows no evidence of uniform populations either at any one place or over a stretch of shore, as occurs in the Exe. In fact, Stephen (1930) has emphasized the variability in populations at any one place. He excavated four $\frac{1}{4}$ m.^{2} areas within a few yards of each other at St Andrews and found the following numbers in each: 114, 136, 111 and 163 respectively. These show a coefficient of dispersion of 4·4, which indicates a significant degree of aggregation. It is

possible, however, that there may have been drainage or other differences in conditions between the four areas.

Although the even distribution in the Exe might be due to an even spat settlement, the results with artificially increased populations indicate that the spacing can be taken up in the adult stage. It is not at all clear, however, how such an even spacing over a distance of 215 ft. up the shore has occurred.

Certain other lamellibranchs, notably *Macoma*, *Abra* and *Scrobicularia* have a similar mode of life to *Tellina*; and it would be of interest to examine their distribution where they occur in fairly dense beds.

Summary

A population of the lamellibranch *Tellina tenuis* in the Exe estuary is shown to be uniformly distributed, indicating a significant degree of 'over-dispersion'.

By plotting the position of each shell in squares of $\frac{1}{10}$ m.^{2} area it is shown that fewer individuals than would be expected occur less than 1 in. from their nearest neighbour, and none occurs closer than 0·6 in.

When the population density was artificially increased on the shore the same characteristic spacing was found at a moderate density, but not at a rather higher density.

It is suggested that spacing is correlated with the foraging activities of the inhalent siphon on the soil surface.

Very dense populations have been found by Stephen in other areas, indicating that the size of the 'territory' does not limit density. His results show no evidence of the same phenomena as observed in the Exe.

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GREGARIOUSNESS DURING SETTLEMENT IN THE BARNACLE *ELMINIUS MODESTUS* DARWIN

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(Text-figs. 1–3)

CONTENTS

Introduction

Many species of marine animals have been described as local or gregarious. Jeffreys (1863–9) and Eales (1939), for instance, made occasional use of the latter term. It implies crowding, often in a restricted habitat, usually in a search for food or shelter. Such crowding must facilitate breeding. Thorson (1946) reviewed the evidence that even non-copulatory species are stimulated to spawn by crowding, and quoted a few observations suggesting that certain forms specifically seek the company of their fellows. In the present account the term gregariousness will be reserved for such behaviour, rather than for automatic crowding in restricted habitats.

Thorson also reviewed the gradually accumulating evidence that the settlement of marine larvae at the end of their planktonic phase is generally not haphazard. The idea of 'hit-or-miss' settlement advanced, for instance, by Colman (1933), for several species, including barnacles, is now out of date. Surprising powers of discrimination have been revealed in certain forms, but up to the present time, so far as we are aware, the only larvae shown to be gregarious during settlement are those of the oyster, *Ostrea edulis*. This was demonstrated by experiments in the oyster-breeding tanks of the Ministry of Agriculture and Fisheries at Conway (see Cole & Knight-Jones, 1949). In those experiments, two or three times as many larvae attached themselves to shells which already bore recently settled oyster spat, as to similar shells from

which all previously settled spat had been removed with the point of a needle. This happened consistently, day after day. In general, most larvae attached themselves to those shells which bore most spat, up to a density of from 50 to 100 spat per shell. Once this density had been reached they settled apparently at random upon the more and the less crowded shells, but much less readily on the bare ones. The gregarious tendency was most marked when the spatfall was light. When numerous larvae were settling they quickly covered both spat-shells and bare shells alike.

Spärck's (1949) observations in the Limfjord tended to confirm that oysters are gregarious during settlement, 'since restocking only took place in any considerable degree in places where the density of the left native stock was fairly great and since the continued restocking slowly spread from these places'. Gregariousness was found to be of great importance on Essex oyster beds, where several small widely separated areas were selected and heavily stocked (Knight-Jones, 1949). The subsequent spatfall was much more heavy on these areas than on neighbouring ground where oysters were sparse or absent. It is most unlikely that these arbitrarily selected areas were more suitable for settlement because of such factors as the nature of the bottom or exposure to tidal currents. Some of them were unproductive when unstocked but became productive when stocked. It is highly probable that the heavier settlement upon them was due to the gregarious tendency demonstrated by the critical experiments in the Conway tanks.

Lest it seem incredible that small, simply organized, planktonic larvae should be capable of such behaviour, it may be explained that the mechanism of gregariousness in *O. edulis* need not necessarily be very complex. Larvae which have reached the stage at which they are ready to settle crawl, by means of a ciliated and very mobile foot, upon any substratum with which they may happen to come into contact (Cole & Knight-Jones, 1939). After crawling for a period they usually swim off again. Their discriminatory powers suggest that they can to some extent postpone attachment until they happen to find a place particularly favourable for it. In Essex creeks tidal currents carry swimming larvae several miles in a few hours, enabling those ready to settle to visit a variety of widely separated places. It appears that the presence of other oysters is one of the factors which encourage settlement. The stimulus may perhaps be olfactory, but there is no evidence on this point from work on oysters. On the other hand, laboratory experiments on ascidian larvae (Grave & Nicoll, 1940; Grave, 1941) showed that metamorphosis was hastened by crowding and also by aqueous extracts of larvae, later developmental stages, and adult tissues. It may therefore be expected that ascidian larvae will prove to be gregarious during settlement, stimulated by the water-borne secretions of their fellows, but direct evidence of this has not yet been obtained in the field, so far as we are aware, though it is a matter of common observation that adult simple ascidians usually occur in clumps.

Gregariousness during settlement must be of great biological importance to a sessile form, such as the oyster, in facilitating breeding. Moreover, the individual is likely to find, in a situation where the species is already established, suitable conditions for its own survival.

In the Burnham-on-Crouch district the most serious competitor of newly settled oyster spat is the barnacle *Elminius modestus*, a recent immigrant from the Antipodes (Knight-Jones, 1948). Smooth slates, which were exposed for weekly periods during the summers of 1947, 1948 and 1949 to record the settlement of oyster larvae, were usually covered with these barnacles in a few days. When settlement was very intense the distribution of the barnacles over the surface of a slate was remarkably even. When settlement was light the barnacles tended to settle first in groups but, as colonization of the surface proceeded, the later arrivals rarely settled amongst the grouped individuals but rather upon the bare areas in between the groups. In this way their distribution gradually became even, provided the light settlement was sufficiently prolonged. Like many other barnacles *Elminius* settles particularly abundantly in scratches or irregularities of the surface, but the test-slates used were smooth, and the initial formation of the groups generally appeared to be unrelated to surface irregularities. The impression gained was that the early arrivals on the bare surfaces were gregarious but that the later arrivals on the crowded surfaces tended to space themselves out. Another point which appeared significant was that slates exposed at certain places consistently caught very few barnacles, though settlement elsewhere was very intense and cyprids were abundant in all plankton samples. The only feature which these places appeared to have in common was a bottom of bare mud, from which barnacles were absent. The slates on which settlement was heavy were from places where the bottom was covered with shells, on which *Elminius* was abundant. It seemed possible that gregariousness might have been responsible for the differences observed.

There is plenty of evidence suggesting that settling barnacles have considerable powers of discrimination. The literature is too lengthy to review here, but it seems particularly relevant to note that Visscher (1928) observed cyprids of *Balanus improvisus* and *B. amphitrite* crawling over the substratum for distances of more than 12 mm. and periods of over an hour, apparently testing different areas in a search for a place for attachment. *B. amphitrite* had been observed to attach within 7 days after hatching, yet Visscher kept some cyprids of this species under observation for 10 or 11 days. By then some had attached but many were still active, which suggests that metamorphosis in this species can be delayed if conditions are unfavourable for attachment. One of us (E. W. K. J.) has observed that cyprids of *B. balanoides*, which had been attached anteriorly to the side of a glass vessel and dislodged by a jet of water from a pipette, were capable of swimming about and then attaching themselves again. Burton (1949) wrote 'the first settled larvae (of *Balanus*) seem to attract others to settle in the same spot'. Dr D. J. Crisp and Dr P. N. J. Chipperfield, with whom we had the

good fortune to discuss this subject, kindly informed us that field observations had led them to suppose that barnacles might well be gregarious, but that they had also observed that barnacles often settled alongside surface projections, as though the cyprids had been sheltering there from currents. The tendency to settle in groups upon a uniform surface might therefore be due wholly to the later arrivals obtaining some shelter amongst previously settled barnacles. If so it could not accurately be described as gregariousness.

This point is of considerable practical importance in oyster research. The extremely productive French oyster industry is based on the use of artificial collectors for spat (see, for instance, Dalido, 1948). Experiments with such collectors in Essex creeks have shown promising results, and the chief factor militating against their successful use there is the overwhelming prolific *Elminius*. Critical tests for gregariousness in *Elminius* were therefore carried out, with the positive results recorded here, as part of a study of its settlement behaviour. Further work will be directed towards finding out how far the smothering of collectors by barnacles can be delayed by placing them far from shelly shores where the barnacles are abundant. It is also hoped to offer for publication later some information regarding the spacing-out tendency on crowded surfaces.

It would be interesting to carry out critical experiments on other barnacles. Should a gregarious habit prove general it would have a bearing on the problem of ships' fouling, for it might prove worth while to take special measures for the cleaning of docks and wharves. Without gregariousness this would appear to be useless so far as organisms with lengthy planktonic stages are concerned.

Methods

Small concrete slabs were prepared, each of which held a pair of rectangular plates of smooth glass (Fig. 1). The plates, which measured $23{\cdot}8 \times 13{\cdot}3$ cm., were held on each side by a long coach-bolt, the head of which was embedded in the concrete. They rested horizontally upon the nuts of the bolts, 4 cm. above the upper surface of the slab, and were secured by rubber washers, cut from pressure-tubing. Wire hoops protected the plates and served as carrying handles.

For the small-scale experiments the slabs were buoyed and placed close together below L.W.E.S.T., near Burnham. For the comparison between settlement on muddy and shelly shores they were placed at L.W.O.T., near Paglesham. They were exposed for short periods during late July, August and September 1949. By then the main settlement of *Elminius*, which had occurred as usual during June and early July, was over. Settlement during the period of the experiments was moderate or sparse. In this respect conditions were ideal for testing for gregariousness, in that the spacing-out tendency observed at times of heavy settlement (see above) scarcely came into effect.

A wire counting-frame and a hand-lens were used for counting. In the small-scale experiments counts were made of the barnacles which had settled on certain areas of the plates, details of which are given below and on p. 289. We have not yet learned to distinguish the earliest settled stages of *Elminius modestus* from those of *Balanus improvisus*, which they resemble in size, but we are confident that the results presented here relate to *Elminius modestus*, since plates exposed at the time of these experiments and under similar conditions, but for longer periods, became covered with the characteristically shaped *Elminius*, amongst which were very few *Balanus improvisus*. Over 99% of the barnacles settling at this time on test plates on or near the shore were *Elminius*.

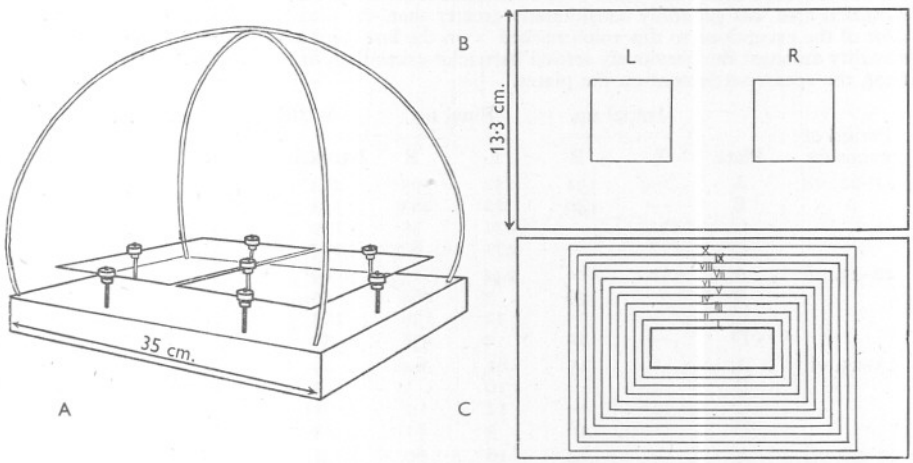

Fig. 1. A, concrete slab, with protecting wire hoops, holding a pair of rectangular glass plates; B, plate marked with areas 5 cm. square, L and R, for preliminary small-scale experiment; C, plate with microscope slide stuck to it. These were exposed in pairs, one with the slide barnacled, the other with the slide bare. When counting the barnacles which settled subsequently, each plate was placed over graph paper marked with the rectangles I–X, and the numbers settling on each narrow area at gradually increasing distances from the slide were obtained. Mean densities on these areas are shown in Fig. 2.

Preliminary Small-scale Experiment

Two areas, 5 cm. apart and each 5 cm. square, were drawn with a diamond on each of four glass plates and marked respectively L and R (left and right, see Fig. 1B). The plates were placed in position with the side which had been scratched by the diamond downwards. This orientation was adopted because it had previously been found that settlement on glass plates was much heavier on the upper than the lower surfaces. It was therefore decided to use the upper surfaces for small-scale experiments and it was desirable that this experimental surface should be uniformly smooth, since barnacles tend to settle in scratches and may well discriminate between scratches of various depths. The scratches delimiting the experimental squares could be clearly seen through the glass.

The two slabs bearing the four plates were exposed to settling barnacles for a day. The entire lower surface of each plate and all the upper surface except for one of the 5 cm. squares was then wiped with clean cotton-wool. The number of barnacles left in the square was counted and the remainder of the plate was examined to ensure that no barnacles had been left upon it. The plates were exposed for another day, the two slabs being placed near to one another.

TABLE I. SETTLEMENT OF *ELMINIUS MODESTUS* ON PAIRS OF AREAS 5 CM. SQUARE

Areas, 5 cm. square, L and R, marked on glass plates A, B, C and D. Of each pair one area was initially bare whilst the other bore a recorded number of barnacles. The increment on the barnacled area was generally considerably greater than the number settling on the bare area. Most of the exceptions to this rule (marked × in the last column) appear to have been due to mortality amongst the previously settled barnacles exceeding, in the later stages of the experiment, the sparse settlement on the plates.

Period of exposure	Plate	Initial no.		Final no.		Settlement		Ratio Barnacled : bare	
		L	R	L	R	Barnacled	Bare		
21–22. vii	A	—	131	152	595	464	152	3 : 1	
	B	—	140	22	263	123	22	5·6 : 1	
	C	132	—	271	35	139	35	4 : 1	
	D	177	—	471	82	294	82	3·6 : 1	
22–23. vii	A	152	—	241	15	89	15	5·9 : 1	
	B	—	149	7	164	15	7	2·1 : 1	
	C	—	35	12	138	103	12	8·6 : 1	
	D	—	82	2	138	56	2	28 : 1	
23–25. vii	A	—	15	81	64	49	81	1 : 1·7	×
	B	7	—	10	3	3	3	1 : 1	×
	C	12	—	11	1	(−1)	1	—	×
	D	—	48	3	61	13	3	4·3 : 1	
25–26. vii	A	—	64	16	60	(−4)	16	—	×
	B	10	—	21	4	11	4	2·7 : 1	
	C	11	—	59	15	48	15	3·2 : 1	
	D	—	51	7	148	97	7	13·9 : 1	
26–27. vii	A	—	60	26	73	13	26	1 : 2	×
	B	21	—	17	4	(−4)	4	—	×
	C	59	—	127	4	68	4	17 : 1	
	D	6	—	4	7	(−2)	7	—	×
27–28. vii	A	26	—	30	3	4	3	1·3 : 1	
	B	17	—	Plate lost					
	C	127	—	99	10	(−28)	10	—	×
	D	—	7	10	28	21	10	2·1 : 1	

At the beginning of this period each plate therefore presented to settling barnacles two similar squares, one of which was bare whilst the other contained a known number of barnacles. The object of the experiment was to compare the settlement on these squares. At the end of the day the number of barnacles on each square was counted. The results for this and subsequent days are given in Table I.

After counting, each plate was again wiped bare except for one of the squares, which was left barnacled. On a few occasions some of these barnacles were removed, with the object of making subsequent counting easier, and the number

on the square recounted. The plates were then exposed for a further period. Where practicable the square left barnacled was that which had been wiped clean on the previous day. The number of times this change between the two squares L and R was effected for each of the plates can be deduced from Table I, where the plates are designated A, B, C and D.

Table I shows that, in general, settlement was much heavier on the squares which were initially barnacled than on those which were initially bare. A total of 1610 barnacles settled upon the former, 521 on the latter. During the first 2 days, when the initial numbers on the barnacled squares were fairly large and settlement was moderate, the ratios were consistently in favour of the barnacled squares. Later, when the initial numbers were smaller and settlement sparser, inconsistencies appeared, but even some of these supported the idea that the settling barnacles were gregarious. For instance, of the eighty-one barnacles which settled on the bare area of plate A on 23–25 July, sixty-nine settled in a small cluster in a corner of the square. In half of these inconsistencies the final number of barnacles on the barnacled square was less than the initial number, showing that mortality amongst settled barnacles was exceeding settlement. We have often seen evidence of mortality amongst young *Elminius*, and we are inclined to think that most of the inconsistencies in Table I were due to the mortality amongst the relatively large numbers of previously settled barnacles being great compared with the rather small numbers of new arrivals. Giving due weight to this point it is concluded that the squares which initially bore barnacles were considerably more favourable for settlement than those which were bare. This is not indisputable evidence for gregariousness. First, it does not answer the question whether the effect may not be due to mere sheltering amongst the previously settled barnacles, as amongst surface irregularities, and secondly, the bare surface was wiped immediately before exposure, whilst the barnacled surface had not been wiped for 1 or 2 days. Settling larvae of several forms have been shown to favour surfaces covered with bacterial or diatomaceous films (for references see Miller, Rapean & Whedon, 1948; Cole & Knight-Jones, 1949) and such films are acquired after short periods of immersion, though it is doubtful whether one affecting appreciably the behaviour of cyprids would be acquired in such short periods as a day or two.

Critical Small-scale Experiment

A better experimental technique was derived from the account of settlement in *Tubularia* by Pyefinch & Downing (1949), who set a glass microscope slide which bore a colony of *Tubularia* in the centre of a wooden panel and hung it from a raft which itself bore practically no *Tubularia*. A control exposure consisting of a bare slide set in the middle of a similar panel was immersed close beside it at the same time. Much heavier settlement subsequently occurred on the panel to which the *Tubularia* colony was attached (although

this suggests gregarious behaviour it may have been due solely to larvae from the colony settling immediately after liberation).

Accordingly glass slides measuring 2·6 × 7·5 cm. were stuck with 'Durofix' adhesive to the centres of several glass plates. These were exposed to settling barnacles for a few days. They were then taken up and some were wiped thoroughly all over with clean cotton-wool, whilst others were wiped in the same way but leaving the slides barnacled. A pair of these plates was placed side by side, slides uppermost, in each concrete holder, one with the slide barnacled, the other with the slide bare. These pairs were exposed for periods of 2 or 3 days. After each period of exposure the numbers of barnacles on each slide and on the surrounding 199 cm.^{2} of the upper surface of each plate were

TABLE II. SETTLEMENT OF *ELMINIUS MODESTUS* ON PAIRS OF GLASS PLATES

To one plate of each pair a microscope slide bearing a recorded number of barnacles was fixed, to the other a bare slide. Settlement was consistently much heavier on the plate which bore the barnacled slide.

	Plate with barnacled slide				Plate with bare slide		
			Settlement		Settlement		Ratio in favour of plate with barnacled slide
Period of exposure	Initial no. on slide	Final no. on slide	On slide	On plate	On slide	On plate	
6–8. viii	212	287	75	480	Plate lost		—
	249	304	55	599	8	173	3·5 : 1
8–10. viii	287	369	82	354	3	69	5·1 : 1
	304	403	99	540	0	117	4·6 : 1
10–12. viii	369	413	44	66	14	31	2·1 : 1
	403		Plate lost		3	25	—
12–14. viii	14	1	(−13)	23	0	7	3·3 : 1
	413		Plate lost		0	5	—
3–6. ix	160	167	7	141	1	20	6·7 : 1
	85	89	4	116	1	24	4·8 : 1
	410	497	87	230	5	106	2·2 : 1

recorded (see below for details of the counting-frame used), and the plates and one of the slides of each pair were again wiped bare before exposure for a further period. The results are set out in Table II.

Consistently, many more barnacles settled on the plate which bore the initially barnacled slide than on that which bore the initially bare slide. It seems highly probable that these differences were due to gregariousness. They cannot be regarded as due to sheltering, for the recently settled barnacles on the slide were small compared with the thickness of the slide (2 mm.), so that virtually the same degree of shelter was afforded by the bare slide as the barnacled slide. The increment on the barnacled slide was also consistently greater than the number settling on the bare slide, except for one occasion when no barnacles appeared on the bare slide whilst those on the barnacled slide were considerably reduced in number by mortality.

While counting, each plate was placed slide uppermost over graph paper on

which the outline of the slide had been drawn surrounded by ten other concentric rectangles, gradually increasing in area (Fig. 1 C). The plate was orientated so that the slide was superimposed upon its outline on the paper. This outline measured $2{\cdot}6 \times 7{\cdot}5$ cm., the adjoining rectangle $3{\cdot}5 \times 8{\cdot}5$, the next $4{\cdot}5 \times 9{\cdot}5$, and so on. Between the outlines of adjoining rectangles there was therefore a series of areas, gradually increasing in size and distance from the slide, each 0·5 cm. wide. The number of barnacles in each of these areas was recorded and is shown in Table III. The areas are numbered consecutively

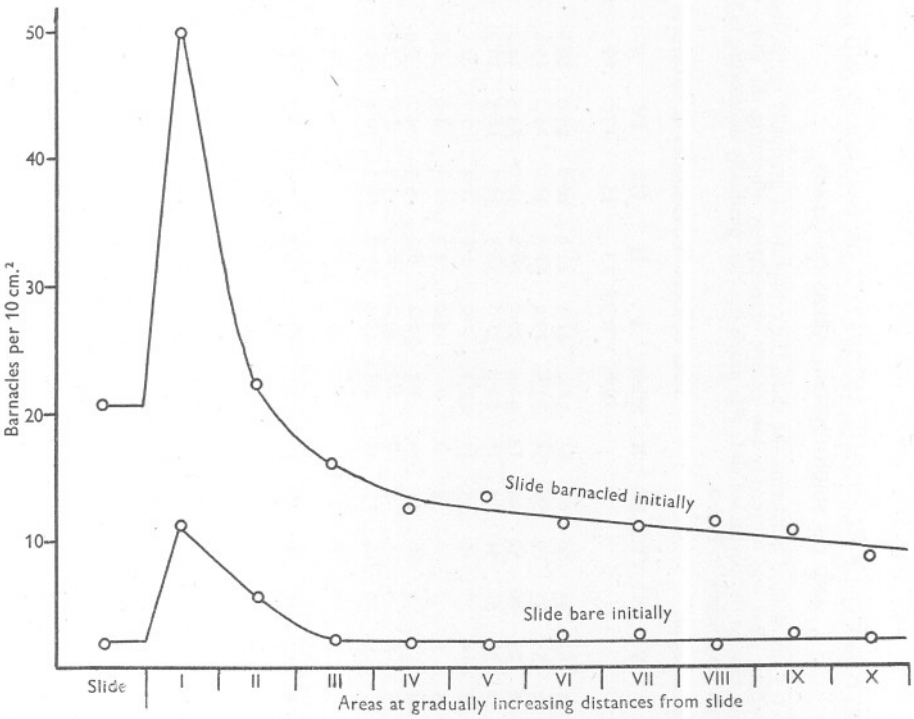

Fig. 2. Mean densities of settlement on slides and on surrounding areas at gradually increasing distances from them (see Fig. 1 C). Data from Table III.

I–X, I being that immediately surrounding the slide. The results relating to the barnacled slides and the bare slides are grouped separately. On the right of Table III the sizes of the areas and the densities of settlement on each are shown. Fig. 2 shows graphically the mean densities of settlement on the slides and at varying distances from them.

Considering first the plates with the slides which were initially bare, it will be seen that while the mean density of settlement on the slides and on the general surfaces of the plates was uniformly low, that on area II was more than twice as great and that on area I five times as great. Evidently the cyprids tended to shelter round the edges of the slides. The densities of settlement on

TABLE III. DENSITIES OF SETTLEMENT OF *ELMINIUS MODESTUS* ON BARNACLED AND BARE MICROSCOPE SLIDES AND ON SURROUNDING AREAS OF GLASS

Areas of glass were marked I–X, each 0·5 cm. wide, I bordering the slide, the remainder at gradually increasing distances from it. Settlement on the initially bare slides and the surrounding glass was uniformly low except immediately adjoining the slide, where increased densities suggest a sheltering tendency. Settlement on and around the barnacled slide was much heavier, gradually decreasing in intensity with increasing distances from the slide. Mean densities are shown graphically in Fig. 2.

	Nos. of barnacles on											Sizes of areas and densities of settlement (nos. of barnacles per 10 cm.²)										
Date	Slide	I	II	III	IV	V	VI	VII	VIII	IX	X	Slide	I	II	III	IV	V	VI	VII	VIII	IX	X
												19·8	9·95	13	15	17	19	21	23	25	27	29 cm.²
	Slide barnacled initially																					
6–8. viii	75	41	16	30	46	51	63	45	60	63	65	38·0	41·2	12·3	20·0	27·0	26·8	30·0	19·6	24·0	23·3	22·4
	55	79	67	48	36	49	53	71	79	59	58	27·8	79·4	51·5	32·0	21·2	25·8	25·2	30·8	31·6	21·8	20·0
8–10. viii	82	50	60	45	40	46	23	20	32	24	14	41·4	50·2	46·2	30·0	23·5	24·2	11·0	8·7	12·8	8·9	4·8
	99	131	76	49	28	31	30	52	51	64	28	50·0	131·7	58·5	32·7	16·5	16·3	14·3	22·6	20·4	23·7	9·7
10–12. viii	44	7	1	2	0	0	11	7	0	13	25	22·3	7·0	0·8	1·3	0	0	5·2	3·0	0	4·8	8·6
12–14. viii	0	3	3	2	5	3	1	1	0	3	2	0	3·0	2·3	1·3	2·9	1·6	0·5	0·4	0	1·1	0·7
3–6. ix	7	52	8	8	8	14	11	9	16	12	3	3·5	52·2	6·2	5·3	4·7	7·4	5·2	3·9	6·4	4·4	1·0
	4	40	11	8	12	15	8	5	5	5	7	2·0	40·2	8·5	5·3	7·0	7·9	3·8	2·2	2·0	1·8	2·4
	87	45	23	28	18	21	19	20	14	17	25	4·4	45·3	17·7	18·7	10·6	11·1	9·0	8·7	5·6	6·3	8·6
								Mean densities				20·82	50·02	22·67	16·29	12·60	13·46	11·58	11·10	11·42	10·68	8·69
	Slide bare initially																					
6–8. viii	8	16	17	11	14	9	16	26	16	22	26	4	16·1	13·1	7·3	8·2	4·7	7·6	11·3	6·4	8·1	9·0
8–10. viii	3	5	20	4	1	5	5	10	2	10	7	1·5	5·0	15·4	2·7	0·6	2·6	2·4	4·3	0·8	3·7	2·4
	0	13	7	5	10	6	18	10	9	20	19	0	13·1	5·4	3·3	5·9	3·1	8·6	4·3	3·6	7·4	6·6
10–12. viii	14	8	7	4	1	1	7	1	2	0	0	7·1	8·0	5·4	2·7	0·6	0·5	3·3	0·4	0·8	0	0
	3	1	1	5	3	6	0	3	3	2	1	1·5	1·0	0·8	3·3	1·8	3·2	0	1·3	1·2	0·7	0·3
12–14. viii	0	0	1	0	0	1	4	0	1	0	0	0	0	0·8	0	0	0·5	1·9	0	0·4	0	0
	0	0	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0	0	0	0·8	0	1·0
3–6. ix	1	7	3	0	1	2	0	1	2	4	0	0·5	7·0	2·3	0	0·6	1·1	0	0·4	0·8	1·5	0
	1	12	0	2	0	1	2	0	2	4	1	0·5	12·0	0	1·3	0	0·5	1·0	0	0·8	1·5	0·3
	5	51	16	5	4	5	2	6	4	8	5	2·5	51·3	12·3	3·3	2·4	2·6	1·0	2·6	1·6	3·0	1·7
								Mean densities				1·96	11·35	5·55	2·39	2·01	1·88	2·58	2·46	1·72	2·59	2·13

the slides which were initially barnacled and on the plates which bore them were much greater. Also the mean density on the barnacled slides was twice that on the areas remote from the slides. On area I settlement was particularly intense and on II it was about as intense as on the slide, probably because the gregarious and sheltering tendencies were acting together in these areas. On III and subsequent areas the densities decreased gradually, as the distance from the slide increased. This gradual decrease contrasts strikingly with the uniformly low densities upon the plates with the bare slides. It suggests that gregariousness in *Elminius* is not entirely a habit of settling in small groups, perhaps as a result of contact between crawling cyprids and previously settled barnacles, but that it affects settlement at considerable distances. The results presented in the next section also support this conjecture, which seems plausible to us, since we are inclined to suppose that olfactory perception may be involved (though evidence on this point is lacking). It may be objected that if gregariousness is a response to the diffusion of a water-borne substance the intensity of settlement should vary inversely with the cube of the distance from the group of previously settled barnacles, but it seems unlikely that this relation would hold under the conditions of these experiments, in which the plates were exposed almost continuously to tidal currents of varying intensity.

Comparison between Settlement on Plates exposed in Muddy Areas, where Barnacles were Absent, and in Neighbouring Shelly Areas, where Barnacles were Numerous

As already mentioned (p. 283) settlement of *Elminius* on test-slates used in routine work on oyster production was usually sparse at stations where the bottom was of bare mud. For example, Table IV gives the 1948 records for two such stations and for two other stations where shells (and barnacles) were abundant. The 1949 records showed a similar phenomenon. The length of river covered by these four stations is about 2 miles (Fig. 3), whilst the tidal currents cover over 4 miles on a moderate tide. *Elminius* cyprids were well distributed in plankton samples, so it seems unlikely that inequalities in their distribution could have been responsible for the differences in intensity of settlement in these areas. The slates were held horizontally about 5 cm. clear of the bottom and did not catch much silt. The tidal currents at these stations seemed of similar strength.

Table V records the settlement on sets of glass plates placed on areas of bare mud and areas covered with shell about 50–100 m. apart. The sets on the Shop Laying each consisted of four plates, the others of two plates. They were put down at L.W.O.T., at places where patches of shell lying on the surface of the mud adjoined extensive areas of bare mud. The shores were fairly straight and uniformly sloping, and there were no differences between adjoining areas in respect of exposure to currents or wavelets. At least one of the patches of shell,

that on Potton shore, had been made within recent years by dredgermen dumping ashore *Crepidula* (the American slipper limpet), and it is probable that most of the patches were originally man-made.

TABLE IV. SETTLEMENT OF *ELMINIUS MODESTUS* ON SMOOTH SLATES

Numbers counted on slates (upper/lower surfaces) exposed just below L.W.E.S.T. for weekly periods at four stations near Paglesham, in 1948. Settlement was usually sparser at stations where the bottom was of bare mud.

Period of exposure	Areas of shell		Bare mud	
	Broadrakes	Shop laying	Upper Paglesham Pool	Opposite Potton point
8–17. vi	188/516	714/916	14/8	No record
17–24. vi	404/2705	467/282	210/1016	0/0
24. vi–1. vii	24/64	53/10	7/58	0/0
1–8. vii	47/107	22/44	1/0	0/1
8–15. vii	1/1	26/64	No record	0/0
15–22. vii	9/39	118/136	1/7	77/43
22–29. vii	203/77	1740/899	0/0	308/80
29. vii–5. viii	35/45	1029/349	0/0	96/92
5–12. viii	24/42	3/2	1/0	93/24
12–19. viii	22/15	10/11	0/0	1/2
19–24. viii	2/2	1/1	0/0	13/1
Means	87·2/328·5	380·3/246·7	23·4/108·9	58·8/24·3

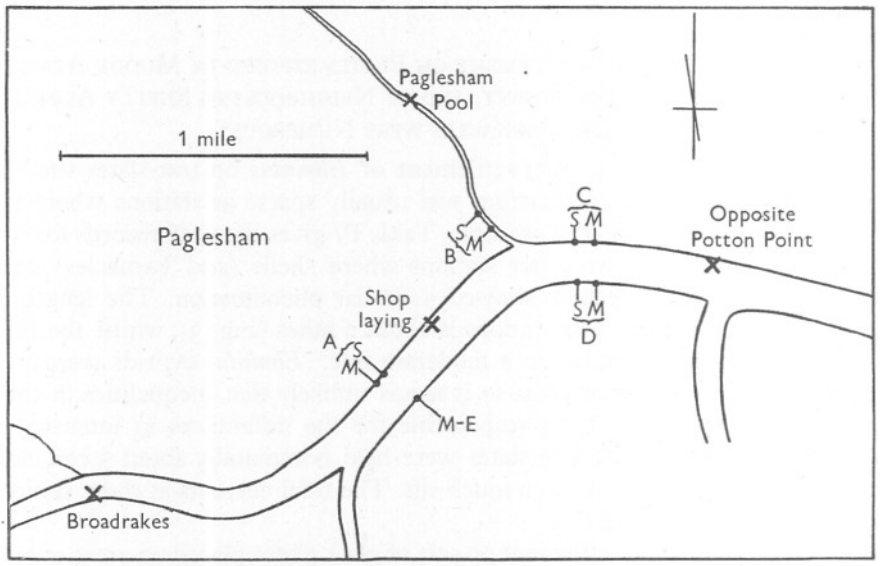

Fig. 3. River Roach near Paglesham at L.W.O.T., showing stations (X) referred to in Table IV. Also, A to D, shore stations referred to in Table V, at each of which plates were exposed on areas of mud (*M*) and shell (*S*); E, muddy area on Potton shore at which plates were exposed for 8 weeks for comparison with plates exposed for the same period on the area of shell at A (p. 294).

Settlement on the plates exposed on the patches of shell was consistently much heavier than on those on adjoining bare mud. The difference was not due

TABLE V. COMPARISON BETWEEN SETTLEMENT OF BARNACLES ON GLASS PLATES EXPOSED AT L.W.O.T., ON NEIGHBOURING AREAS OF SHELL AND MUD

Period of exposure	Nos. on plates placed on an area of shell		Do. area of mud about 50 m. away		Ratio shell/mud		Silt on mud plates compared with shell plates
	Upper surface	Lower surface	Upper surface	Lower surface	Upper	Lower	
			A. On the Shop laying, Paglesham.				
18–19. vii	470–532–668–511	2–1–5–11	97–2–63*	0–0–0*	10·1 : 1	—	Similar
19–20. vii	470–218–713–260	13–5–6–30	52–41–20–22	2–3–3–0	12·3 : 1	6·9 : 1	Similar
20–21. vii	252–125–231–80	26–5–10–6	0–3–0–0	0–0–4–0	229·3 : 1	11·75 : 1	Slightly more
21–22. vii	451–455–347–291	24–37–10–24	109–79–67*	11–2–9*	4·5 : 1	3·2 : 1	Similar
22–26. vii	6120–5960–6420–3640	610–1196–588–100	726–1620–1140–1640	22–7–6–9	4·3 : 1	56·7 : 1	Similar
26–27. vii	1622–956–1438–1795	121–41–12–11	74–86–140–133	1–0–14–11	13·6 : 1	7·1 : 1	Slightly more
27–28. vii	178–105–646–104	17–39–7–14	0–34–13–7	0–3–1–0	19·1 : 1	19·25 : 1	Similar
			B. In Paglesham Pool.				
19–20. vii	1764–1958	10–8	234–512	14–0	5·0 : 1	1·3 : 1	Similar
20–21. vii	2798–2883	41–74	250–84	2–36	17·0 : 1	3·0 : 1	Slightly more
21–22. vii	2272–3249	162–143	502–755	56–91	4·4 : 1	2·1 : 1	Similar
22–26. vii	6810–7650	1184–972	2660–2560	671–364	2·8 : 1	2·1 : 1	Similar
26–27. vii	1774–826	17–59	234–58	0–20	8·9 : 1	3·8 : 1	Similar
27–28. vii	674–1042	19–7	88–153	1–3	7·1 : 1	6·5 : 1	Similar
			C. On Wallasea Shore, below Paglesham Pool.				
3–4. viii	39–29	1–1	2–4	0–0	11·0 : 1	—	Similar
8–10. viii	325–406	24–2	6–2	2–7	91·4 : 1	2·8 : 1	Slightly more
10–11. viii	85–101	97–12	54–45	34–21	1·9 : 1	2·0 : 1	Similar
			D. On Potton Shore, opposite Paglesham Pool.				
2–4. viii	169–91	0–3	7–11	0–1	14·4 : 1	3·0 : 1	Similar
8–10. viii	421–311	13–41	133–189	10–0	2·3 : 1	5·4 : 1	Similar
10–11. viii	88–120	36–8	30–16	12–20	4·5 : 1	1·4 : 1	Similar

* One plate missing. This was allowed for when calculating ratios.

to varying muddiness of the plates, for there was little difference between the muddiness of the upper surfaces of plates from the two types of ground, whilst the lower surfaces were equally clean. The possibility that it was due to varying turbidity of the water must be considered, for in this respect there were probably frequent slight differences between the muddy and shelly areas. Much of the silt in the water is derived from the muddy bottom, particularly from the shores. It is swirled up by wavelets at low water and, in places, by the current when the tide is running. It would not be surprising to find that settlement is discouraged by turbidity, for such behaviour would be adaptive, leading to avoidance of places liable to smothering by mud, but such behaviour has not yet been demonstrated in *Elminius modestus*. On the contrary, Darwin (1854) remarked on the peculiar ability of this species to live under muddy conditions. Moreover, the plates were held about 5 cm. above the bottom, and the differences in turbidity between adjoining areas were probably small, because the patches of shell were also muddy and were limited in area. It is much more likely that the comparatively heavy settlement on the plates from the areas of shell was principally due to the gregarious tendency, since the small-scale experiments have shown the existence of such a tendency. At each locality there were virtually no barnacles on the bare mud surrounding the one set of plates, but millions, the vast majority *Elminius*, on the shells within a few metres' radius of the other.

A comparison was also made between settlement on sets of plates exposed on muddy and shelly shores for a long period. Areas were chosen on opposite sides of Paglesham Reach, which is a straight stretch of the River Roach. The shelly area was on the shore of the Shop Laying and the other on the almost uniformly muddy Potton shore (Fig. 3). The two sets, each of eight plates, were put out on 12 August 1949. They were visited occasionally. *Ulva* was found to collect round the protecting wire hoops and on the plates themselves, particularly on the Potton shore. This was removed at infrequent intervals. On 7 October 1949 the plates were taken up, having been down for 8 weeks during which settlement was very sparse. The upper surfaces of all plates were covered with almost continuous layers of mud, which were noticeably thicker on the plates from Potton shore. The lower surfaces were clean. Amongst the mud were sparse filaments of *Enteromorpha*, but the only attached animal, besides *Elminius*, was a single specimen of *Balanus improvisus*. The numbers of *Elminius* on these plates (upper/lower surfaces—as usual with glass plates, settlement was much heavier on the upper surfaces) were as follows:

Area of shell (Shop Laying): 1680/88, 1980/55, 1270/213, 1620/500, 1560/111, 970/280, 1360/127, 2140/480.
Bare mud (Potton shore): 3/1, 2/2, 2/0, 0/0, 5/0, 24/0, 1/0, 0/2.

Some of these were recently settled but the majority were large and had probably settled during August.

These great differences could not have been due to the greater muddiness of the Potton shore plates, since the lower surfaces of all plates were equally clean. It is doubtful whether differences in turbidity contributed to them and though it is quite likely that they were partially due to greater blanketing of the Potton shore plates by *Ulva*, they were probably largely due to the gregarious tendency.

Gregariousness as a Factor affecting the Distribution of *Elminius*

Elminius is abundant on the shores of Essex creeks and becomes very crowded on stable substrata, such as pier piles. It is a small, short-lived form which achieves population densities even greater than those of native shore barnacles, since its individuals readily settle one on top of the other. Doubtless its gregarious habit during settlement tends to maintain its littoral distribution.

Away from the shores, at depths of about 5 fathoms for instance, it is comparatively sparse. The majority of shells dredged from these deeper grounds in 1949 bore no *Elminius*, but occasional shells bore many; isolated individuals were rare. In November 1947, *Elminius* was well established, but not common, in the Helford River, Cornwall. On the shore at Calamansack only about one stone in twenty bore any specimens, but some bore groups of from five to twenty. Several isolated individuals were observed in this locality. It was even less common on the oyster-layings in mid-river, where only about one shell in a hundred bore any specimens, yet one shell was observed bearing a group of eight. In the Fal and Truro Rivers few were seen during a week's survey of shores and oyster grounds in June 1949, except at the wharf at Malpas, where the species was abundant.

The tendency to settle in groups and in places where the species is well established must tend to prevent wastage through individuals settling in unsuitable localities and in isolation. It will not prevent the colonization of new areas, for occasional individuals settle in such areas even when settlement is sparse. Groups will gradually form round the majority of these pioneers, so that their breeding capacity will not be wasted and suitable areas will eventually become fully colonized. Far from restricting the spread of *Elminius* in this country, gregariousness will make it more certain, though more gradual. Craft in Essex creeks become heavily fouled with *Elminius* during the summer, and coastal shipping must play an important part in widening its distribution. This fact, together with the gregarious tendency, may partially account for its apparent predilection for wharves, although this is doubtless largely due to intolerance of wave action and insolation.

Summary

A gregarious tendency during settlement, similar to that already demonstrated in oyster larvae, was suspected in *Elminius*, because cyprids settled in groups during the initial stages of colonization of surfaces (crowded later arrivals

showed a spacing-out tendency) and because settlement on test-plates was peculiarly sparse at stations with a muddy bottom, where barnacles were absent.

Settlement was much heavier on areas of smooth glass, which already bore recently settled barnacles, than on similar adjoining areas which were bare.

When barnacled microscope slides were stuck to one set of glass plates, bare slides to another and the two sets exposed side by side, settlement was consistently much heavier on the plates which bore the barnacled slides. The mean density of settlement on the bare slides and the surrounding plates was uniformly low, except for a greater density immediately adjoining the slides, probably due to sheltering alongside their edges. On the barnacled slides density of settlement was much higher and on the plates immediately alongside still more so, whilst at increasing distances from the slides it became gradually smaller but was still much heavier than on the plates with the bare slides. This suggests that the sensory basis for gregariousness can act at a distance. It may possibly be olfactory.

Settlement was very much heavier on glass plates placed on areas of shore where shells were numerous and barnacles abundant, than on similar plates on areas of bare mud 50–100 m. away, where barnacles were absent. This was probably largely because of gregariousness.

In localities where the species was sparse it usually occurred in small groups, loss of breeding potential through isolation being thus at a minimum.

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SOME OBSERVATIONS ON THE EFFECT OF FIBROUS GLASS SURFACES UPON THE SETTLEMENT OF CERTAIN SEDENTARY MARINE ORGANISMS

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(Plate I and Text-fig. 1)

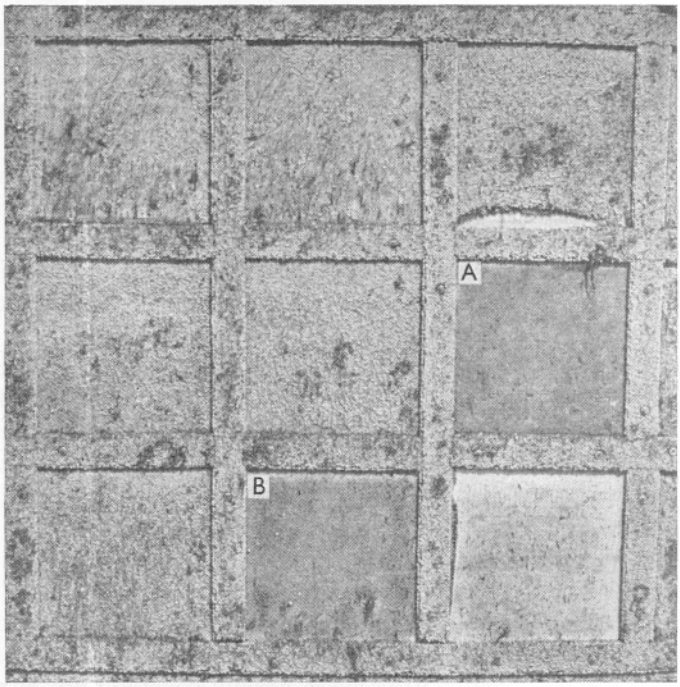
The work of Wilson (1948, q.v. for further references) has emphasized the importance of the nature of the substratum for the settlement and metamorphosis of a number of marine worms, while Pomerat & Weiss (1946) and Pyefinch (1948) have drawn attention to the effect of surface conditions upon the settlement of barnacles. Observations during some recent tests on a number of glass cloths, manufactured by Fibreglass Ltd., have resulted in further evidence concerning the marked effect of surface texture on the settlement of certain sedentary marine organisms.

Samples of these cloths were mounted on both sides of a wooden board and the latter attached to an iron frame which was suspended 2 ft. below the surface from a raft moored close inshore. Duplicate specimens of nine types of cloth were tested, the positions on each side of the board being allocated randomly. Control panels of seasoned Bakelite were exposed at the same time. (No toxic panels were under test on the raft during these exposures.)

The cloths and controls were immersed on 25 March 1949. A barnacle settlement, which subsequently developed into one of the heaviest for many years, began between 1 and 3 April, was heavy by the 5th and continued for some time (Barnes, 1950). At the first inspection (15 April, 21 days' exposure) most of the cloths and the controls were heavily covered with either newly settled cypris larvae or young barnacles.

The exposure was continued and a further examination made on 9 May (45 days' exposure). Four of the samples were almost completely free from barnacles; the remainder and the Bakelite controls were more or less uniformly and very thickly covered with young barnacles, determined later to be *Balanus crenatus* (Text-fig. 1). In marked contrast to this inhibiting effect of four of the Fibreglass panels on the settlement of barnacle larvae, all the panels and the controls were similar with regard to other attached forms, which consisted only of mixed diatom species and some short filaments of *Ectocarpus sandrianus* at the first inspection, with the subsequent addition of traces of *Cladophora* sp. and *Ulothrix flacca*.

The four panels almost free from barnacles were duplicates of two types of cloth and, as a result of inquiries, Fibreglass Ltd. pointed out that these duplicates, while similar to one another, differed from the others in that they were what is termed 'staple' cloths. As such, they are made up of comparatively short lengths of glass fibre spun together to form a strand before weaving into cloth. The other samples, which had not inhibited settlement, were 'continuous' cloths, consisting basically of very long glass filaments. A microscopic examination showed the continuous cloth to have an extremely smooth surface (Pl. I, fig. 1), in marked contrast to the rough spinous surface of



Text-fig. 1. Nine samples of Fibreglass cloth after 45 days' exposure. Note almost complete absence of barnacles on the staple cloths, panels A and B. $\times \frac{3}{20}$.

the staple cloth, resulting from the projecting and partially interlocking free ends of the short, fine glass filaments (diameter 8 μ approx.) comprising the individual strands. The general impression of the surface of these staple cloths was, therefore, of a stiff fibrous weft, beyond which numerous longer fibres (about 1·0 mm. in length) projected (Pl. I, figs. 2, 3).

In view of the strikingly different effect of these two types of cloth upon settlement of barnacles, a second set of panels and controls was put out on 26 July 1949, to ascertain whether there was any similar effect with respect to settling forms prevalent later in the season.

At the first inspection (12 August, 17 days' exposure) only diatoms and traces of algal sporelings were present on all panels and controls. After a further 6 weeks' exposure all had a heavy growth of *Tubularia larynx*, together with some *Laomedea* (*Campanularia*) *flexuosa*, and some panels had a number of newly settled *Pomatoceros triqueter*. At the next inspection (22 October, 88 days' exposure) it was evident that there was a clear distinction with regard to this *Pomatoceros* settlement. The staple cloths that had virtually prevented the settlement of barnacles were quite free from *Pomatoceros* which was, however, present on all the smooth cloths and frequent on some, although no cloth was as heavily covered as the control panels. Continued exposure throughout a further period of heavy *Pomatoceros* settlement, as clearly indicated by the control panels, confirmed the effectiveness of these staple cloths in preventing attachment of this species. The control panels showed that during this period there was a settlement of *Anomia ephippium*, the light character of which settlement makes confirmation of the results necessary, but examination of the cloths suggested that its settlement had been inhibited by the staple yarns.

It appears, therefore, that the texture of the surface of the staple cloth prevents the settlement of *Balanus crenatus* and *Pomatoceros triqueter*, whose larval forms differ widely in both structure and size, but is without effect on the settlement of *Tubularia larynx*.

Visscher (1928) states that cypris larvae, in a series of exploratory movements, may cover appreciable distances before attaching. It is possible, therefore, that during these movements the projecting bristles of the staple cloths by their number and stiff character may prove a source of irritation or may mechanically restrict such exploratory movements, either effect causing the cypris larvae to move away. It is of interest to note that settling oyster larvae are sensitive to the physical texture of the surface, and that they also carry out exploratory movements before settlement and metamorphosis (Prytherch, 1934; Cole & Knight-Jones, 1939). Further, according to these authors, these larvae do move away from an unsuitable surface. It is not clear, however, why such a surface as this staple cloth presents, if actively irritating, does not prevent the settlement of the actinula larva of *Tubularia*, although of course the latter may be less sensitive to this type of mechanical irritation. This larva, according to Pyefinch & Downing (1949), also moves over a surface before settling, but the length of the aboral tentacles would be sufficient to penetrate the fibrous surface weft. A similar explanation has been advanced by these authors to explain the lack of settlement of *Tubularia* on a surface covered by long tufts of filamentous algae, in contrast to its ready settlement on a surface covered by shorter (less than 2 mm. in length) algal tufts. In addition, any irritation of an actinula larva may stimulate discharge of the nematocysts contained within the swollen tips of the attaching aboral tentacles, thus facilitating attachment.

Wilson (1948), working with the larva of the polychaete *Ophelia bicornis*, found that substrata consisting of more angular grains were unfavourable to

settlement and metamorphosis, and he suggested that the size and shape of the interstices between the grains were more important than the grain size or shape, a critical amount of surface area being requisite for the initial attachment stimulus and subsequent metamorphosis. From this point of view the character of the surface of the staple cloth may not provide the appropriate stimulation.

The development of the actinula larva of *Tubularia* is much more direct than the metamorphosis of a barnacle or polychaete larva, and may not require so critical a stimulus for its initiation.

The courtesy of Fibreglass Ltd. throughout these investigations, and in particular the help of their representative, Mr H. Cameron, is acknowledged.

Summary

A description is given of a glass cloth surface which prevents the settlement of larvae of *Balanus crenatus* and *Pomatoceros triqueter*, whilst not affecting that of *Tubularia larynx*. A number of possible causes for this are examined, and its relation to other work on the settlement of sedentary forms is briefly considered.

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EXPLANATION OF PLATE I

Fig. 1. A photomicrograph of surface and folded edge of a smooth continuous cloth. ×60. (N.B. Folding has caused the slight irregularities seen along the edge.)

Fig. 2. The same of folded edge of staple cloth A. The projecting fine glass filaments have diameters of about 8 μ. ×50.

Fig. 3. The same of surface of staple cloth B. ×30.

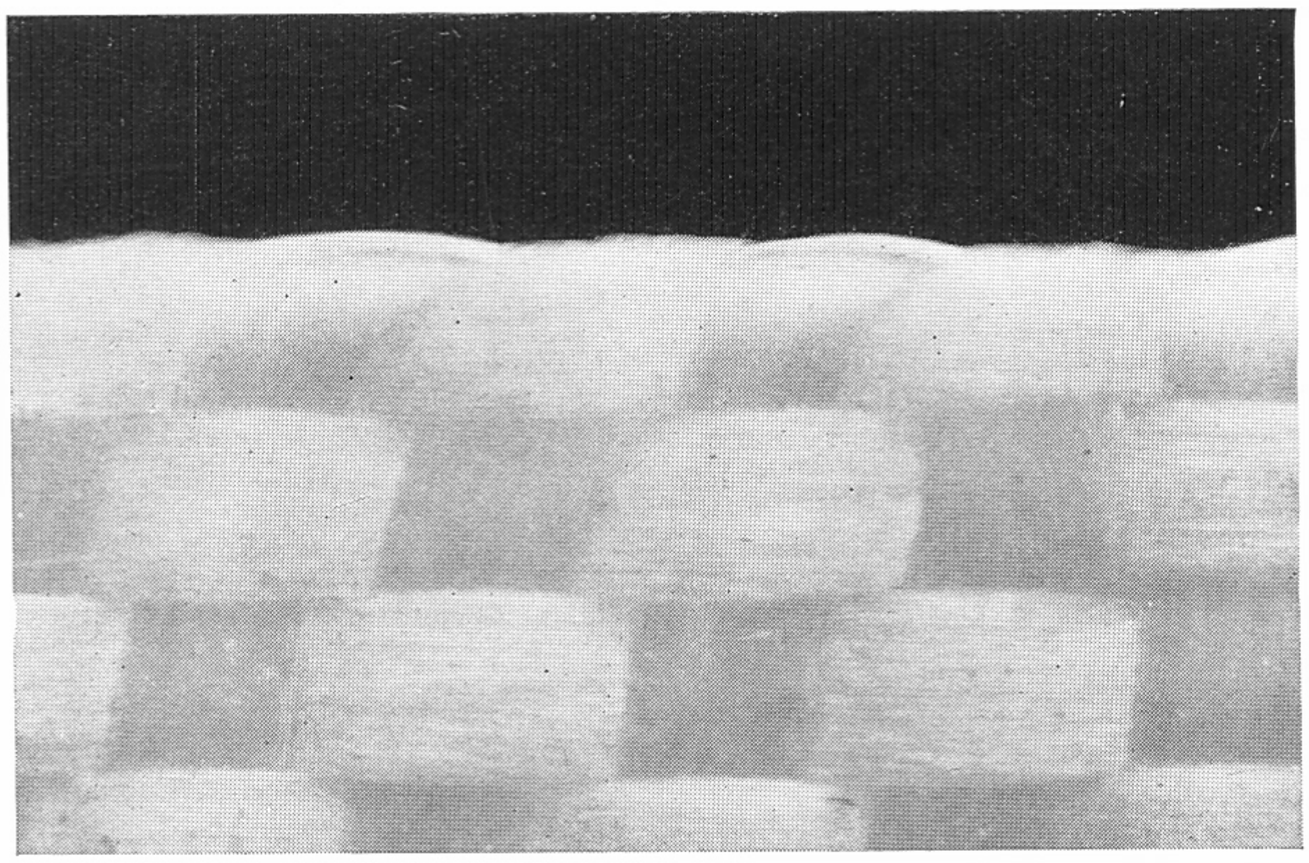

Fig. 1.

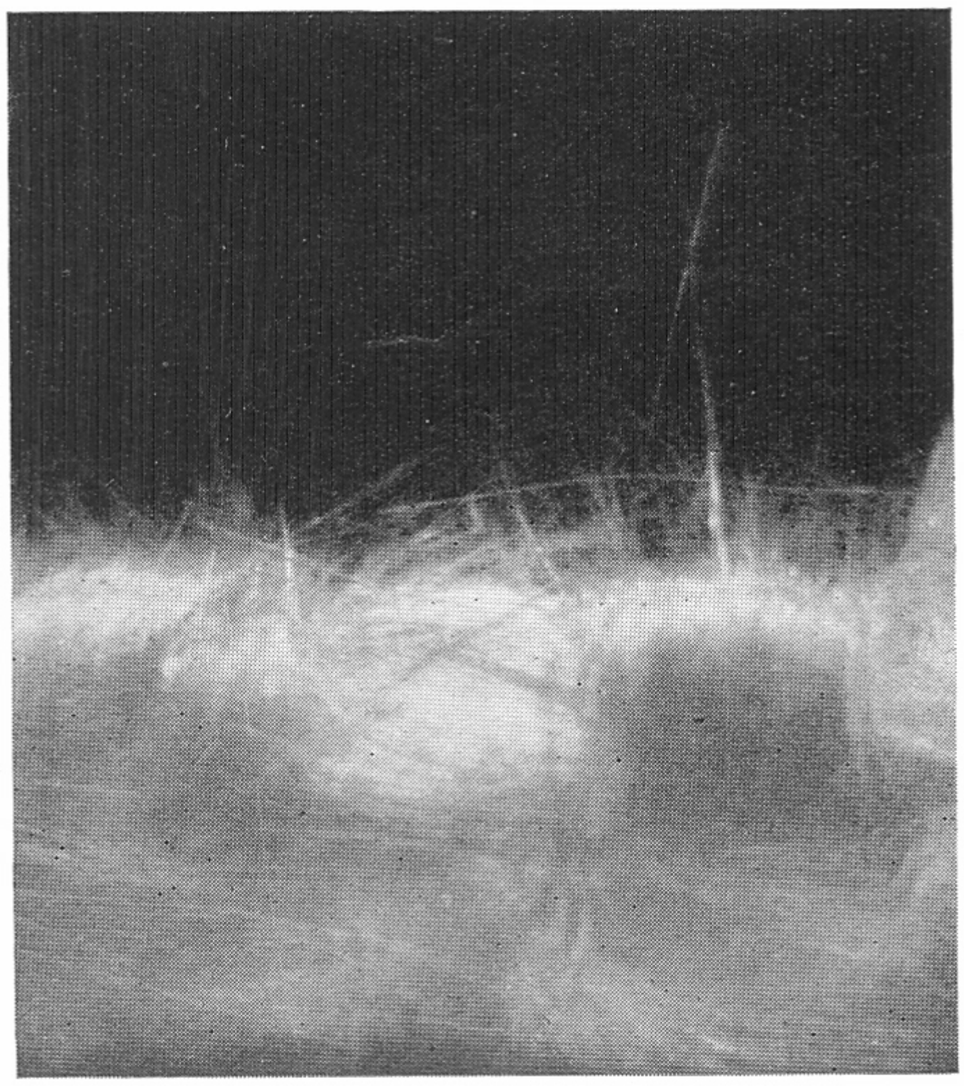

Fig. 2.

Fig. 3.

RESPONSES OF *BRANCHIOMMA VESICULOSUM* (MONTAGU) TO PHOTIC STIMULATION

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(Text-figs. 1–6)

CONTENTS

Introduction

The light sensitivity of sabellid and serpulid polychaetes has been investigated on a number of occasions, but this subject is still poorly understood. Early workers commented on the extreme sensitivity of certain species to various stimuli, including changes in illumination. These animals are tubicolous, and normally they protrude their branchial crowns from the mouths of their tubes. When disturbed the animal usually jerks back into its tube. This quick withdrawal is the result of synergistic contraction of the longitudinal muscles, and it is intermediated through a giant axon system (review by Nicol, 1948*a*).

Many, perhaps all, species of the Serpulimorpha retreat into their tubes on interruption of the light or during the passage of shadows. This response is reported for: *Sabella spallanzanii* (Viviani), *S. microphthalma* Verrill, *Bispira volutacornis* (Montagu), *Potamilla reniformis* (O. F. Müller), *Branchiomma vesiculosum* (Montagu), *B. vigilans* Claparède, *Dasychone bombyx* (Dalyell), *Myxicola infundibulum* (Montagu), *Eudistylia polymorpha* (Johnson), *Hydroides dianthus* (Verrill), *H. uncinata* (Philippi), *Serpula vermicularis* L., *Pomatoceros*

triqueter L., *Protula intestinum* (Lamarck) (Dalyell, 1858; Gosse, 1863, 1877; Claparède, 1868, 1870; Soulier, 1891; Andrews, 1891; Hesse, 1899; Hargitt, 1906, 1909*a*, *b*, 1912; Buddenbrock, 1913, 1928; Hess, 1914; Loeb, 1918; Ricketts & Calvin, 1939; Nicol, 1948*b*; *et al.*). Observers have noted that animals react to sudden decreases in light intensity, to moving shadows, and to slight movements of the observer within view of the animal. These are largely qualitative impressions. A response certainly occurs to a sudden decrease, but not to a sudden increase, in light intensity, for example in *Hydroides dianthus* (Hargitt, 1906) and *Serpula vermicularis* (Hess, 1914).

Evidence from ocular structure is ambiguous. *Branchiomma vesiculosum*, which possesses ocular spots near the tips of its branchial filaments, withdraws into its tube when the light dims; it still gives this response when the ocular spots are removed (Hesse, 1899). In *Hydroides dianthus*, which possesses no such special branchial receptors, the withdrawal reflex is equally well developed. Photo-sensitivity is greatest in the distal quarter of the filaments; total ablation of the filaments abolishes the reflex (Andrews, 1891; Hargitt, 1906). Consequently, it would appear that the specialized ocular organs on the branchial filaments are not necessary for this response (cf. Hesse, 1899).

Constant illumination also acts as a stimulus for other behavioural activities in some of these sedentary polychaetes. Loeb (1906, 1918) claimed that *Sabella spallanzanii* and *Hydroides uncinata* turn their branchial crowns and the anterior portion of their tubes towards the source of the light. This behaviour would constitute a kind of photo-tropism. Hargitt (1909*a*, *b*, 1912), who repeated Loeb's experiments, found no evidence for orientation towards the light, but Fox (1938) considered that *Sabella spallanzanii* is positively phototropic. No conclusion seems possible without reinvestigating the subject.

Again, Fox (1938) found that *S. spallanzanii* is usually retracted within its tube during the day, and emerges at night; other observers also indicate that *S. pavonina* protrudes its crown mainly at night. This is a negative postural response to light intensity.

The following account presents the results of experiments carried out on photo-sensitivity in the sabellid worm, *Branchiomma vesiculosum*. This species was chosen because it is available in quantity, it is large, hardy in the laboratory, and because it displays a well-marked light reflex when compared with *Sabella* and *Myxicola*, the two other large species which are common locally. The photo-receptors and the physiological mechanisms involved will be described in a further paper.

Dr W. R. G. Atkins, F.R.S., and Mr F. J. Warren have provided technical assistance and advice, particularly in the measurement of illumination. I am especially grateful for their calibration of incandescent lamps, a photoelectric cell, and galvanometers. Dr Atkins and Mr F. S. Russell F.R.S., have read the manuscript. I thank them for their advice and criticism.

METHODS

Animals were kept in dishes under circulation in the laboratory, and specimens were chosen at random for any particular experiment. The experiments were carried out in a cellar where the temperature remained fairly constant for long periods; the seasonal variation over 6 months was 6° C.

Intensity measurements were made with a selenium rectifier photocell ('Electrocell', German make) which was calibrated for absolute photosensitivity against a substandard lamp. The sensitivity of this cell ceased to be linear above 25 μA., with a high resistance galvanometer, and a correction was applied to readings at higher intensities. Readings were made on a Gambrell Bros. Onwood patent galvanometer (557·3 Ω at 17·75° C.) and on a Cambridge unipivot galvanometer (9.99 Ω at 17·75° C.). These were calibrated in terms of each other and against a potentiometer and accurate resistances. Their sensitivities, respectively, were 0·27 and 1·92 μA. per scale division, and they were read to a 0·2 scale division. Reduction of intensity was achieved on occasion by the use of a Chance ON 31 neutral filter 3·5 mm. in thickness. This filter, according to the manufacturer, gives nearly uniform transmission from 4000 to 7000 A. Its overall transmission measured in the visible spectrum was 8·2 %.

For obtaining light from restricted spectral regions, a set of four Corning coloured filters was used. These same filters have been described and their characteristics presented by Atkins & Poole (1931). These were: C. dark blue (H. lantern blue) with 20 % transmission of visible light, 50 % cut-off at 4800 A., and very slight transmission in the red; C. sextant green, with a transmission of 2·2 % of visible light, and 50 % cut-offs at 5000 and 5700 A.; C.H.R. yellow, green shade, with 50 % cut-off at 5500 A., and 67 % transmission of visible light; C. selenium red G. 24, with 50 % cut-off at 6400 A., and 66 % transmission of visible light.

Unless otherwise specified, the following additional experimental conditions obtained. The light source was a 100 W., gas-filled tungsten 'daylight' lamp (Crompton), maintained at 200 V. by a variable transformer (Variac). The animals, in their tubes, were placed in an aquarium with a glass front. The transmission of this glass, measured with the selenium rectifier photocell and coloured filters specified above, was: 88·7 % in unfiltered ('white' light); 88·3 % in blue light; 89·7 % in green light; 88·9 % in orange light; 83 % in red light. These figures were used to correct the intensity measurements made in front of the aquarium glass. No allowance was made for absorption by sea water; the animals lay 1–5 cm. behind the glass; usually some part of the crown was within 2 cm. of the glass. The inside of the tank was dark brown; a piece of matt-black paper covered the rear wall. At very low intensities, when it was difficult for the partially dark-adapted eye to distinguish the animals, a piece of white paper was placed at the back of the tank. Under these conditions, reflectance was not measurable with the photocell. The arena in front of the

tank contained a movable lamp housing; this area was enclosed and was painted matt-black.

Branchiomma is extremely sensitive to mechanical stimuli, and reacts promptly to vibrations of low intensity. The aquarium was mounted on a brick column topped with a slate slab, and the column rested on a concrete floor founded on solid rock. Even with this rigid arrangement, and with two inches of felt between the slate and the bottom of the aquarium, it was not possible to damp all vibrations to below the threshold of sensitivity of the animals.

Observations

Photic stimulation and the withdrawal reflex

Effect of sudden alteration in intensity

Specimens of *Branchiomma vesiculosum* frequently withdraw into their tubes when the light is suddenly extinguished. In several thousand trials no specimen ever withdrew in response to sudden increase in intensity of illumination. Response to intensity change, therefore, is to decrease, not increase, in intensity. This agrees with results obtained for *Hydroides dianthus* and *Serpula vermicularis* (Hargitt, 1906; Hess, 1914; cf. also Buddenbrock, 1928).

Adaptation to photo-stimulation

When the light is suddenly diminished, the animals respond to the first stimulation or first few photic stimuli by a withdrawal, but thereafter cease to react. In Fig. 1 are shown the results of subjecting the worms to repeated

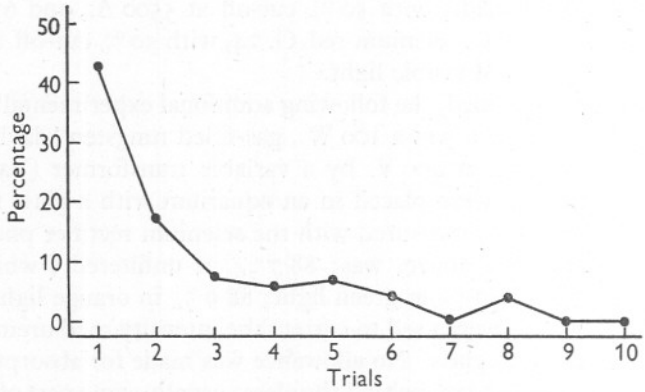

Fig. 1. Course of adaptation to photic stimulation (sudden decrease in intensity). Ordinates, proportion of animals responding; abscissae, successive trials.

stimulation. The animals were placed in white bowls underneath a white (pearl) tungsten lamp (100 W., 200–230 V. input). The measured intensity at the level of the containers was about 419 lux. Successive stimuli were delivered

usually at intervals of 1–10 min. It was not possible to standardize the interval because of great variability in times of emergence in different animals. About half the animals responded to the first stimulus; thereafter the number responding rapidly decreased to zero at the ninth trial. Adaptation or habituation to photic stimulation has been reported for other Serpulimorpha, namely, *Hydroides dianthus*, *Serpula vermicularis* and *Bispira volutacornis* (Bohn, 1902; Hargitt, 1906; Hess, 1914).

Minimal effective intensity change

The limen for decrease in light intensity at different initial intensities was determined as follows. Two daylight lamps were used at empirically dermined distances so as to give a certain initial intensity and a certain decrease in

TABLE I. LIMEN FOR DECREASE IN PHOTIC INTENSITY AT EIGHT DIFFERENT INITIAL INTENSITIES

Further explanation in text.

Initial intensity i (lux)	Lowest effective decrease in intensity tested δi_e (lux)	Highest ineffective decrease in intensity tested δi_i (lux)	$\delta i_e/i$	$\delta i_i/i$
407·2	17·2	12·9	0·0423	0·0317
308·1	12·9	8·6	0·0406	0·0279
185·3	12·9	8·6	0·0698	0·0465
64·6	4·3	2·2	0·0666	0·0334
34·7	2·9	2·2	0·0870	0·0620
17·9	2·9	2·5	0·1600	0·1400
5·3	1·2	1·1	0·2300	0·2030
2·3	0·5	0·4	0·2240	0·1550

intensity when one lamp was extinguished. At each initial intensity animals were tested to determine the minimal intensity change necessary to evoke a response, and the maximal intensity change that failed to evoke a response. All samples used in these tests were drawn from one laboratory group.

The results have been plotted in Fig. 2 as $\delta i/i$, where δi is the minimal intensity change that evoked a response. The vertical lines represent the interval between this effective value and the maximal non-effective intensity change that was determined. Absolute values are presented in Table I. The procedure was very slow and tedious, and to obtain these figures many more observations were required than those shown and utilized. The variability of this biological material will be discussed in a later section. Here it is noted that these results are not interpreted as representing the absolute photosensitivity limits of this species under manifold conditions. The stimulus-response method as here employed does give an indication of what these animals can do under these particular conditions but not necessarily of their ultimate discriminatory powers. These observations were all obtained on a given lot of worms in which all animals were kept under similar conditions,

and were tested in one period of time. It is therefore submitted that the observations are of value as relative and comparative data.

The curve in Fig. 2 shows that a relatively greater intensity change is required to effect a response at low intensities than at high intensities over the range explored (2·32–407·19 lux.).

These results obviously do not conform to the Fechner-Weber law for intensity discrimination. Comparable results are not available for other polychaete species. Hess (1914) sought the minimal decrease in intensity that would evoke a response in *Serpula vermicularis*. He found that moving a lamp from 60 to 61·5 cm. called forth retraction of the crown. The relevant

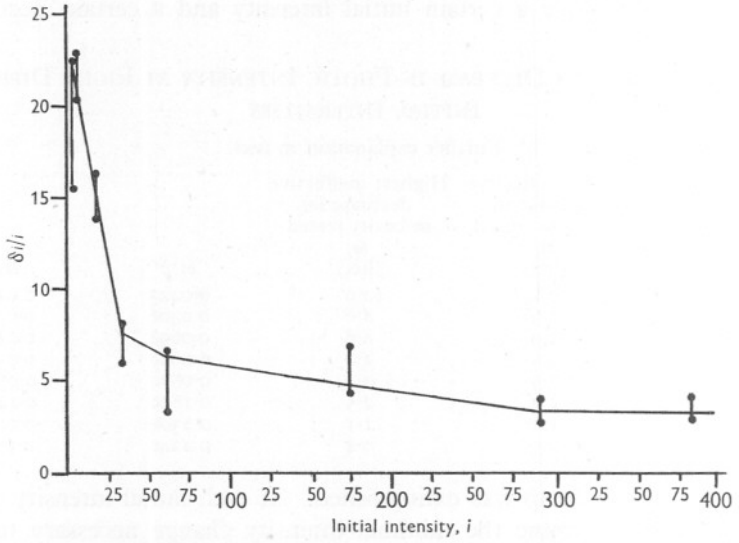

Fig. 2. Relation of minimal decrease in intensity necessary to evoke a response to initial intensity. Ordinates, $\delta i/i \times 100$; abscissae, intensity i, in lux. The data are grouped in pairs for a given value of i. The upper point of each pair represents the minimal value at which a response occurred; the lower point the maximal value at which no response occurred; vertical lines represent the unexplored range. Each point is based on trials of at least 10 specimens.

intensities were as 1:0·95; this gives a value for $\delta i/i$ of 0·05. This is within the range determined for *Branchiomma*. Hecht (1924) has studied an analogous situation in *Mya arenaria*. He utilized retraction of the siphons as an indicator of discrimination, and he tested for sensitivity to increases in light intensity. Hecht also found that the ratio $\delta i/i$ is not constant for this species at different initial intensities; the ratio decreases as intensity is increased up to a certain point, beyond which the ratio increases. However, the Fechner-Weber law for visual discrimination does not hold even in man, the subject for which it was erected. 'For visual intensity discrimination $\Delta I/I$ is approximately constant over the range from medium to very high light intensities, and below these

increases very markedly' (Rawdon-Smith, 1938, p. 18). Since *Mya* is responding to an increase in intensity, and *Branchiomma* to a decrease, it is suggested that the underlying photochemical reactions are similar, but that differences exist in the nature of the central correlatory mechanisms.

Sensitivity in lights of different spectral composition

The following experiments were designed to obtain information for sensitivity to lights of different spectral composition. The lowest initial intensities of light at which a response could be obtained by reduction of intensity were sought. Animals were tested in white and coloured lights of different initial intensities by cutting off the light (reduction to zero intensity). 'White' light from a daylight bulb, blue, green, orange and red lights were used (spectral composition described above under methods). Experiments were carried out on a single sample of worms kept under similar conditions.

White light. The minimal light intensity at which a response occurred to complete extinction of illumination was 2·5 lux. Only one animal in ten contracted at this intensity. At higher initial intensities a greater proportion of animals responded amounting to 80 % at 175 lux (Fig. 3).

Coloured lights. The minimal intensities at which a response could be elicited, and the maximal intensities at which no response occurred to diminution of intensity were determined for blue, green, yellow and red light. The coloured filters used have been described above under methods. The values obtained were weighted for the spectral composition of light from the source, and the spectral sensitivity of the photocell. The results are presented in relative units as the reciprocals of the intensities determined. This gives some indication of relative sensitivity to different spectral regions. The values obtained are green 6–18, blue 3–8, yellow 7–10, red 1·6–2·4 (units of relative sensitivity). The wide spread between the values in green and in blue light is due to the fact that the photoelectric cell has maximal sensitivity in green light (5700 A.) and sensitivity falls off much more rapidly in long than in short wave-lengths (Lange, 1940). The difference between the two figures for green light actually represented only 0·1 μA. in photoelectric current.

The data show that *Branchiomma* is sensitive to the whole visual spectrum from 4000–7000 A. Owing to the spread of the data it is not possible to make a firm statement for relative sensitivities in different spectral regions. Sensitivity is least in the red, increases for shorter wave-lengths, and probably has a maximum between 5000–6000 A. These conclusions require confirmation.

Responses of specimens kept in light and darkness

The effect of retention in total darkness on the withdrawal response of *Branchiomma* was investigated as follows. Specimens were kept in an aerated container in the dark for 5 and 10 days. Sensitivity in weak illumination was thereafter determined by permitting the animals to expand at some given

intensity, and then turning off the light. As a control, an equal number of specimens was kept in constant illumination (257·5 lux) for 5 and 10 days.

Specimens retained in darkness:
(i) For 5 days. Tested at 1·97 lux. Proportion of animals responding: 60 %.
(ii) For 10 days. Tested at 0·36 lux. Proportion of animals responding: 70 %.

Specimens retained in constant illumination (257 lux):
(i) For 5–8 days. Tested at 0·72 lux. Proportion of animals responding: 30 %.
(ii) For 9–10 days. Tested at 0·36 lux. Proportion of animals responding: 27 %.

The data show that animals kept for periods up to 10 days in either constant light or darkness are sensitive to light of intensity at least as low as 0·36 lux. It is probable that the animals are sensitive to weaker intensities, but 0·36 lux was about the lowest intensity at which it was possible to observe the animals. There is slight evidence for greater responsiveness of animals maintained in darkness than in light, but not for greater sensitivity to weak light. Owing to voltage variation in the power mains the light occasionally flickered. Illumination of specimens kept in the light was therefore constant, but light intensity occasionally dropped momentarily. These sudden decreases in light intensity were sufficient to cause the animals to react. If these results are compared with the figure for minimal intensity of white light given on p. 309 it will be seen that the minimal intensity at which the animals responded is only one-seventh as great in the present experiments. Corresponding observations on other tubicolous polychaetes are conflicting. Hargitt (1905) found that in *Hydroides dianthus* specimens obtained from deep water (20 fathoms), or kept in a dimly lighted basement over winter, failed to respond to shadows. Bohn (1902), however, noted that in *Hermella ascolata* prolonged exposure to sunlight tended to weaken the sensitivity of the worm to reduction in photic intensity. He explained the reaction to shadows as a learnt response, based on mechanical factors as the unconditioned stimuli. Copeland (1930) has demonstrated the possibility of establishing a conditioned response in a specimen of *Neanthes virens* by associating feeding with light diminution and increase. Yerkes (1906) selected two specimens of *Hydroides dianthus* that failed to respond to shadows, and she repeatedly subjected them to reduction of photic intensity, followed by weak tactile stimuli. After a training period the animals became conditioned to react negatively to shadows.

Interspecific variation may explain some of the differences listed above. But apart from this factor it is clear that the previous history of the animal has considerable influence upon its responsiveness to decrease in light intensity, and upon the threshold of light intensity at which a response can be elicited. The operating factor in *Branchiomma* seems to be not the level of light intensity to which it was generally exposed, but the frequency or infrequency of stimulating decreases in intensity. When animals are kept for some time in either light or darkness and are undisturbed, more react to decrease in light

intensity, and at much lower initial intensities, than when kept under other laboratory conditions where they are frequently subject to variations in light intensity. Repetitive photo-stimulation leads to a lasting state of apparent habituation in which the energy change required to evoke a response is also raised.

Variability in response

It has already been intimated that different animals show considerable variability in their response to photic stimulation. For this reason, when determining critical values, a sample of at least ten specimens was tested (occasionally increased to eleven or twelve specimens). In Fig. 1, which illustrates the course of adaptation to repeated photic stimulation, two aspects of variability are depicted. This graph is based on examination of fifty-six specimens, of which only twenty-four (43 %) responded to the first photic stimulation (intensity 419·13 lux, p. 306). Considerable variation thus exists in the responsiveness of different animals within a population to intensity diminution as a stimulus-signal. The second aspect lies in different rates of adaptation in different animals, some ceasing to respond after the first stimulus, others continuing to respond for nine or more stimuli. Fig. 3 shows still another aspect of individual variation, namely, differences in the number of animals that respond to diminution of illumination at different intensities. In these experiments samples of ten animals were tested at different initial intensities by turning off the lamp. The observations form a fairly regular series from the lowest intensity tested, 2·51 lux, at which 10 % of the animals responded, to 174·6 lux, at which 80 % of the animals responded. In the previous section it has been noted that animals kept under conditions of minimal disturbance have greatly enhanced sensitivity at low intensities. Presumably the behaviour of these animals approaches that of animals living under natural conditions.

Individual differences in the responses of different worms to light have been noted by Andrews (1891) and Hargitt (1906) for *Potamilla* and *Hydroides*. In practice one would expect to find a normal variability in behaviour such as one encounters in investigating any species of animal. The data for *Branchiomma*, however, also suggest a process of adaptation akin to learning, which can modify the withdrawal reflex. Adaptation leads to cessation of the withdrawal response on repeated stimulation, and it raises the limen for photic stimulation.

Following withdrawal there is great variation in the time taken to re-emerge in different animals. The length of time during which the animals remained within their tubes following repetitive photic stimulation was recorded for 35 specimens. In the first three trials, the average periods of withdrawal were 3·9, 3·8, 3·9 min. The means of the differences between the periods of withdrawal in the first and second, and second and third trials, were 0·19 and −0·06 min. respectively. Thereafter, as the number of observations greatly

declined, the mean figures became very variable, without any apparent trend. The observations from the first three trials would indicate that, on the average, animals tend to remain the same length of time in their tubes before expanding their branchial crowns again.

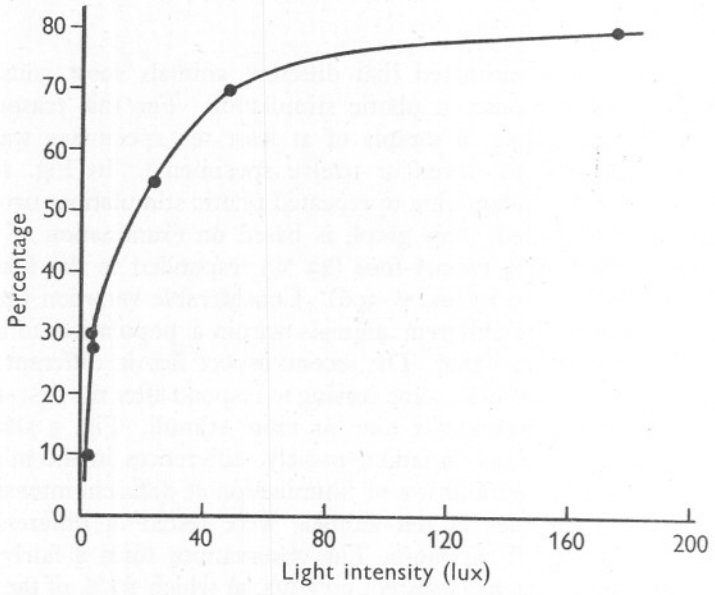

Fig. 3. Proportion of animals that respond to decrease in illumination at several initial light intensities. Ordinates, proportions of animals responding at selected initial intensities; abscissae, light intensities in lux.

Differential responsiveness to intensity change and movement

Two lots of animals were repeatedly stimulated by turning off the light for ten successive trials. Immediately following the last (tenth) trial with this stimulus, a black card was moved across the field between the lamp and the animal for another ten trials. The source of light was a white (pearl) 100 W. tungsten lamp. The intensity at the level of the animals was 419 lux. When the lamp was turned off, the intensity fell to zero. When the card was removed in front of the lamp the intensity fell to about 29 lux. The results are depicted graphically in Fig. 4.

The results show that after the animals have become adapted to a sudden decrease in intensity, they are still sensitive to a moving shadow or moving intensity change of nearly the same magnitude. Slightly less than half the animals responded to a sudden decrease in intensity and to a moving shadow (38·1 and 42·9 % respectively). There is a distinct difference, on the other hand, in the course of adaptation which takes place more slowly to a moving shadow, than to sudden decrease in light intensity. To both events the response

is the same, and the effective stimuli involve diminution in photic intensity, slightly less in movement of the card than in sudden extinction of the illumination. The different adaptation curves show that two distinct sensory processes are involved. This difference arises ultimately from the fact that the one stimulus (the moving shadow) includes a varying temporal and spatial component, as well as an intensity change. Further experiments to elucidate the processes and the photo-receptors involved will be described in a later paper.

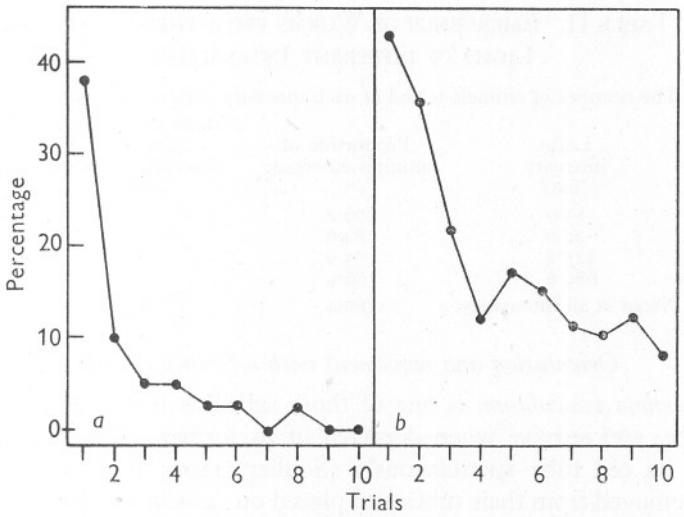

Fig. 4. Course of adaptation to photic stimulation: (*a*) sudden decrease in intensity; (*b*) moving shadow. Observations of 42 specimens. Initial intensity 419 lux. Ordinates, proportions of animals responding; abscissae, successive trials. Trial *b* 1 followed immediately after *a* 10.

Light intensity and emergence from the tube

The following experiments were designed to seek whether the intensity of illumination governs protrusion of the branchial crown from the mouth of the tube. It was not practicable to secure the necessary observations from animals in their natural habitat; consequently, laboratory study had to suffice. Animals were chosen that had recently been collected from their natural habitat, and they were tested within 48 hr. of reaching the laboratory. Twenty-three animals were used. These were placed in the aquarium, which was successively illuminated at four different intensities. Each lot of animals was kept under observation for 30 min.; time of emergence and number of animals that emerged were recorded for each group. The data obtained are presented in Table II. The intensities used were 13·93, 20·04, 125·22, and 689·56 lux. The mean proportion of animals that emerged at all intensities in 30 min. was 80·4 %, and the average time to emerge at all intensities was 10·05 min. There is no apparent trend in the numbers of animals that emerged at different

intensities. The mean times of emergence might be taken to indicate that the animals tend to protrude their branchial crowns sooner in strong than in weak light. However, the length of time which different animals spend in their tubes is very variable; on this basis a difference of 5·3 min. is not significant. In any event, there is no evidence, from these observations, that *B. vesiculosum* is principally a nocturnal form and that it tends to withdraw or remain in its tube when illuminated, as does *Sabella* (cf. Fox, 1938).

TABLE II. EMERGENCE OF WORMS FROM THEIR TUBES IN LIGHT OF DIFFERENT INTENSITIES

The number of animals tested at each intensity varied from 19 to 23.

Light intensity (lux)	Proportion of animals emerging (%)	Mean time to emerge (total time of observation, 30 min.) (min.)
13·9	76·2	12·5
20·0	84·6	10·3
125·2	73·9	10·2
689·6	86·9	7·2
Mean at all intensities:	80·4	10·05

Orientation and movement with reference to light

Branchiomma vesiculosum is one of those sabellids that can burrow, build a new tube, and survive when deprived of its former tube. On occasion it abandons its old tube spontaneously (Soulier, 1891; Buddenbrock, 1913). Animals removed from their tubes and placed on sand immediately commence to burrow; they are positively geotropic (Buddenbrock, 1913). When placed on a hard surface, such as a glass dish in which burrowing is impossible, they

TABLE III. ORIENTED LOCOMOTION AWAY FROM THE LIGHT

Time (hr.)	No. of animals in Light	No. of animals in Shade	Proportion of animals in shade (%)
1417 (start)	6	5	45·5
1517	3	8	72·7
1618	1·5	9·5	86·4
1715	0	11	100·0

usually glide along backwards by slow undulatory waves. Since the animals are capable of free locomotory movement, it is necessary to consider whether light acts as a token stimulus by which they can orientate themselves.

To test orientation to light, groups of 10–11 animals were placed in a white enamel pan, 24 × 33 cm., with overhead illumination. The light source was a white (pearl) tungsten lamp. One half of the dish was covered by a black card. The intensity in the illuminated half of the dish was about 145 lux. A protocol of an experiment is given in Table III, and the data are plotted in Fig. 5.

In these experiments all the animals moved into the shaded half of the container in 4 hr. Consequently, they display negative orientation to light. Orientation under these conditions could be to an intensity difference, or to direction of the light (lateral reflectance from the walls of the dish; cf. Ullyott, 1936). Further experiments are in progress to determine the mechanism of orientation in this species.

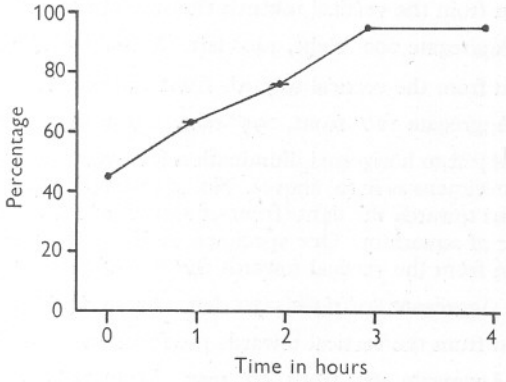

Fig. 5. Oriented movements away from light into shaded region. Ordinates, proportion of animals in shaded portion of container; abscissae, time in hours. Data obtained from two experiments and twenty-two animals. One animal apparently was injured; this would account for the leveling off of the curve slightly below 100 %. Further explanation in the text.

Orientation of tubes to direction of the light (photo-tropism)

The possible influence of the direction of incident illumination on the orientation of the animals' tubes was investigated as follows. Specimens were removed from their tubes, and placed on the surface of clean sand in the bottom of an aerated aquarium. Black matt paper was used to cut off unwanted illumination. Diffuse light was obtained from a 100 W. white (pearl) tungsten lamp. Animals were subjected to total darkness, and to lateral illumination.

About twenty specimens were placed in the aquarium for each test. Most of the animals immediately started to burrow downwards into the sand. A few animals failed to burrow and these were discarded after 2–3 days. The remaining animals were examined. The general direction in which the branchial crowns pointed was noted, and two measurements were made for the protruding section of each tube, namely, the angular deviation from the vertical towards either side of the aquarium, and towards the front or rear of the aquarium. The data obtained are shown below and in Fig. 6.

Specimens building new tubes and subject to horizontal illumination (from front of aquarium). Two days.

(1) No. of specimens—19 (two failed to burrow). Fourteen specimens directed their crowns towards the light. Four specimens directed their crown laterally and towards the light.

Angular deviation from the vertical towards the sides of the aquarium:

Aggregate 190° right, 190° left. Mean 0°

Angular deviation from the vertical towards the front and rear of the aquarium:

Aggregate 630° front, 0° rear. Mean 37° front

(2) Specimens building new tubes in total darkness. 3 days. No. of specimens—19 (1 failed to burrow). Branchial crowns pointed randomly in all directions.

Angular deviation from the vertical towards the side of the aquarium:

Aggregate 200° right, 140° left. Mean 3·3° right

Angular deviation from the vertical towards front and rear of the aquarium:

Aggregate 120° front, 295° rear. Mean 9·7° rear

(3) Specimens subject to horizontal illumination for five days after previous sojourn in darkness (same specimens as in (2) above). No. of specimens—17. Eleven specimens directed their crowns towards the light (front of aquarium). Four specimens directed their crowns to rear of aquarium. One specimen directed its crown to one side.

Angular deviation from the vertical towards the side of the aquarium:

Aggregate 80° right, 230° left. Mean 8·3° left

Angular deviation from the vertical towards the front and rear of the aquarium:

Aggregate 460° front, 90° rear. Mean 22° front

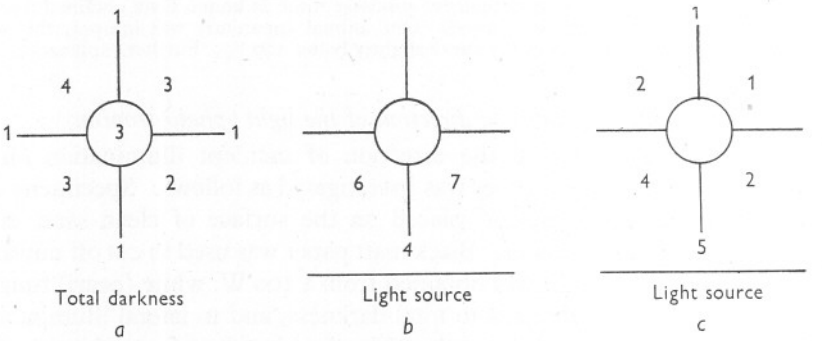

Fig. 6. Diagrammatic representation of the effect of light on direction in which tubes point. The figure in the central circle represents the numbers of animals that directed their tubes and branchial crowns vertically upwards. The figures opposite each radius represent the numbers that directed their crowns and tubes towards the left, right, front or rear of the aquarium. The figures in each quadrant represent the numbers of animals that inclined their tubes and crowns in that direction. It is to be noted that rarely is a tube bent so that it is parallel to the ground; the mean angular deviation from the vertical is given above. A horizontal line beneath the diagram represents the relative position of the light source. (*a*) Total darkness for 3 days. (*b*) Horizontal unilateral illumination for 2 days. (*c*) Horizontal unilateral illumination for 5 days after previously being in the dark for 3 days.

There is definite evidence from these experiments that *Branchiomma* directs the distal portion of its tube and, in consequence, its branchial crown towards the light. Specimens kept for 3 days in total darkness built new tubes which inclined randomly in all directions, but predominantly upwards (Fig. 6*a*). Specimens kept for 2 days in an aquarium illuminated from one side built

new tubes, all of which inclined towards the light. The mean deviation from the vertical towards the light source (90° to the vertical) was 37° (Fig. 6*b*). Finally, specimens which had been in the dark for 3 days, were subjected to unilateral illumination for 5 days. At the end of this period 69 % of the specimens were pointing towards the light, and the mean deviation from the vertical towards the light source was 22°, an increase of 37 % and 31·7° for unilateral deviation over corresponding values for previous sojourn in darkness (Fig. 6*c*). It is concluded that *Branchiomma* tends to direct the exposed extremity of its tube towards the light when building a new tube, and can alter the direction in which the tube points, to conform to a change in the direction of incident illumination.

Discussion

There is no lack of explanation for the value of the withdrawal reflex to tubicolous polychaetes. Jenkins (1940, p. 479) summarizes the prevalent concept when he says: 'It is a common observation that various species of flatworms, annelids and nematodes respond in characteristic fashion to sudden changes of intensity....For instance, the tubicolous annelids, such as *Hermella ascolata* [Sabellariidae] usually retract the tentacles into their tubes with the onset of shadows. This is probably a type of anticipatory response, as if to shadows cast by carnivorous swimming animals.' (cf. Buddenbrock, 1928, p. 12). Known enemies of tubicolous polychaetes are certain species of flatfish, notably the lemon dab (*Pleuronectes microcephalus*) and the sole (*Solea vulgaris*) (Steven, 1930; Wilson, 1935). The evidence is presumptive that they would feed upon *Branchiomma vesiculosum* when available. All stimuli to which *Branchiomma* responds by a withdrawal reflex, namely touch, mechanical vibrations, and decrease in photic intensity, could be token signals of the approach of a predator. In this regard the animal's sensitivity to a moving shadow or intensity change is of particular interest. To a sudden decrease in intensity the animal soon adapts itself, but adaptation to a moving shadow, in general, is considerably slower. Predation involves movement, and it is of advantage to the animal to maintain considerable sensitivity to a token stimulus of a predator's approach. On the other hand, tidal movements and currents in the lower littoral and sublittoral zone can create conditions in which there are regular and repetitive changes of light intensity and, accordingly, photic stimuli without biological significance to the animal. Presumably, adaptation represents a compromise between two conflicting needs of the organism, withdrawal to escape from enemies, and maintained expansion for feeding and respiration. Adaptation also occurs to certain qualities of mechanical stimuli, namely water currents and vibrations; the proportion of animals that respond is greater, and the course of adaptation is slower, than to photic stimulation. Adaptation, apparently, does not occur to tactile stimuli (above the levels of muscular and nervous fatigue). These mechanical

stimuli have greater biological significance and urgency to the animal, in terms of survival value.

For the animal, normally living in its tube, the steady or slowly varying intensity of illumination is apparently without significance in daily behaviour. *Branchiomma* expands its branchial crown in light or darkness in contrast to *Sabella* which is nocturnal (Fox, 1938). This may explain why the light reflex is more highly developed in *Branchiomma* than in *Sabella*, two closely related species living side by side in practically the same niche. The light reflex has greater biological value to *Branchiomma*, which feeds in the daytime, than to *Sabella*, which tends to stay withdrawn during the day. Moreover, the reflex is more efficacious in strong light: a greater proportion of animals respond and a smaller intensity change produces a response at greater light intensities (in these experiments, intensities above about 80 lux were most effective).

It is not certain to what depths in the sublittoral zone *Branchiomma* descends. Locally, in the Salcombe estuary (South Devon), it is found on the lower shore at low spring tide level, and slightly above. The tidal range in this estuary is 17·3 ft. (Evans, 1947). Absolute values for submarine light intensities are not available for the Salcombe estuary, but Atkins (1945) has summarized information for coastal and inshore waters near Plymouth. At a depth of 5 m., transmission of light would be reduced to about 10 % of subsurface illumination. This would permit bottom illuminations of about 5400 and 1800 lux at high-water springs on clear days in June and December respectively. Higher intensities would be encountered of course as the animals approached emergence during low water. In somewhat turbid water maximal transmission occurs in green light, and transmission decreases somewhat in the blue, and markedly in the red (Atkins, 1939, 1945; Atkins & Poole, 1940). In conjunction with this information we may observe that *Branchiomma* is sensitive to light in all parts of the visual spectrum (blue to red, 4000–7000 A.), but is more sensitive to light of short and medium wave-lengths, than to red light.

Most workers on the behaviour of tubicolous polychaetes have considered only the withdrawal or giant axon reflex. This reflex must have considerable survival value in terms of predation-pressure. Light can be one sensory modality eliciting this response, but for various sabellids and serpulids, light influences the character of other responses as well. Protrusion of the branchial crown in light and darkness has already been considered; the influence of light on this activity varies in two species of sabellids (*Branchiomma* and *Sabella*). The orientation of the branchial crown and anterior end of the tube towards the light would ensure that the feeding organs were directed towards the open, when the animals were in confined surroundings. This response is of particular interest since the effectors concerned in orientation of the tube appear to be glands in the body wall (Loeb, 1906; Fox, 1938). Finally, *Branchiomma*, divested of its tube, executes locomotory movements in which light has a directive value, and which lead it into darker regions.

SUMMARY

In *Branchiomma vesiculosum* decrease in light intensity causes the animal to contract and withdraw into its tube. A decrease, never an increase, in illumination is the effective stimulus. When repeatedly stimulated the animals quickly become adapted to intensity changes and no longer respond.

The minimal effective intensity change has been determined for a range of intensities. $\Delta I/I$ is found to increase in low light intensities, and to be fairly constant in intensities over 50 lux. The animals are least sensitive to red light; sensitivity increases in shorter wave-lengths.

Animals show considerable sensitivity in weak light. They respond to intensity changes in illumination at least as low as one-third of a lux. Animals kept under undisturbed conditions show enhanced sensitivity and responsiveness. Frequent stimulation raises the stimulation-threshold and establishes a lasting state of habituation.

Animals respond both to a sudden diminution of illumination and to a moving intensity change. Adaptation to the former does not necessarily abolish response to the latter, which shows an independent course of adaptation.

Branchiomma protrudes its branchial crown in light and darkness.

Tubes and branchial crowns are directed towards the light (positive phototropism).

Branchiomma, removed from its tube, shows negative orientation to light in its locomotory movements (retrograde creeping). Animals congregate in dark places.

The sensitivity and responses to light are discussed in terms of the life habits of the animal.

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THE REPRODUCTION AND LARVAL DEVELOPMENT OF *NEREIS DIVERSICOLOR* O. F. MÜLLER

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(Plate I and Text-figs. 1–13)

CONTENTS

Introduction

It is somewhat surprising that although *Nereis diversicolor* O. F. Müller is one of the commonest of all shore polychaetes in the British Isles and north-western Europe, its early development has hitherto been unknown. The species has, however, attracted considerable attention and many divergent views have been expressed about its reproductive habits.

The present paper presents a reasonably complete account of the larval life history, and also a discussion of the diverse views expressed about various aspects of its reproductive habits.

The most interesting points discussed, apart from the development of the larvae in the mud, are the existence of a form of pseudo-copulation, the absence of an epitoquous stage, and the general absence of the phenomena of hermaphroditism (Mendthal, 1889), parthenogenesis (Schultze, 1856; Herpin, 1923*a*, 1925, etc.), and viviparity (Schröder, 1886; Gravier, 1905; Benham, 1910; MacGinitie & MacGinitie, 1949) previously attributed to the species by these authors.

I am glad to have this opportunity of expressing my thanks to Dr G. E. Newell, of Queen Mary College, for the original suggestion of the subject of this work and for constant encouragement and help during its progress, and to Dr J. E. Forrest, of Queen Mary College, for kindly reading the typescript.

Methods

All observations on breeding habits, unless otherwise stated, were made on a single population at Chalkwell, Essex, on the north side of the Thames Estuary, and the larvae figured and described were collected from the same part of the beach, which for convenience was near the upper limit of the intertidal flats.

Artificial fertilizations were successfully carried out by opening the coeloms of males and females and mixing the ripe gametes in shallow glass dishes. A minimum admixture of blood was obtained by slitting or puncturing the body wall at the bases of the parapodia, where it is relatively thin. The oocytes did not spurt out under pressure of the coelomic fluid on puncturing the body wall as in many polychaetes, and fairly extensive slitting was found necessary to obtain an appreciable quantity of oocytes. Sperm was more easily obtained, and sufficient quantity to fertilize a Petri dish full of oocytes could be obtained by pricking a single parapodium. Surplus sperm was washed off the oocytes after fertilization had taken place. Decantation was relatively easy as the oocytes are appreciably heavier than sea water. The fertilized eggs were found to develop well, as far as young chaetigerous larvae, if allowed to remain in shallow dishes in which the sea water was changed daily, no further attention being required.

Larvae were obtained from the mud by digging trenches through areas in which the worms were most numerous, stirring the sea water which percolated into the trench, well rinsing the overturned mud containing the adults back into the trench, and then passing this water through a fine silk net. This method which has been used to collect larvae of other polychaetes, is described by Newell (1949), and is fairly efficient when the larvae are numerous. On return to the laboratory, the water containing the larvae was poured out into Petri dishes and the silt allowed to sediment out. The larvae were then searched for under a binocular microscope, and picked out with a fine pipette.

Drawings were made with a camera lucida, those of larvae having been made from typical living specimens temporarily narcotized with a drop of 8 % magnesium sulphate and examined without a cover-glass. When larvae are left in this fluid for some time, the cilia continue to beat for about 10 min. after the larvae have ceased other movements, so that the ciliary tracts may be made out fairly well. If not allowed to remain too long in the narcotic, larvae were found to revive completely when replaced in fresh sea water.

Permanent mounts of larvae either unstained or stained with borax or alum carmine in euparal or balsam revealed no more anatomical detail than in the living state. However, details of such structures as the jaws and chaetae could be seen more easily in benzyl alcohol. This medium was found most satisfactory for examination of fixed, unstained larvae, providing these were not left too long in the fluid before examination.

The larvae fixed well in 5 % formalin in sea water, after being narcotized in 8 % magnesium sulphate. They were allowed to remain in the formalin for about 2 days, and were then transferred and stored in 30 % alcohol.

Sections of adults were cut at 8 and 10 μ, after fixation in cold Bouin's fluid, and stained with Ehrlich's haematoxylin with eosin as a counterstain.

The beach temperatures shown in Text-fig. 11 were recorded by a combined maximum-minimum thermometer lying at a depth of about 10 cm. in the mud, and protected by a heavy brass cylinder loosely plugged with cotton-wool at each end.

Reproduction

Sex Ratio

McIntosh (1907), at St Andrews, found that the great majority of individuals examined in December were females; and Dehorne (1925) also notes that the number of females is greatly in excess of the males. Schröder (1886) found three males in a sample of forty-eight (6·25 %), and Herpin (1925) found the ratio of males to females at Cherbourg to be 1 : 7 (about 14·3 %). Durchon (private communication), on the other hand, reports the males to form as much as 30 % of the population at Luc-sur-Mer. It is this scarcity of males which has been partly responsible for the suggestion that the worm reproduces parthenogenetically. It would appear from these references and from numerous observations made by the writer that this predominance of females is probably universal.

The proportion of males to females naturally varied in any one sample taken during early spring, and this was probably due to the samples being too small, since owing to the relative scarcity of the males comparatively large samples have to be taken to obtain a significant result. It is also possible that the proportion of males to females is different in different localities. At

Chalkwell, in various samples taken before spawning had taken place the percentage of males varied between 1 and 10 (3 in 35, 5 in 153, 3 in 218, 4 in 109, 9 in 138).

Differentiation of the Sexes

In the autumn the sexes are externally indistinguishable, although by October the coeloms of the females contain small oocytes and the sexes may be determined by slitting open the body cavity. The oocytes at this stage are rather small (100 μ) and cannot be seen without the aid of a good lens.

In summer and autumn all the worms assume a reddish brown colour, but in early spring become bright green. The mature males have a bright grass-green colour and may thereby be distinguished from the females, which have a much darker green colour which is often lacking on the ventral side at this stage. The ripe males, that is, males containing free sperm, are completely green, and the red and brown pigments, which are usually still recognizable in the ripe female, cannot be seen in the male. The white mass of sperm which by then packs the coelom of the male gives the sex its lighter green colour, and when the sperm has been shed the males are appreciably darker in colour.

Apart from colour differences, the mature female may be recognized on the shore by slightly stretching the animal between the fingers when the oocytes, which by then are quite large (200 μ) and visible to the naked eye, may under favourable conditions be seen moving with the coelomic fluid.

In many nereids the males when mature may be distinguished by the development of an anal rosette, the sperm being discharged through the anus after histolysis of the gut (Gravier, 1923 *a*). This does not appear to be so in *N. diversicolor*, and no anal rosette could be distinguished in mature or spawned males.

Changes Occurring at Maturity

Most recent authorities agree that *N. diversicolor* is typically atoquous. Changes, or instances of partial metamorphosis (i.e. change of body form as a preliminary to spawning usually resulting in a free-swimming epitoquous or 'heteronereid' phase) which have been described may be regarded as atypical or exceptional; while the occurrence of completely epitoquous forms ascribed to this species is probably due to a confusion of species. These problems are considered in more detail in the discussion.

Although the process of metamorphosis of normal individuals into an epitoquous form is normally lacking in *N. diversicolor*, some well-marked changes do, however, occur. Thus, early in the development of the female germ cells, the coelom becomes filled with a large number of coelomic corpuscles which eventually come to form a very loose parenchyma or pseudo-tissue. Claparède (1868) was one of the first to comment on this phenomenon which since then has received attention from several workers, especially Romieu (1921 *a*, *b*), Dehorne (1922 *a*, *b*, 1924, 1925), Herpin (1921, 1925) and

Thomas (1930*b*). McIntosh (1907, 1910) also refers to the formation of this loose 'ovigerous tissue' as being possibly derived from the dorsal organ of Goodrich, and becoming attached to the vessels and the bases of the parapodia. He also notes an increase in the vascularity of the gut in December and that, when the oocytes become free in the coelom, masses of coarsely granular cells appeared sometimes in lobular masses in the region of the dorsal ciliated organ. He considered these masses of cells to be correlated with the growth of the oocytes. Herpin (1925) found, in individuals in which the sexual products were in an advanced state of development, that the coelomic corpuscles (*éléocytes*) contained fusiform bodies which were in fact fragments of muscle fibre. These *éléocytes* (he remarks) evidently have the same role as in nereids, which metamorphose at the breeding season into 'heteronereids', that is, in becoming actively phagocytic and digesting the muscle which undergoes histolysis towards maturity. This phenomenon has been studied by Romieu and Dehorne primarily in *Perinereis cultrifera*, but also in *Nereis diversicolor*. In the four papers mentioned above, Dehorne made a close study of these changes and found that there was no doubt that the spindle-shaped bodies in the phagocytes were in fact muscle fibres. He pointed out (1922*a*, *b*) that this process of phagocytosis is probably not due to a precocious invasion of the tissues by the phagocytes, but that it is more likely a result of the muscle fibres breaking up spontaneously, and their fragments then being taken up by the cells. This process is carried out over a fairly prolonged period, and the phagocytes may be regarded as specialized coelomic corpuscles.

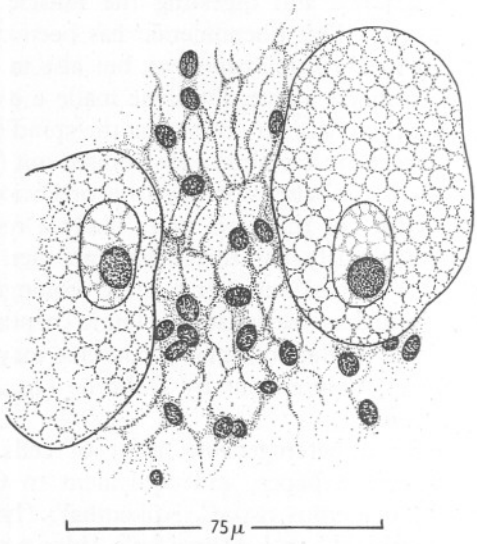
Two phases of activity of the coelomic corpuscles may therefore be distinguished. These phases, pointed out by Dehorne (1924), were identified in the Chalkwell population.

(i) Coelom filled with a heterogeneous mass of cells. (Referred to as 'parenchyma' in the present paper, and equivalent to Claparède's 'tissue connectif', McIntosh's 'ovigerous tissue', Kükenthal's 'lymphoiden Zellen', Heinen's 'Protoplasmaschicht' and Schneider's 'blasigen Gewebes'.) The formation of this loose parenchyma is presumably correlated with the development of the female germ cells, for its cells appear to be largely responsible for the deposition of yolk in the oocytes (Kükenthal, 1885; Schröder, 1886; McIntosh, 1907, 1910; Herpin, 1925; and also in *Perinereis cultrifera*; Romieu, 1921*a*, *b*). According to Dehorne the nuclei of the oocytes during this early stage are rather irregular in shape, and most of the coelomic corpuscles remain in the region of the dorsal ciliated organ. The muscles remain intact.

(ii) This loose coelomic parenchyma disappears. The mature oocytes come to fill most of the coelom, and histolysis of the muscle layers begins. The nuclei of the oocytes are now spherical and the coelom contains, apart from the oocytes, fragments of muscle fibre and phagocytes.

This gradual digestion of the muscle layers by the phagocytes enables the

oocytes to be released by the splitting of the body wall, which has become very thin by the time that spawning is ready to take place. In the specimens of *Nereis diversicolor* from Chalkwell, however, the degree to which histolysis had proceeded at the onset of the spawning period was rather variable, and was not readily detected even in some apparently mature females. Generally, however, the worms were abnormally fragile in early spring some time before spawning, and this was presumably due to the histolysis of the body-wall muscles described above. Sections of some adults showed almost complete histolysis in some instances, but in others reduction in the muscle layers was hardly noticeable. The appearance of the coelom during these various phases is shown in Text-fig. 1, and Plate I, figs. 1, 3–5. Histolysis of the muscle layers is also referred to by McIntosh (1907, 1910).



Text-fig. 1. Young coelomic oocytes. Young oocytes are seen imbedded in the parenchyma.

Thieren (1909) concluded that this histolysis is caused by unfavourable conditions and insufficient oxygen supply, and that breaking down of the tissues occurs where the oxygen consumption is normally highest; and also that this, in *N. diversicolor*, facilitates spawning before the assumption of an epitoquous stage is completed by the individual. He suggested that histolysis may also be caused by internal secretions, or as a corollary of normal metamorphosis. Thieren's suggestion, however, that spawning takes place before metamorphosis into an epitoquous stage has begun, thus explaining the atoquous habit, cannot be supported since no further change appears to occur in unspawned individuals in which the oocytes eventually break down, and which usually die off before the next winter without showing any signs of

metamorphosis. Dehorne (1922*b*), indeed, concludes that as phagocytosis occurs in *N. diversicolor* which is atoquous, the process may be regarded as independent of metamorphosis.

In the male, the first phase in the activity of the coelomic corpuscles, that is the formation of a loose parenchyma, is of very short duration, and this supports the hypothesis that the formation of the coelomic matrix in the female is concerned mainly with the growth of the oocytes and the deposition of yolk. On the other hand, histolysis occurs in the male as well as in the female, and often appears to be taken much further in the male. The relation of this to spawning is discussed below.

Colour Changes

The colour change occurring at maturity is one of the most interesting aspects of the reproduction of this species, and has been noted by several previous workers (Mendthal, 1889; de St Joseph, 1906; McIntosh, 1907, 1910; Herpin, 1923*a*, 1925; Dehorne, 1925; Thomas 1930*a*).

Mendthal considered this green colour to be due to a diet of green algae. McIntosh, however, who also found green females in January, rejected this explanation and concluded that this colour was due to the presence of 'pale greenish ova', yet he states that the sexes are not always distinguished by colour differences and reports finding both males and females of a greenish or dull yellowish colour, of which the males were usually paler. McIntosh offers no explanation of the cause of the coloration in the male sex; but his general observations on the slight colour differences between the sexes are in accordance with the observations made at Chalkwell.

The coloration of *N. diversicolor* is being investigated, and as it is hoped to publish the results separately, only a brief outline of the process of colour change is given here. In either sex the assumption of the green coloration occurs about the same time as the onset of histolysis, the phagocytes in the coelom being richly charged with granules of a bright green pigment which later becomes deposited under the cuticle. This general green colour is apparently correlated with maturity, and at Chalkwell the percentage of green worms rose steadily to practically 100 % just after the main spawning period, afterwards dropping steadily during early summer. In December, for example, only a very few green worms were found; in late February and March, on the other hand, practically all the worms were green; while by the end of May only very occasional specimens bore traces of green pigment. Such individuals were invariably found to contain mature oocytes in contrast with those with a reddish brown colour, which were either empty or contained a milky fluid formed from broken-down oocytes. This correlation was found to be statistically significant. The females appear to lag behind the males slightly in assuming the green colour. No support was found for the explanations of the presence of green pigment made by Mendthal or McIntosh.

It is also interesting to note here that *N. japonica* which appears to be closely related to *N. diversicolor*, and with which it was originally confused, also becomes green at maturity (Izuka, 1908), although, unlike *N. diversicolor*, *N. japonica* possesses an epitoquous phase.

Maturation and Structure of the Oocytes

Schröder (1886), Mendthal (1889), Schneider (1902), and Heinen (1911) agree that the female sex cells arise in the ventral region of the body in relation to the ventral vessel and between the bases of the parapodia, and it was confirmed that the germinal epithelium appears to proliferate in the ventral part of the coelom in the septal region in the worms collected at Chalkwell. The cells which eventually divide to form the female germ cells, however, break loose into the coelom at a very early stage.

TABLE I. MEASUREMENT OF OOCYTES

Size (μ)	Sept. 1949	Oct. 1948	Nov. 1948	Dec. 1948	Jan. 1949	Feb. 1949	Mar. 1949
0–25	—	—	—	—	—	—	—
25–50	—	—	—	—	—	—	—
50–75	3	4	—	—	—	—	8
75–100	6	5	—	—	—	—	1
100–125	28	32	—	—	—	—	—
125–150	13	19	—	—	—	—	—
150–175	8	56	32	8	—	—	—
175–200	—	7	46	41	4	5	4
200–225	—	1	21	46	38	14	11
225–250	—	—	5	7	80	59	51
250–275	—	—	—	—	19	24	17
275–300	—	—	—	—	1	17	9

McIntosh (1907, 1910) noted that the size of the oocytes was somewhat variable, but these oocytes from St Andrews were much smaller than those collected from Chalkwell. McIntosh gives the diameter of a mature oocyte as 152·4 μ. Herpin (1925) found the maximum oocyte size to lie between 200 and 250 μ, and emphasizes that the size variation is much more variable in *N. diversicolor* than in other nereids, noting that the mature oocytes may have a diameter of less than 200 μ. This is confirmed by Durchon (private communication), who found the diameter to vary between 190 and 240 μ. The size of the mature oocytes at Chalkwell varied between about 200 and 275 μ in diameter, the mean oocyte size at the time of spawning being about 220 μ. The actual range in size of coelomic oocytes is shown in Table I.

The coelomic germ cells in the female are first recognizable in young worms about 7 cm. in length, when they are at least 6 months old. Dehorne (1925), it is true, found oocytes free in the coelom of worms only 5 cm. in length, but it is likely that these would actually appear longer if measured after narcotization with 10 % magnesium sulphate as here employed.

Apart from the first few segments in the pharyngeal region and the most posterior segments, oocytes may be found throughout the length of the body.

At Chalkwell, samples of worms were taken throughout the year and about twenty specimens randomly selected. A few oocytes were taken from each, and about 100 measured. The range in size is shown in Table I. The mean oocyte size was calculated and was found to increase steadily over the winter months, reaching a constant maximum size rather before the main spawning period. This provides a useful method of prediction of spawning time, as pointed out by Newell (1948, 1949). Oocytes were found in the coelom from early September to early May, but were absent during the summer months.

When mature, the oocytes come to fill the main body cavity and the spaces in the parapodia, frequently becoming crushed together. On slitting open the coelom of a mature female the oocytes which are released are often dented and rather irregular in outline through being crammed together, but when not dented are practically spherical. On contact with sea water they quickly round off. They are a very pale straw colour, and not pale green as noted by McIntosh (1907). A large central germinal vesicle is surrounded by a highly granular cytoplasmic area composed of rounded yolk globules (Text-fig. 1).

The larger oily droplets observed in some other species of *Nereis* (E. B. Wilson, 1892; Herpin, 1925; D. P. Wilson, 1932, etc.) are not visible in *N. diversicolor*. This may be correlated with the typical bottom development of the larvae of this species, since these droplets appear to occur in typically pelagic nereid larvae.

After the spawning period has passed, the oocytes in the females which have not spawned gradually break down into a white milky mass in the coelom, the observations made by the writer being in accordance with those made by McIntosh (1907). Oocytes remain in the coelom for nearly 2 months after the main spawning period before finally breaking down. Thomas (1930*b*) found that the oocytes were invaded by a chromolipoid pigment, the cytoplasmic constituents disappearing, the corpuscles becoming actively phagocytic, and surrounding the degenerating oocytes during this process.

Maturation and Structure of the Spermatozoa

In the male the loose parenchyma is transitory, and the sperm mother cells, which presumably originate from the coelomic epithelium in much the same position as the oocytes, break away into the coelom in small groups. These 'sperm plates' as they may be called, are very characteristic flattened groups of cells found in many polychaetes, though differing much in size and appearance in different species. In *N. diversicolor* at Chalkwell they were found in the coelom from December until February. The number of cells in each plate or disk increases with age, but free spermatozoa are not formed until the normal breeding season is reached. The young sperms acquire their tails while still attached to form a sperm plate, but soon after they break away

into the coelom. Males containing mature sperm were found for some 2 weeks before spawning apparently took place.

The ripe spermatozoan (Text-fig. 4) bears a sharply defined acrosome anteriorly, and a tail about 40 μ in length posteriorly.

Parasites

In a very large proportion of the males found at Chalkwell the coelom was found to contain quantities of a single form of unidentified ciliate which apparently fed on the spermatozoa. The amount of sperm left by the time the spawning period was reached was negligible in some instances, and in these the general body cavity and parapodial spaces were crammed with ciliates.

Spawning Mechanism

Unfortunately, in spite of much observation, spawning was observed neither under natural conditions on the shore, nor in the laboratory.

There are theoretically four ways in which the germ cells may be released from the coelom: (1) through the nephridia; (2) by the coelomic ducts (ciliated organs) acquiring openings to the exterior during the breeding season; (3) through the anus after histolysis and perforation of the gut; (4) by rupture of the body wall.

Release of the Oocytes

The first of these methods was maintained by Mendthal (1889), though the oocytes are manifestly too large for it to occur. Regarding the second method, Benham (1910) suggested that the ciliated organs might acquire openings to the exterior, but this may be discounted in light of recent work by Goodrich (1945). Goodrich, however, was obviously not convinced or did not realize that *N. diversicolor* is atoquous, since he suggested that atoquous nereids might have functional ducts. This has not been found to be so. Regarding the third method, it may be assumed that it is extremely unlikely that oocytes would ever be discharged through the anus. Release of the oocytes by rupture of the body wall has been observed by Herpin (1925), who describes the shedding of oocytes as being preceded by contraction of the posterior end of the body. McIntosh (1907) also expresses the opinion that they are shed by this means, and this is confirmed by Durchon (private communication).

Emission of the Spermatozoa

As in the female there is no evidence that the ciliated organs acquire openings to the exterior, nor is there any evidence that the sperm is discharged through the anus, since spawned males appeared to have the gut intact, showed no sperm in the gut, and lacked the anal rosette which is developed in *Perinereis*

marionii (Herpin, 1923*a*; Gravier, 1923*b*), *P. cultrifera* (Herpin, 1923*b*; Gravier, 1923*a*; Gravier & Dantan, 1928) and other species.

As a few spawned males which showed no signs of damage to the body wall were found in late February, the sperm is almost certainly discharged through the nephridia, though in some instances emission may accidentally occur by rupture of the body wall.

General considerations

In the laboratory, apparently, fully mature females could not be induced to spawn in the presence of males, whether placed in glass dishes or in the aquarium in fresh sea water under various conditions of light and temperature; nor in the presence of motile sperm from ripe males. Conversely, ripe males could not be induced to emit sperm when placed together with ripe females, ripe oocytes, or in 'egg-water' from crushed ripe oocytes. Other workers seem to have been rather more successful in this respect with this somewhat temperamental species. Herpin (1925) watched ripe females spawning under laboratory conditions. Just (1940) also found at Roscoff that mature individuals released their gametes into dishes in the laboratory during January and February, and this writer was apparently successful in making artificial fertilizations with these naturally spawned gametes, and in rearing the larvae for 3 months afterwards. Unfortunately, no details are given of the subsequent development, nor is it stated whether the males and females spawned in separate dishes or together, or how this spawning actually took place.

Under natural conditions Dehorne (1925) described a kind of copulation or sexual congress, in which several females were found coiled round a single male. Müller (1771, see Dehorne, 1925) had also apparently seen tangled masses of worms under stones and compared them with tangled masses of macaroni. Dehorne regards this observation of Müller's to have been similar. Herpin (1925) also found males and females coiled or knotted together posteriorly and more or less agglutinated with mucus on the surface of the mud, a condition known locally as 'Roi de rats'. This knotting together is not, of course, specifically related to reproduction, and may be observed in the laboratory whenever too many individuals are confined together in a tank, and Durchon (private communication) also concludes that this is probably a purely accidental phenomenon. Herpin supports Dehorne's conclusion that a form of sexual congress occurs in which clusters of females come to surround a single male. Herpin concludes that the ripe females swim in search of the males during the night, and that a tangle of females forms round each male, the oocytes being gradually released and fertilized by the sperm emitted by the male.

Dehorne (1925) also mentions that the females are positively attracted by the secretions of the male, and that when in contact provoke the emission of sperm. He points out that usually, as in epitoquous nereids, it is the males

which stimulate the females to release their oocytes, but here, owing to the rarity of the males, the reverse seems to occur. Thorson (1946) states that it may be regarded as a general ecological rule that it is the males which stimulate the females, but he notes that there are exceptions. Galtsoff (1940), for example, found in *Gryphaea virginica* that though chemical stimulation was specific for females, this was not so for males. Townsend (1939), confirming the 'fertilizin' theory of Lillie, and Just (1930*a*, *b*) found that the reaction of the male of *Nereis limbata* was extremely specific to glutathione which is present in the unfertilized oocyte, and this appears to be fairly general, though no experiments appear to have been performed on *N. diversicolor*. Although Dehorne concludes that this species is an exception to the general rule in relation to the comparative rarity of the males, it does not necessarily follow from this fact that it is the females which seek out the males and prompt spawning. It may well be that having come in contact with a male by chance or by attraction by some other stimulus, it is the male which actually initiates the simultaneous emission of the gametes.

Conditions Governing the Time of Spawning

At Chalkwell, spawning took place in 1949 within 2 weeks centred around the third lunar quarter in late February. At this time both males and females had apparently been mature for about 2 weeks. At the time of spawning a sharp rise in temperature occurred. Authorities seem to differ as to the actual time of year when spawning takes place, but this is discussed later.

The fact that the spawning period centred round the third lunar quarter is interesting in that it is at this phase that many epitoquous nereids spawn. Whether this is in fact a lunar effect, in *N. diversicolor*, is not known, and can only be determined after study for a number of years. This problem has been given much attention by Fox (1932) and by Amirthalingham (1928), who concluded that apparent correlation with lunar phase was due to several practicably inseparable effects. It is worth noting, however, that Newell (1948) found a correlation with a lunar phase at which spawning took place over a sharply defined period, in the common lugworm *Arenicola marina*, whose habitat is not widely different from that of the species under consideration.

Although factors relating to the lunar effect may possibly be correlated with the growth of the gametes, the actual stimulus required to initiate spawning is frequently the attainment of a definite threshold temperature or temperature change (Orton, 1920; Thorson, 1946). At Chalkwell, as already mentioned, spawning took place at a time when there was a marked rise in temperature, and may have been stimulated in this way. The temperature during the week when the main spawning took place varied between 5 and 8·8° C.

From a study of size distributions of adult populations obtained from various stations on British coasts, it may be concluded that spawning generally takes place in early spring, and the fact that McIntosh found spawning to take

place in east Scotland about a month later than the writer found in southern England again suggests that a threshold temperature may be the factor initiating spawning.

Duration of Spawning Season

The variability of the reproductive habits within a single species of nereid is notorious, and this, together with the possibility of confusion of the species of *Nereis* to which the various larvae have been ascribed, makes it difficult to assess the value to be attached to reports of *N. diversicolor* larvae occurring at widely different seasons of the year. Information from various sources which throw light on these points is summarized in Table II.

TABLE II. BREEDING PERIOD OF *NEREIS DIVERSICOLOR*

Author	Locality	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Present paper	Chalkwell, England	O	O, S	O, L	O, L	—	—	—	—	O	O	O	O
McIntosh	St Andrews, Scotland	O	O	O, S	—	—	—	—	—	—	O	O	O
Thamdrup	Skallingen	—	—	O	O	O	O	O	—	—	—	—	—
Just	Roscoff	S	S	—	—	—	—	—	—	—	—	—	—
Smidt	Copenhagen	—	—	—	L	L	L	L	L	L	L	L	—
Herpin	Cherbourg	S	S	S	S	S	S	S	S	S	S	S	S
Nunn	Plymouth	—	—	—	O	—	—	—	—	—	—	—	—
Hofker	Zuidersee	—	—	—	—	—	—	L	L	—	—	—	—
Thorson	Øresund	—	—	L	L	L	L	L	L	—	—	—	—
Blegvad	Nyborg	—	—	—	O	—	—	—	—	—	—	—	—
Mendthal	B. of Pillau	—	—	—	—	—	O	—	—	—	—	—	—
Durchon	Luc-sur-Mer	—	S	S	S	—	—	—	—	—	—	—	—

O = oocytes in the coelom; S = spawning; L = occurrence of larvae.

Thorson (1946) points out that the length of the breeding season of any marine organism may depend on three main factors. With reference to *N. diversicolor* these may be summarized as:

(i) Vertical distribution on the shore, with resulting effects, *e.g.*, a graded temperature, so that a possible optimum spawning temperature will be reached progressively later at greater depths.

(ii) Variation in the time taken by populations or individuals to mature.

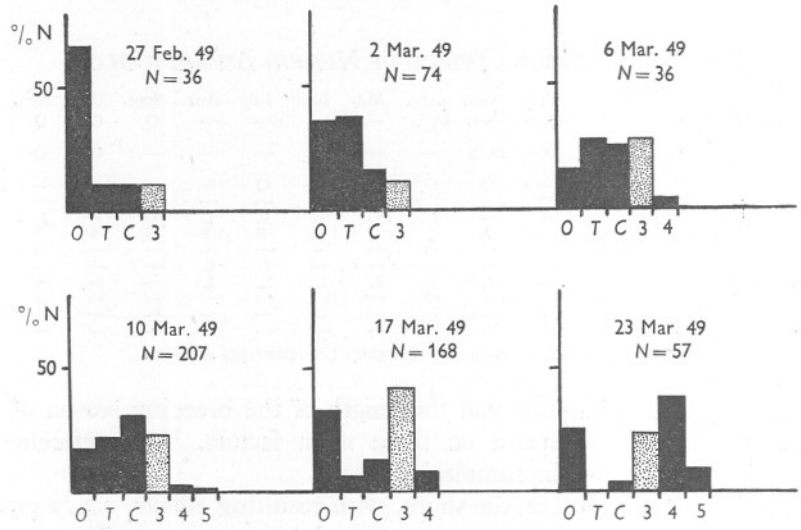
(iii) Repetition of spawning by the same individuals within one season, or protraction of spawning over a period.

The first factor seems most likely to promote an extended breeding season, Herpin (1925) regards this and the variability of habitat to cause spawning to take place all the year round at Cherbourg. Also, if this occurs together with migrations of individuals between the levels, the breeding season may actually be extended at any one locality.

With regard to the second factor, it may be noted that a small number of individuals of both sexes are sometimes slow in maturing. In late summer one or two mature worms may be found, and these may be successful in spawning. Usually these late maturing females are so few that the chance of coming in contact with a ripe male is remote, but the possibility remains, especially when the number of males is relatively high.

The third effect is not found in this species. Individuals die soon after spawning, and unspawned worms may last only the summer, for the length of life does not appear to cover more than one breeding season. Also, in any one worm the gametes are all much in the same state of development, which suggests that the spawning period is restricted. McIntosh (1907, 1910) found females in January and February which he considered to have partially spawned, but these may have been immature worms.

As already noted, spawning at Chalkwell took place between 13 and 27 February, and from that time onwards larvae were obtained from the natural habitat in sufficient numbers to make quantitative counts of the



Text-fig. 2. Histograms of relative numbers of larvae at various stages. *O*, unfertilized oocytes; *T*, trochophores; *C*, early chaetigerous larvae; 3, 4, 5 larvae with three, four or five chaetigerous segments respectively.

various larval stages possible. The numbers of larvae at different stages are represented as percentages of the total on each date, and shown as a series of histograms in Text-fig. 2. These represent counts of larvae taken at 3-day or weekly intervals, up to a month after the main spawning date. Further samples were taken, but these merely show a steady drift along the abscissa. Larvae were not found later, in summer. The diagrams also show that some oocytes continue to be discharged into the sand after the spawning period, but owing to the absence of males or for some other reason, these were not fertilized. In artificial fertilizations unfertilized oocytes retained their original appearance and showed no signs of degeneration for as much as 10 days in fresh sea water, but it seems unlikely that even in the natural habitat oocytes would remain in a healthy state for as long as 5 weeks. Presumably these are released accidentally by unspawned females.

Larval Development

Early Development

Early development seems to follow the general plan already described for other species. Cleavage is spiral and is dextrorotatory, as described by Wilson (1892) for *N. limbata* and *N. megalops*. The thick gelatinous envelopes described in these and other species (Herpin, 1925) are not always present in *N. diversicolor*.

The early development was followed from artificial fertilizations. Fertilization membranes are thrown off between 0·5 and 2 hr. after mixing the gametes (Text-fig. 3). The membrane gradually crumples off the surface of the egg and eventually stands away from its surface at a distance which varied in different fertilizations (Costello & Young, 1939) and with gametes at different stages of maturity.

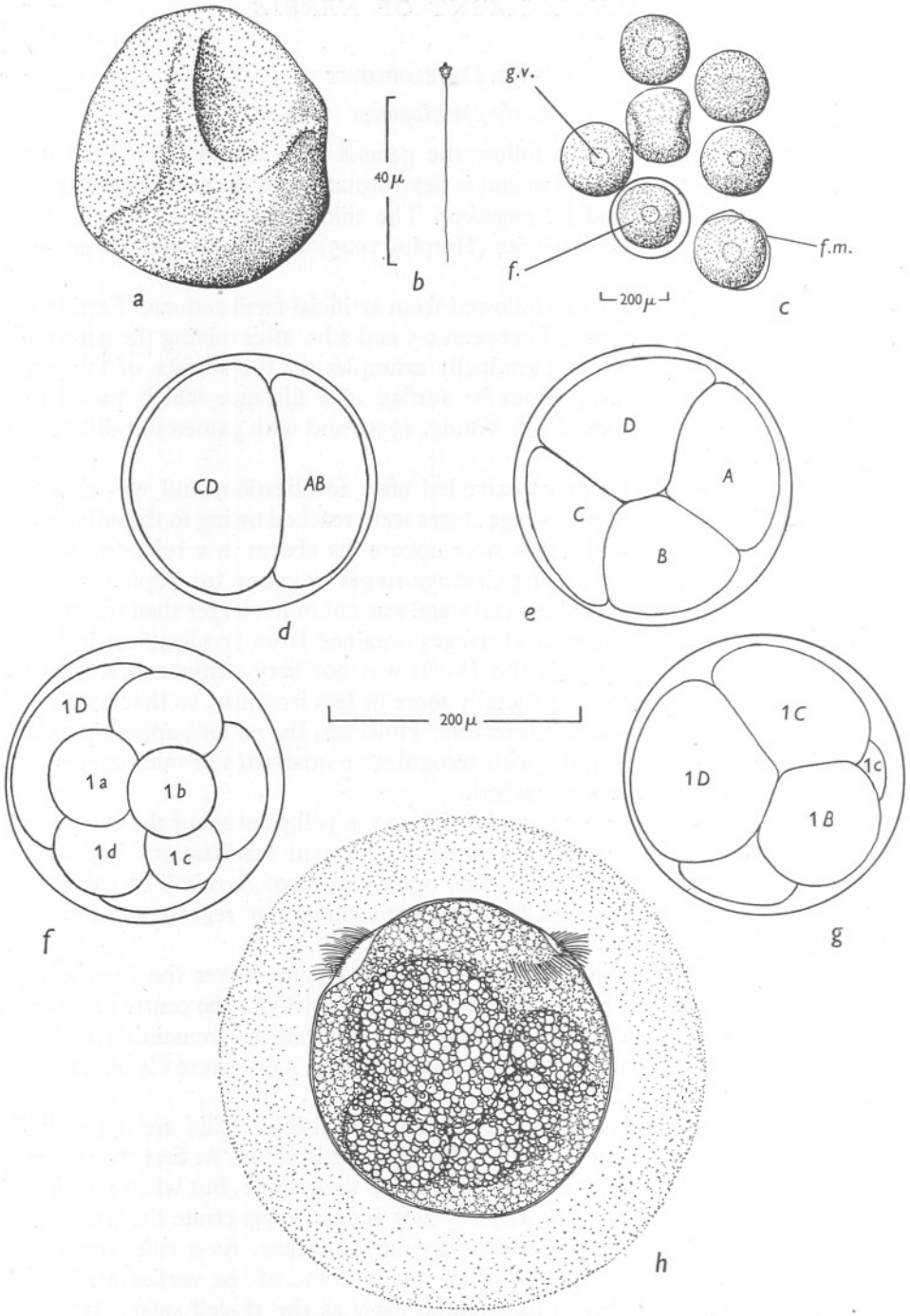
A jelly layer was sometimes extruded after fertilization, and was clearly visible by the time the later cleavage stages were reached owing to the adhering sperm and bacteria. These layers were apparently absent as a rule, and were never seen in nature surrounding cleavage stages or young trochophores.

In cleavage, the *D*-cell of the 4-cell stage was not much larger than the other three blastomeres, and in early cleavages obtained from fertilizations in late January and February (1949), the *D*-cell was not very distinct. Cleavages with immature gametes were generally more or less irregular, so that no well-defined cleavage pattern was discernible. However, the pattern approximated more nearly to the spiral type, with recognizable quartettes of micromeres as the spawning period was approached.

Polar bodies were very small, and owing to the yolky nature of the egg were difficult to detect. Cleavage times varied in different fertilizations but were generally slow, as compared with some other species of *Nereis*. The cleavage stages figured were drawn 20 hr. after fertilization but represent different phases of development.

Quartettes of micromeres became cut off and spread over the remaining megameres which could be seen rather indistinctly lying in the centre of a ball of cells forming the gastrula. The number of megameres remaining varied slightly, and although later larvae had usually only 4, 5 or 6 were visible in the monotrochophore.

When the larva begins to rotate, cilia are not visible. Cilia are not easily distinguishable until about the fourth day after fertilization. At first the rotary movement appears to be inside the fertilization membrane, but when the cilia begin to grow out near the animal pole, they appear to penetrate the fertilization membrane, which then becomes the larval cuticle. As a rule, rotation begins about 3 days after fertilization, but in some of the earlier artificial fertilizations the larvae began to rotate as early as the 16-cell stage. At first rotation is never continued for periods of more than a few seconds, separated



Text-fig. 3. *a*, unfertilized oocyte on release from coelom; *b*, spermatozoan; *c*, spawned eggs (*f*, fertilized egg, *f.m.*, fertilization membrane, *g.v.*, germinal vesicle); *d*, 2-cell stage; *e*, 4-cell stage; *f* and *g*, 8-cell stage, seen from animal and vegetable poles; *h*, young monotrochophore with jelly layer. The scale in the centre applies to all except *b* and *c*.

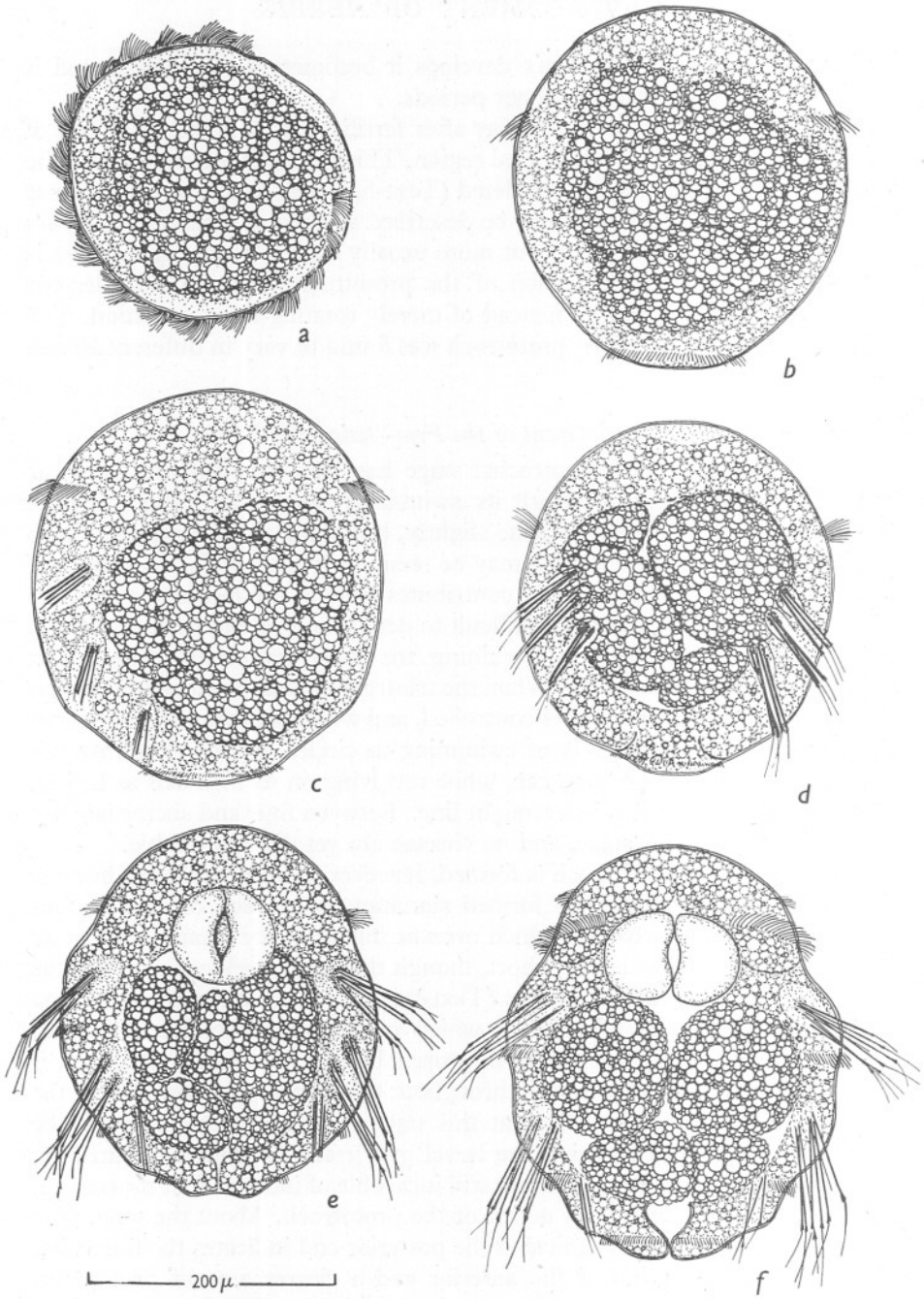
by long pauses, but as the larva develops it becomes more vigorous and is continued over progressively longer periods.

At the beginning of the fourth day after fertilization only one large tuft of cilia may be seen in the prototrochal region. This gradually extends round the larva, but is probably never completed (Text-figs. 3*h*, 4*a*). If a jelly layer is present, the larva, which may now be described as a monotrochophore, breaks through the layer at this stage; but more usually such a 'hatching' process is absent and the gradual extension of the prototroch eventually enables the larva to swim off the bottom instead of merely rotating in one position. The degree of development of the prototroch was found to vary in different larvae.

Later Development of the Free-Swimming Larva

By the time that the monotrochal stage has been reached the larva has become free-swimming, although its swimming powers are rather limited. Soon after this it begins to elongate slightly, becoming more conical in shape and in side view a faint telotroch may be seen (Text-fig. 4*b*). This consists of very fine short cilia and probably contributes little to the locomotory powers of the larva. In many larvae it is difficult to detect, and cannot be seen without narcotization, the prototroch remaining the most important ciliary tract throughout the early larval life. When the telotroch is well developed, however, the swimming is probably better controlled, and whereas previously the monotrochophore was capable only of swimming in circles, by the time that this later stage is reached the larva can, while revolving on its own axis as before, now progress more or less in a straight line. Between four and six megameres can still be seen at this stage, and no chaetae are yet distinguishable.

Very soon after the telotroch is formed, however, chaeta rudiments become visible. Three chaetal sacs are formed simultaneously, each containing four or more rudimentary chaetae, which even at this stage are clearly compound although the distal part is very short, though this quickly elongates when the chaetae project beyond the cuticle (Text-figs. 4*c*, *d*). By the time the first three pairs of bundles of chaetae, which correspond with the first three chaetigerous segments, have come to project beyond the cuticle, the larva is about 10 days old. (Age of larvae throughout this paper is reckoned from the time of fertilization.) Very often at this stage four megameres may still be seen quite clearly, but a cavity, the larval gut, gradually comes to surround them (Text-fig. 4*d*). The chaetae are still incapable of independent movement, and the larva swims mainly by action of the prototroch. About the same time a slight invagination of the cuticle at the posterior end indicates the formation of the proctodaeum; and at the anterior end a clearer area of protoplasm devoid of any yolk granules may be seen in some larvae. This last feature is of doubtful significance, since it was only clearly recognizable in a few instances. By now the larvae have grown to about 280 μ in length.



Text-fig. 4. Early stages of the larva: *a*, 'hatching stage' (viewed from animal pole); *b*, slightly later stage showing telotroch (side view); *c*, larva showing early formation of first three chaetal sacs (side view); *d*, early larva with three chaetigerous segments (dorsal view); *e*, larva with three chaetigerous segments (ventral view); *f*, slightly older larva with three chaetigerous segments (ventral view).

The young chaetigerous larva

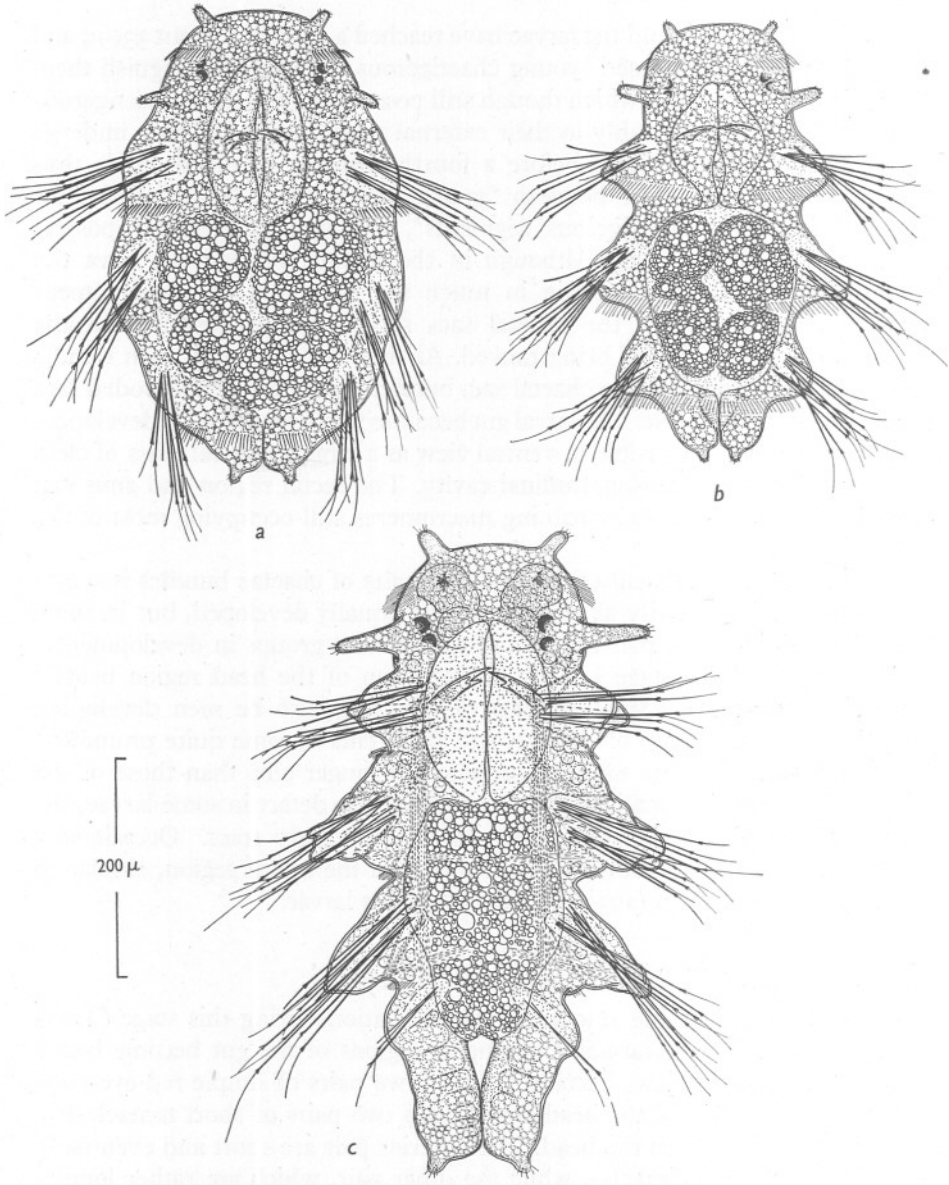
When about 2 weeks old the larvae have reached a length of about 330 μ, and may be conveniently termed 'young chaetigerous larvae' to distinguish them from slightly later larvae, which though still possessing only three chaetigerous segments, differ considerably in their external morphology, for they undergo great morphological changes before a fourth segment is added. It is thus convenient to distinguish between 'young chaetigerous larvae' and later 'larvae with three chaetigerous segments', although both stages possess three pairs of chaetal sacs. Although in the young chaetigerous larva the prototroch and telotroch remain in much the same state of development as in the earlier stages, the chaetal sacs soon acquire muscles, and the chaetae become capable of being moved. At first the chaetae in each bundle appear to arise from a single chaetal sac, but neuropodial and notopodial sacs soon become recognizable. The larval gut becomes much more highly developed, the pharynx becoming visible in ventral view as a large spherical mass of clear cells enclosing a median longitudinal cavity. The rectal region and anus can now also be seen, the four remaining macromeres still occupying most of the gut cavity.

The state of development of the different pairs of chaetae bundles is somewhat variable. Frequently all three pairs are equally developed, but in some (Text-fig. 4*e*) the third pair lag behind the anterior groups in development.

By the end of this stage a slight demarcation of the head region usually makes its appearance. Small patches of cilia may also be seen developing posteriorly to each group of chaetae, and these cilia become quite prominent in some larvae. They are usually composed of longer cilia than those of the telotroch, but are still small enough to be difficult to detect in some larvae, the prototroch remaining the only really prominent ciliary tract. Occasionally a few short cilia-like processes were detected in the apical region, similar to those figured by Wilson (1932) in *Nereis pelagica* larvae.

The Later Larva with Three Chaetigerous Segments

There is a considerable amount of differentiation during this stage (Text-figs. 4*f*, 5*a*, *b*). The rectal and pharyngeal regions of the gut become better developed and simple jaws become visible. Two pairs of simple red eye-cups appear on either side of the head region, and two pairs of short tentacle-like processes grow out from the head. The anterior pair are short and eventually form the prostomial tentacles, while the other pair, which are rather longer, form the first pair of prostomial cirri. Palps are not visible at this stage. The chaetae become more prominent and come to be borne on recognizable, though rudimentary, parapodia (Text-fig. 5*b*). Anal cirri may also be seen growing out on either side of the anus. They bear fine hair-like processes, similar to those on the prostomial tentacles and peristomial cirri, and are



Text-fig. 5. *a*, larva with three chaetigerous segments (dorsal view); *b*, larva with three chaetigerous segments, about 3 weeks old (dorsal view); *c*, larva with four chaetigerous segments, about 4 weeks old (dorsal view).

presumably sensory structures, which are also characteristic of the adult. By now the larva is about 400 μ long, and is quite active, the chaetae, which are now provided with muscles attached to the bases of the chaetal sacs, being moved fairly vigorously during swimming or crawling.

The Larva with Four Chaetigerous Segments

By the time that a fourth chaetigerous segment is becoming differentiated the larva is about 4 weeks old and is about 570 μ in length (Text-fig. 5*c*). The ciliated bands remain in much the same condition as in larvae with three chaetigerous segments, but the parapodia are becoming more complex in structure and their musculature greatly increased. The general musculature of the body wall now becomes more prominent; septal muscles are visible in the mid-gut region, and longitudinal muscles may be seen lying on either side of the gut in the dorsal region.

The fourth chaetigerous segment is represented at first by slight outpushings of the body wall, with two or three chaetae in an apparently simple sac. As in all segments during their early phases of growth, definite neuro- and notopodial sacs are not recognizable, and apparently only separate later.

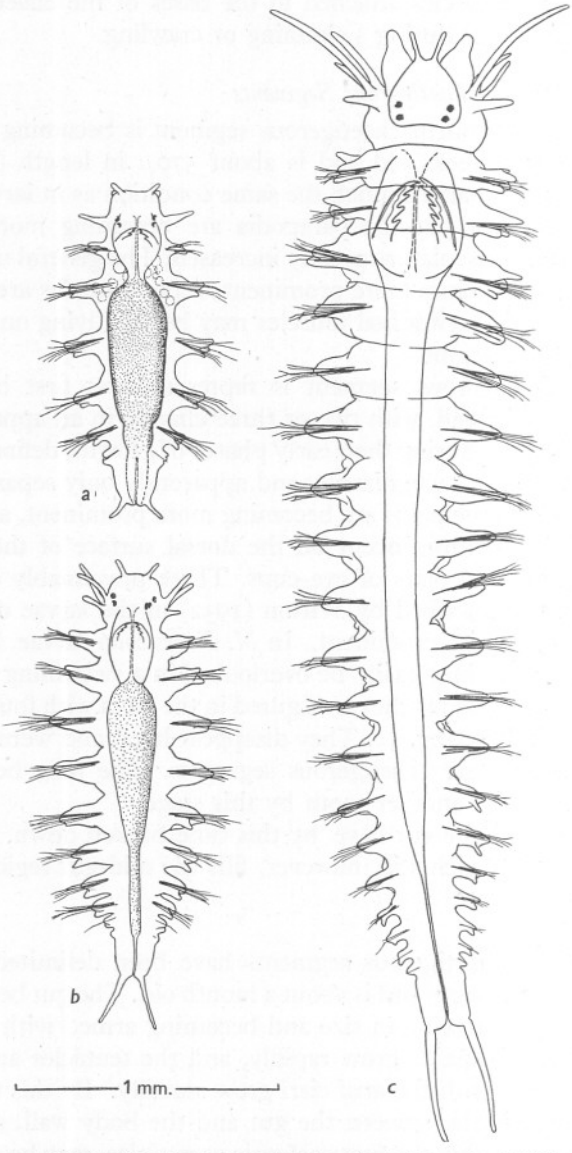
In the head region the palps are becoming more prominent, and small light pigment patches sometimes occur on the dorsal surface of the prostomium just anterior to the two pairs of eye-cups. These presumably correspond to the similar patches described by Wilson (1932) in the larvae of *N. pelagica*, where they may be quite prominent. In *N. diversicolor* larvae, however, they are never obvious and may easily be overlooked in a swimming larva, and are frequently absent. These patches are figured in the larva with four chaetigerous segments shown in Text-fig. 5*c*. They disappear later, and were never seen in larvae with five or more chaetigerous segments. The jaws become further elaborated and possess another tooth by this stage.

The megameres in the gut have by this time broken down into an amorphous mass of yolk, which still, however, fills the mid-gut region.

Later Development

By the time five chaetigerous segments have been delimited, the larva is rather over 1 mm. in length and is about a month old. The gut becomes further elaborated, the jaws growing in size and becoming armed with an increasing number of teeth. The palps grow rapidly, and the tentacles and cirri of the head region together with the anal cirri grow steadily. By this time coelomic spaces are clearly visible between the gut and the body wall, and masses of rounded cells, presumably the first coelomic corpuscles, may be seen tumbling about in the coelom with the movements of the larvae.

Larvae with six, nine and nineteen chaetigerous segments are shown in Text-fig. 6, from which it will be seen that septa become externally visible when about seventeen or eighteen segments have been formed. By the time



Text-fig. 6. *a*, larva with six chaetigerous segments, about 5½ weeks old (dorsal view); *b*, larva with nine chaetigerous segments, about 7 weeks old (dorsal view); *c*, young worm with nineteen chaetigerous segments, about 10 weeks old (dorsal view).

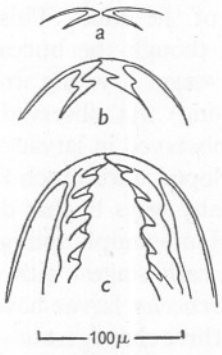
this last stage (Text-fig. 6*c*) has been reached, the young worm, which is by then between 2·5 and 3·0 mm. long, is still quite colourless, but orange pigment appears in the anterior dorsal region soon afterwards, and in the larvae with nineteen chaetigerous segments the dorsal blood vessel may be clearly seen as a deep red mid-dorsal line. By now the adult mode of life has been assumed, and the larva is virtually a miniature adult, burrowing in the mud.

Development of the Jaws and Chaetae

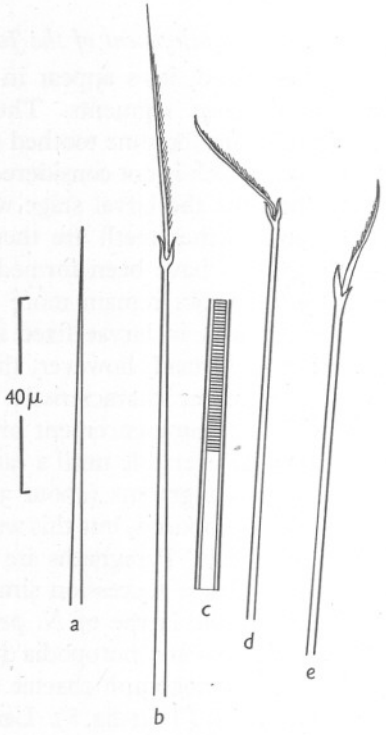
As already mentioned, jaws appear in the pharyngeal region of the larva with three chaetigerous segments. They are at first simple transparent structures and only later become toothed (Text-fig. 7). One tooth (apart from the apex of the jaw which is not considered as a 'tooth' in this description) has developed by the time the larval stage with four chaetigerous segments has been reached, and further teeth are then added until, by the time that six chaetigerous segments have been formed, five teeth are borne on each jaw. Up to this stage the jaws remain more or less transparent, and the details could be made out only in larvae fixed in benzyl alcohol. By the time that five teeth have been formed, however, the jaws are beginning to harden and assume the amber colour characteristic of those of the adult. This change corresponds with the commencement of feeding, though the buccal region does not appear to be eversible until a rather later stage. A young worm with eighteen chaetigerous segments (about 3·2 mm. long) was observed on one occasion to evert its proboscis, but this was never observed in larvae or young worms smaller than this. Paragnaths are not developed until much later.

Larval chaetae follow a succession similar in many ways to that described by Wilson (1932) in the larvae of *N. pelagica*. Homogomph spinigers predominate in both neuro- and notopodia during the early stages, with very few simple capillaries. Homogomph chaetae in *N. diversicolor* larvae have the tip turned over very slightly (Text-fig. 8). Larvae with three chaetigerous segments have, on the average, about five chaetae in each notopodium and four or five in each neuropodium. Usually there are slightly more chaetae in the notopodia than in the neuropodia. Wilson described *N. pelagica* larvae with three chaetigerous segments as having between seven and ten chaetae in each group, which is almost twice that of *N. diversicolor*. It is interesting to note in this connexion that Wilson's larvae were essentially pelagic, whereas those of *N. diversicolor* are typically bottom forms. Again, capillaries seem to be commoner in *N. pelagica* larvae than in the *N. diversicolor* larvae described in the present paper. Wilson also describes homogomph falcigers from *N. pelagica* larvae with three chaetigerous segments, but these are absent in the corresponding stage in *N. diversicolor*, though intermediate forms between homogomph spinigers and falcigers occur in slightly later larvae. All the compound chaetae have the distal parts closely toothed with long fine teeth. Heterogomph falcigers appear in later larvae, and by the time that the larva has acquired

eighteen segments heterogomph falcigers predominate in the first few segments, but in the more posterior segments homogomph bristles still remain more numerous. Young worms with thirty chaetigerous segments have a predominating number of heterogomph falcigers, but a few homogomph spinigers remain, mainly in the notopodia. This condition approaches that of the adult.



Text-fig. 7.



Text-fig. 8.

Text-fig. 7. Jaws from larvae with: *a*, three; *b*, four; *c*, six, chaetigerous segments.

Text-fig. 8. Larval chaetae. *a*, simple capillary; *b*, homogomph spiniger; *c*, fine structure of chaetae (base only); *d*, homogomph falciger; *e*, heterogomph falciger.

Apart from Wilson's close analysis of the succession of the larval bristles of *N. pelagica*, and some previous work on the same species by Herpin (1925), the development of the larval chaetae has not been closely studied. The only other detailed drawing of a larval chaeta of *N. diversicolor* known in the literature, is the drawing of a single chaeta by Hofker (1930). This author based his identification of his larvae partly on the resemblance of these chaetae to those of the adult, but it does not resemble the chaetae here described. Further, it should be noted that the larval chaetae in the very early larvae do not closely resemble those of the adult, either in character or composition.

Aciculae occur first in larvae with ten chaetigerous segments, and after this stage has been passed, develop with the chaetae as the new segments are added. The formation of the acicula is not, therefore, initiated when the parapodia attain a certain age or size after the formation of the chaetae, the two sets of structures arising concurrently after the formation of about ten chaetigerous segments. It would seem to be some function of the size or age of the larva itself, rather than that of the individual parapodium. Typical larval chaetae are shown in Text-fig. 8.

Elaboration of the Parapodia

The formation of the parapodium is of interest since its form in the adult, like that of the chaetae, is of taxonomic importance. In *N. diversicolor* the adult form is not approached by any of the parapodia until thirty or forty chaetigerous segments have been formed, and even then the older parapodia are by no means identical with those of the adult.

In very early larvae with three chaetigerous segments there are virtually no parapodia, but by the end of this stage simple notopodial and neuropodial lobes are recognizable (Text-fig. 9*a*). In larvae with four chaetigerous segments these two main lobes each begin to be divided into two main parts and the ventral cirri are plainly visible (Text-fig. 9*b*). This pattern persists over much of the strictly larval life and is much the same in larvae with ten chaetigerous segments, though the two main lobes are then much longer and supported by acicula. In a young worm with thirty-one chaetigerous segments notopodial and neuropodial lobes conform mainly to the adult plan (Text-fig. 9*e*). By this time the dorsal cirri have also appeared and the noto- and neuropodia are composed of three subsidiary lobes, which are not, however, as distinctly separated as in the adult (Text-fig. 9*f*).

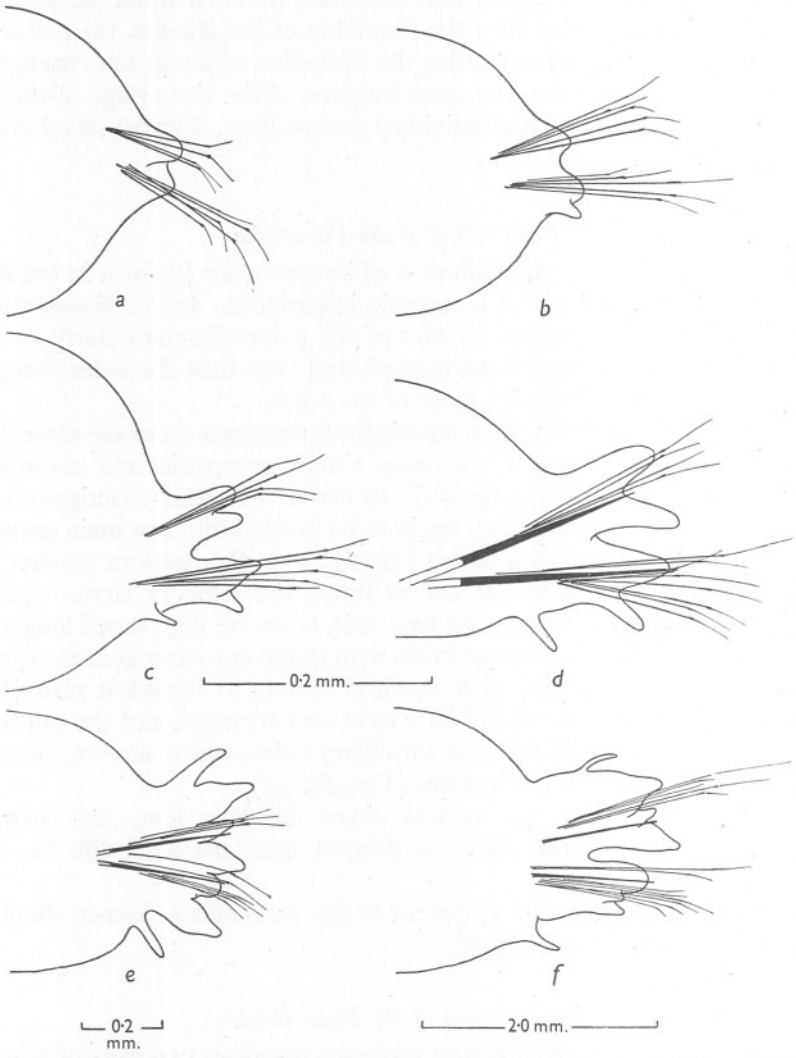
It is interesting that the ventral cirrus develops first, and that the development of the dorsal cirrus is delayed until the adult life has been assumed.

For more details of the development of the parapodia reference should be made to the work of Finke (1936).

Development of the Head Region

The larva with three chaetigerous segments possesses two pairs of tentacle-like processes on the head (Text-fig. 10*a*). The anterior pair are always the shorter of the two, and represent the future prostomial tentacles. The posterior pair represent the first pair of peristomial cirri. Palps do not appear until the larva possesses four chaetigerous segments. Only one pair of peristomial cirri is present in larvae with seven chaetigerous segments, but by the time that a further two chaetigerous segments have been added, three pairs are recognizable. The full complement of four pairs is not developed till the larva

possesses about sixteen chaetigerous segments. The first two pairs of peristomial cirri are derived from the first segment, while the two pairs which are

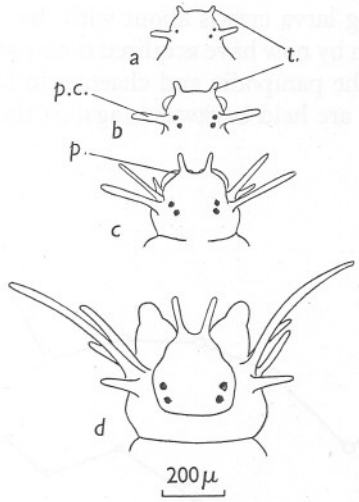


Text-fig. 9. *a*, second parapodium of a larva with three chaetigerous segments; *b*, second parapodium of a larva with four chaetigerous segments; *c*, fourth parapodium of a larva with five chaetigerous segments; *d*, fourth parapodium of a larva with ten chaetigerous segments; *e*, tenth parapodium of a young worm with thirty-one chaetigerous segments; *f*, parapodium of adult in mid-body region. *a*, *b*, *c* and *d* are to the same scale.

added later are derived from the first larval chaetigerous segment which coalesces with the first segment to form the peristomium or 'buccal segment' of the adult (see Table III). A similar mode of development was found by

Hempelmann (1911) in *Platynereis dumerilii*, and by Herpin (1925) in other nereids.

The prostomium is not distinctly separated off by a groove until the young worm has about eighteen chaetigerous segments, when the palps are becoming elaborated into the two parts characteristic of the adult (Text-fig. 10*d*).



Text-fig. 10. Development of head region: *a*, head of young larva with three chaetigerous segments; *b*, head of larva with seven chaetigerous segments; *c*, head of larva with nine chaetigerous segments; *d*, head of larva with eighteen chaetigerous segments; *t*, prostomial tentacles; *p*, palp; *p.c.*, peristomial cirri.

TABLE III. DEVELOPMENT OF THE HEAD REGION

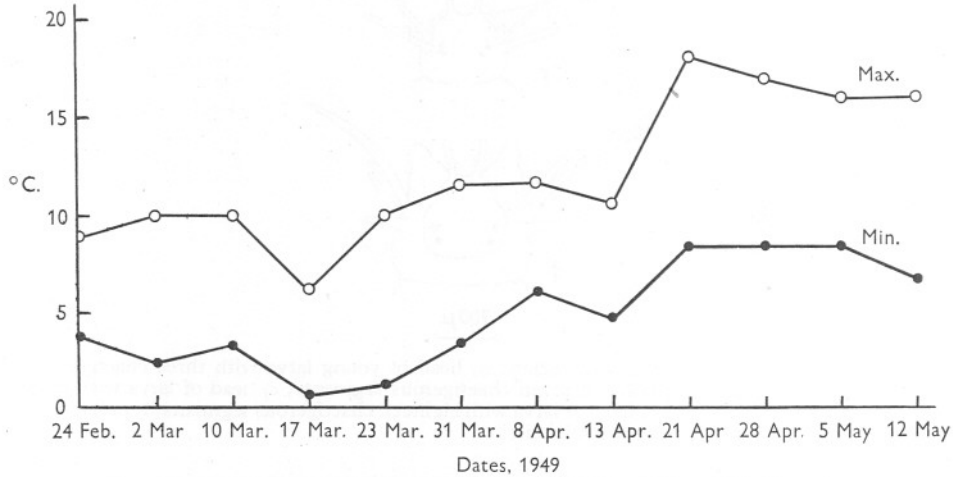
	Appendages	
	Larva with three chaetigerous segments	Larva with more than three chaetigerous segments
Prostomium	Tentacles	Tentacles
First segment	Cirri	Cirri } Peristomium ('buccal
Second segment	First chaetigerous segment	Cirri } segment')
Third segment	Second chaetigerous segment	First chaetigerous segment
Fourth segment	Third chaetigerous segment	Second chaetigerous segment

LARVAL HABITS AND LIFE HISTORY

The young ciliated monotrochophores are weak swimmers and never continue swimming for any length of time, frequently coming to rest on the bottom. They are somewhat denser than sea water, and in nature these swimming movements cannot be of much importance in distributing the species. Young chaetigerous larvae cannot, at first, move their chaetae, but by the end of the larval stage with three chaetigerous segments the chaetal sacs have acquired a good musculature and can be moved backwards and forwards in the

horizontal plane. By this stage, therefore, the larva can crawl on the substratum or on the walls of the parent burrow. Cilia are prominent, however, even in larvae with five or six chaetigerous segments, and in larvae with four chaetigerous segments (Text-fig. 5*c*) the prototroch and subsidiary ciliary bands are still sufficiently well developed to enable the larva to swim off the bottom. Swimming is never continued for more than a few seconds at a time, and for the most part the young larva crawls about with the aid of the anterior three pairs of parapodia which by now have acquired their own intrinsic musculature.

During swimming, the parapodia and chaetae (in larvae with three or four chaetigerous segments) are held backwards against the sides of the body so as



Text-fig. 11. Temperature of natural habitat during early larval life from time of spawning.

to reduce the water resistance. Braking is effected by the parapodia being brought forwards and extended away from the body. The first pair of parapodia are frequently directed forwards in so doing. This action of the parapodia apparently increases the water resistance of the body sufficiently to bring the larva to rest, while the cilia continue beating. This braking action also brings the parapodia into the correct position for crawling to begin again, and with fairly active larvae such crawling and swimming periods alternate.

The larvae are not, however, particularly active until about ten chaetigerous segments have been delimited. Up to this stage the larva is apparently entirely lecithotrophic, but as feeding begins at about this time (when the larva is some 7 weeks old) it is probable that this assumption of a more active life is correlated with the beginning of active feeding. Probably little distribution of larvae occurs until this time. In one instance a burrow was opened which was swarming with scores of larvae with eight and nine chaetigerous segments, and it is highly probable that these larvae resulted from a successful

fertilization in the burrow, or that the fertilized eggs had been washed into the burrow from the surface. The greatly increased activity of the larvae with ten chaetigerous segments coupled with the search for food probably serves to distribute the species, although distribution probably takes place mainly in later life.

Young worms with about twenty chaetigerous segments, and about 4 mm. in length, if placed in a deep dish with a layer of fresh mud, promptly burrow into the mud and construct minute U-shaped tubes the openings of which are only 2 or 3 mm. apart. These burrows may be seen in nature under favourable conditions.

The larvae are, therefore, typically bottom-living. Many authors, however, have ascribed larvae found in the plankton to *Nereis diversicolor* (Hofker, 1930; Smidt, 1944; Thorson, 1946), but all workers seem to be agreed that they do not really represent pelagic forms but are bottom larvae which have

TABLE IV. LARVAL LIFE HISTORY

	Lecithotrophic	Free-living larval life	Adult mode of life
No. of chaetigerous segments ...	3	10	20
Length (mm.)	0·4	1·6	4·0
Age (weeks)	3	7	10
		Jaws harden	
		Colourless	Pigment appears

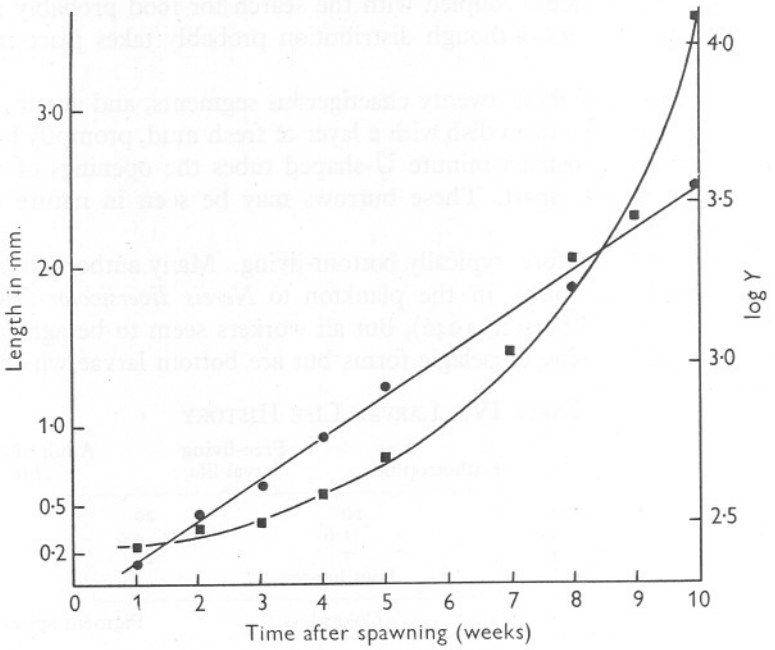
been carried up to the surface. Spärck (1926) found that young adult *N. diversicolor* appeared in cement tanks constructed during the summer in Nykøbing Mors (Limfjord) and these could only have developed from young worms or larvae swept off the bottom by currents.

The early larval life history is summarized in Table IV.

GROWTH OF THE LARVAE

Growth in the length of the larvae continued at a constant geometric rate over the early stages. The length of time elapsing between fertilization and the formation of the monotrochophore, the earliest stage collected in any appreciable numbers from the mud, was determined from the time taken for eggs in artificial fertilizations to reach this stage. The rate of growth of all the later stages was calculated from measurements of larvae obtained from the natural habitat. Collections were made every 3 days at first, and later, at weekly intervals, and all the larvae and young worms so obtained were measured. There was little size variation at first, but this became progressively greater, as would be expected, in later samples. The relative numbers of larvae in each stage were determined during the first month after the main spawning period and the frequency distributions of these samples arranged as a series of histograms in Text-fig. 2 (p. 334). Text-fig. 12 represents the rate of growth

of larvae, constructed from the mean length calculated from the measurements of several dozen larvae in each stage. The curve will be seen to follow the



Text-fig. 12. Growth of larvae during first 10 weeks.

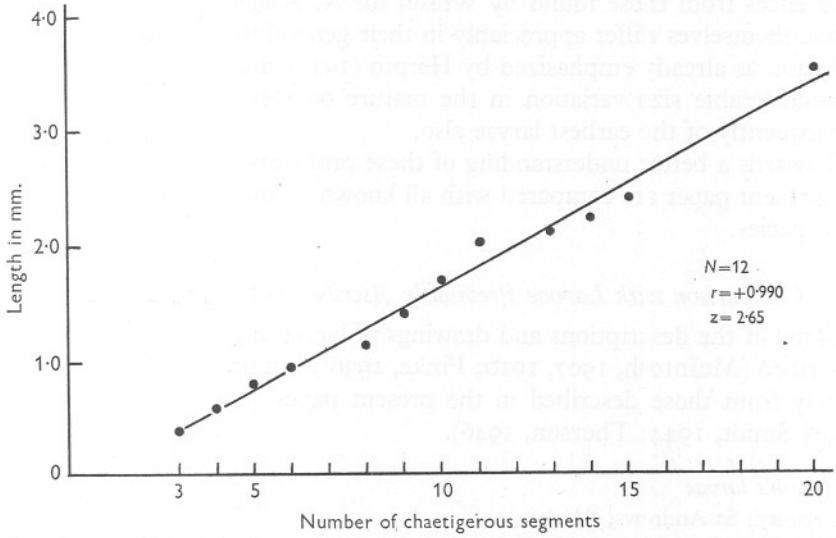
TABLE V. GROWTH OF LARVAE

No. of chaetigerous segments	Length (mm.)	Age (weeks after fertilization)
Egg to monotrochophore	0·220	1–2
Young chaetigerous larvae	0·330	2
Larvae with three chaetigerous segments	0·400	3
,, ,, four ,, ,,	0·570	4
,, ,, five ,, ,,	0·800	5
,, ,, six ,, ,,	0·950	—
,, ,, seven ,, ,,	—	6
,, ,, eight ,, ,,	1·120	—
,, ,, nine ,, ,,	1·480	7
,, ,, ten ,, ,,	1·700	—
,, ,, eleven ,, ,,	2·050	8
,, ,, twelve ,, ,,	—	—
,, ,, thirteen ,, ,,	—	—
,, ,, fourteen ,, ,,	2·300	9
,, ,, fifteen ,, ,,	—	—
,, ,, sixteen ,, ,,	—	—
,, ,, seventeen ,, ,,	—	—
,, ,, eighteen ,, ,,	—	—
,, ,, nineteen ,, ,,	3·600	10

normal logarithmic pattern characteristic of growth with a constant geometric growth rate. This growth rate (geometric, multiplicative, or instantaneous) was calculated, basing the calculations on larvae from 1 to 9 weeks in age, and

was found to be 0·04277. Details of these calculations are given in the Appendix (p. 360).

The length, age, and corresponding number of chaetigerous segments of larvae obtained from the natural habitat is summarized in Table V. During the early stages there is a nearly perfect positive correlation between the total length and number of chaetigerous segments. The graph (Text-fig. 13) shows this relation in larvae up to the age of about 10 weeks. Using the usual statistical methods (see Appendix) the calculation of the correlation coefficient 'r' based on twelve randomly selected larvae from each size-group and having



Text-fig. 13. Correlation between larval length and number of chaetigerous segments.

between three and twenty chaetigerous segments gave a value of 'r' as +0·9900; an almost perfect positive correlation. From this Fisher's term 'z'=2·65. As the worms become older the degree of correlation becomes less, and in 'adult' worms the degree of correlation is too small to have any real significance.

Comparison with other Accounts of Nereid Larvae

Many species of *Nereis* are often found in the same habitat, and this has caused much confusion with regard to the identification of the larvae. Larvae found in the plankton have frequently been ascribed to *N. diversicolor*, solely on the basis that this species is the most abundant in that area. Difficulty in identifying nereid larvae is increased by their variability. Wilson (1932), for example, found certain differences between his *N. pelagica* larvae and those described by Herpin (1925); while the variation in reproduction and development of *Platynereis dumerilii* has been described by Hempelmann (1911).

A larva cannot therefore be ascribed to another species solely on the basis of slight anatomical differences from that of a known species. Conversely, under certain conditions, larvae of two species may appear remarkably similar; as for instance do Herpin's (1925) drawings of *Perinereis cultrifera* larvae and the *Nereis diversicolor* larvae described in the present paper. It would seem probable that the details of chaetae and chaetal succession would be highly specific. Although this may be so, it should be noted that the larval chaetae do not necessarily resemble those of the adult, and in the present investigation a careful study of the succession of larval chaetae did not reveal striking differences from those found by Wilson for *N. pelagica* larvae, although the larvae themselves differ appreciably in their general morphology.

Again, as already emphasized by Herpin (1925) and discussed above, there is considerable size variation in the mature oocytes of *N. diversicolor*, and consequently of the earliest larvae also.

Towards a better understanding of these problems, the larvae described in the present paper are compared with all known accounts of larvae ascribed to this species.

Comparison with Larvae Previously Ascribed to Nereis diversicolor

Some of the descriptions and drawings of larvae agree well with those here described (McIntosh, 1907, 1910; Finke, 1936); but others differ more or less widely from those described in the present paper (Schultze, 1856; Hofker, 1930; Smidt, 1944; Thorson, 1946).

McIntosh's larvae

Locality: St Andrews, Scotland.

Size: Not given (ripe oocyte given as 0·1524 mm.).

Description (1910, figs. 71–73, p. 320; fig. 74, p. 322): Chalkwell larvae correspond well with McIntosh's figures, though these are not detailed. Degree of development of head appendages and anal cirri similar in larva with three chaetigerous segments (probably an early four-chaetigerous segmented larva) and in larva with six chaetigerous segments.

Finke's larva

Locality: Kiel.

Description (fig. 1, p. 244): a larva with four chaetigerous segments closely similar to Chalkwell larvae.

Schultz'es 'larvae'

Locality: Frisches Haff; in the coelom.

Description: in no way resemble nereid larvae. Probably parasites.

Hofker's larvae

Locality: Zuidersee (plankton).

Size: small compared with Chalkwell larvae. Trochophore 140 μ (Chalkwell *diversicolor* larvae were 220 μ, and McIntosh's oocytes were little over 150 μ.)

Description (fig. 12 *a–d*, p. 200; fig. 13 *a–c*, p. 201): previously discussed by Thorson (1946). Early trochophores differ in having well-marked apical tuft; similar in having well-marked prototroch but little or no telotroch. Smaller size. Chaeta figured does not resemble Chalkwell *N. diversicolor* larval chaetae; neither do the jaws from a larva with six chaetigerous segments.

Hofker based his identification on: (1) chaetae, which he regarded as resembling the adult; (2) most abundant adult in the area. Both these points have already been discussed. Hofker's chaeta is provided with large stout teeth, never observed in *N. diversicolor* larval chaetae from Chalkwell, in which the teeth were extremely fine.

Smidt's larvae

Locality: Copenhagen Harbour (plankton).

Size: small compared with Chalkwell larvae. Larva with four chaetigerous segments less than 350 μ (Chalkwell *N. diversicolor* 600 μ). Larva with five chaetigerous segments 700 μ (Chalkwell 800 μ).

Description (fig. 5, p. 254): larvae do not resemble Chalkwell *N. diversicolor* larvae, having three eye-cups on each side. Larva with four chaetigerous segments very small; five chaetigerous segmented larva relatively larger. In larva with four chaetigerous segments prostomial tentacles and peristomial cirri apparently not developed (well developed in Chalkwell larvae) though anal cirri roughly equivalent in length. Pigment (?) on head region in larva with five chaetigerous segments not seen in Chalkwell larvae.

Thorson's larva

Locality: Øresund.

Size: smaller than Chalkwell larvae. Larva with four chaetigerous segments *c.* 450 μ (Chalkwell 550–600 μ).

Description (fig. 30, p. 67): show some resemblance to Smidt's larvae. Unlike Chalkwell larvae—parapodial lobes well developed in larva with four chaetigerous segments, anal cirri much shorter and unlike those of Chalkwell larvae, three eye-spots. Thorson's discussion of this larva, as well as that of Hofker, should be consulted.

Discussion

Many of the interesting features in the reproduction of this nereid have already been discussed. The main points of interest remaining are the alleged occurrences of the phenomena of metamorphosis, hermaphroditism, viviparity, and parthenogenesis.

Metamorphosis. Most recent authorities (McIntosh, 1907, 1910; Fauvel, 1923; Schröder, 1886; Herpin, 1925; Dehorne, 1925) agree that *N. diversicolor* is normally atoquous. Other workers (Heinen, 1911; Thieren, 1909) claim to have found epitoquous forms.

Heinen describes an epitoquous form which he regarded as *N. diversicolor*, but Herpin (1923, 1925) regards this as a confusion of species, and points out that Heinen's figures might equally well refer to *Neanthes succinea* Leuck. Heinen's drawings of the parapodia correspond fairly closely with Fauvel's drawings (1923) of *succinea*, and also the length of the peristomial cirri in Heinen's drawings resemble those of *succinea* rather than those of *diversicolor*, in which they are much shorter. Heinen, however, records the occurrence of

succinea as well, showing that he must have been aware of the similarity. Heinen regards *Nereis diversicolor* to be normally epitoquous and compares it with *N. japonica* (see Izuka, 1908). Heinen quotes Brandt and Riecke as also finding epitoquous forms at Kiel on two separate occasions.

The resemblance of the process of 'metamorphosis' described by Dehorne (1925) is only superficial, as previously pointed out by Herpin (1925). Fage (1924) and Fage & Legendre (1923) do not mention *N. diversicolor*, and the heteronereids described by Sorby (1906) were not referred to this species.

Thieren (1909), on the other hand, agrees with Heinen, and also claims to have found an epitoquous stage. Herpin regards this, as in Heinen's instances, to have been a confusion of species.

Thomas (1930*a*) found that chaetae in mature females sometimes tended to degenerate and suggested that this might be interpreted as an aborted or rudimentary step towards metamorphosis to an epitoquous condition. The significance of histolysis in relation to this problem has already been discussed.

Epitoquous forms, if they do occur, are therefore certainly rare, and it is probable that those reported are not attributable to this species. It may be concluded that *N. diversicolor* is normally atoquous. Epitoquous forms have never been found by the writer, and although a careful examination of maturing worms has been made, no anatomical changes, other than those associated with histolysis and parenchyma formation, were observed.

Hermaphroditism. Mendthal's view (1889) that the species was hermaphrodite was based on the assumption that the pear-shaped bodies which were almost certainly the dorsal ciliated organs of Goodrich (1893, 1945), were testes. He supported his argument by quoting Moquin-Tandon's discovery of an hermaphrodite nereid (*N. massiliensis*) in 1869. This is not unique, since Johnson (1908) found the minute nereid *Lycastis quadraticeps* to be hermaphrodite, while *Platynereis dumerilii* also has an hermaphrodite form (Hempelmann, 1911). Mendthal concluded that, though the worm was hermaphrodite, the male gametes ripened before the ova. Gravier (1905) considered that hermaphroditism might occur exceptionally, but McIntosh doubts Mendthal's statements, and de St Joseph also could not corroborate these views. Herpin (1923*a*, 1925) and more recent workers agree in finding the species dioecious. This is in accordance with observations made by the writer.

Viviparity. Theoretically, ovoviviparity might result from (1) parthenogenetic development of the coelomic oocytes, (2) as a result of internal fertilization, or (3) self-fertilization in the existence of hermaphroditism.

This last explanation may be discounted, although it was suggested by some of the earlier workers.

The second suggestion is also unlikely to occur, in spite of the existence of a form of sexual congress. Schröder (1886), however, thought that the sperm entered via the nephridia to cause internal fertilization, and concluded that the species was viviparous after discovering 'morulae' in the coelom, though this

observation was sceptically treated by McIntosh (1907, 1910) since Schröder failed to find the larvae later in the year. These may have been abortive cleavage stages produced by abnormal conditions, or may even have been young sperm plates. Just (1915) found in the American *N. limbata*, that the oocytes would not fertilize in the tissue juices, and this may have some significance in relation to the present problem.

Parthenogenesis. This might occur in the coelom, or after spawning. The first hypothesis has already been considered, but a further observation may be added here. The discovery by the writer of several oocytes from which the 'fertilization' membranes had become lifted off, in the coeloms of unspawned females, not only supports the theories of Heilbrunn (1924) that the elevation of this membrane is due to a purely physical effect, but also suggests that it is not therefore impossible that cleavage stages might follow, and this would then concur with the views of Smidt (1944), Thorson (1946), and the observations of Schröder (1886).

Regarding the second hypothesis, viz. that the spawned eggs may develop parthenogenetically, Herpin (1923*c*, 1925) obtained cleavage stages from the unfertilized oocytes owing to hypertonicity resulting from evaporation, or other peculiar conditions (Fischer, 1902, 1903; Dehorne, 1925; Herpin, 1925; Just, 1928*a*, *b*).

Herpin noted that the gelatinous envelopes were not always developed in these artificial fertilizations, and the writer has also found them to be frequently absent in artificially fertilized eggs, and in naturally occurring stages. Segmentation was irregular (Herpin, 1925), the cleavage stages being somewhat similar to those obtained artificially by Fischer (1902, 1903) from *N. limbata*, and to those obtained by the writer. For a general discussion of these topics reference should be made to the work by Morgan (1927).

Nereis eggs are very resistant to extreme environmental conditions, as is shown by experiments which have been performed on *N. limbata* (Just, 1928*a*, 1930*a*, *b*; Barron, 1932, etc.). The eggs of this species were found to be particularly resistant to lowered salinity and to temporary exposure to anaerobic conditions (Barron, 1932). No experiments have yet been performed on the eggs of *N. diversicolor*, though if the eggs and larvae of this species are similarly adapted to resist extreme conditions, as seems likely, then in this species this resistance may be regarded as having survival value. The relationship of breeding habits to salinity is being investigated.

Summary

An account is given of the reproduction and development of the larva of *N. diversicolor* O. F. Müller.

In any one population the number of males was found not to exceed 10 %.

The species is dioecious. Both sexes become green at maturity, but may be distinguished externally.

Ripe oocytes, which vary between 200 and 250 μ in diameter mature in a loose coelomic parenchyma, and are released by rupture of the body wall after its partial histolysis. Sperm is released through the nephridia, or possibly by rupture of the body wall as well. In the male histolysis occurs, but the coelomic parenchyma is transitory. Sperm matures in the form of coelomic sperm plates.

Spawning was found to take place over a limited period centred in 1949 round the third lunar quarter in February after a sharp rise in temperature. Spawning has been found to take place generally in early spring; variations are discussed. A form of sexual congress occurs.

Larvae develop in the mud, and there is no true pelagic phase.

Development is relatively slow. Cilia are not well developed in the larvae. The external morphology of the larva is discussed.

The young larvae become active when 7 weeks old, and the adult mode of life is assumed at 10 weeks, when the worm is 4 mm. in length.

The species is atoquous.

Parthenogenesis, hermaphroditism, and viviparity do not normally occur.

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APPENDIX

TABLE VI. GROWTH OF LARVAE

Calculation of the geometric growth rate, based on larvae 0 and 9 weeks after hatching, using the equation

$$G=\frac{\log Y_t-\log Y_0}{0{\cdot}4343t},$$

where Y_0=length of larvae 0 week after hatching, Y_t=length of larvae 9 weeks (63 days) after hatching, t=63 days. Then

$$G=\frac{3{\cdot}54-2{\cdot}37}{(0{\cdot}4343)\,63}=0{\cdot}04277.$$

TABLE VII. GROWTH OF *NEREIS DIVERSICOLOR* LARVAE

Correlation of length and number of chaetigerous segments.

Calculation of the correlation coefficient 'r'

No. of chaetigerous segments (X)	Length (mm.) (Y)	d_X	d_Y	d_Xd_Y	d_X^2	d_Y^2
3	0·40	−6·83	−1·21	8·260	46·650	1·464
4	0·57	−5·83	−1·04	6·063	33·990	1·082
5	0·80	−4·83	−0·81	3·912	23·330	0·656
6	0·95	−3·83	−0·66	2·527	14·670	0·436
8	1·12	−1·83	−0·49	0·897	3·350	0·240
9	1·40	−0·83	−0·21	0·174	0·688	0·044
10	1·70	+0·17	+0·11	0·018	0·289	0·012
11	2·05	+1·17	+0·44	0·515	1·369	0·194
13	2·10	+3·17	+0·49	1·553	10·050	0·240
14	2·20	+4·17	+0·59	2·460	17·390	0·348
15	2·40	+5·17	+0·79	4·084	26·730	0·624
20	3·60	+10·17	+1·99	20·230	103·500	3·960
Σ 118	19·29	—	—	50·693	282·006	9·300

Also

$$N=12,\quad M_X=9{\cdot}83,\quad M_Y=1{\cdot}61;\ \text{and from above}$$
$$\Sigma d_Xd_Y=50{\cdot}693,\quad \Sigma d_X^2=282{\cdot}006,\quad \Sigma d_Y^2=9{\cdot}300.$$

Using the equation

$$r=\frac{\Sigma d_Xd_Y}{\sqrt{(\Sigma d_X^2\,\Sigma d_Y^2)}},$$

$$r=\frac{50{\cdot}693}{\sqrt{(282{\cdot}006\times 9{\cdot}300)}}=+0{\cdot}9900$$

From this, Fisher's term 'z'=2·65.

EXPLANATION OF PLATE I

Fig. 1. Transverse section of an almost mature female showing oocytes in the coelom and parapodial spaces. ×30.

Fig. 2. Sperm plates in the coelom of an immature male. ×120.

Fig. 3. Early stage in the growth of the oocytes: beginning of parenchyma formation. ×120.

Fig. 4. Later stage in the growth of the oocytes: coelom filled with parenchyma. ×120.

Fig. 5. Ripe oocytes: parenchyma breaking down into discrete cells. ×120.

Fig. 6. Living larva with four chaetigerous segments. ×100.

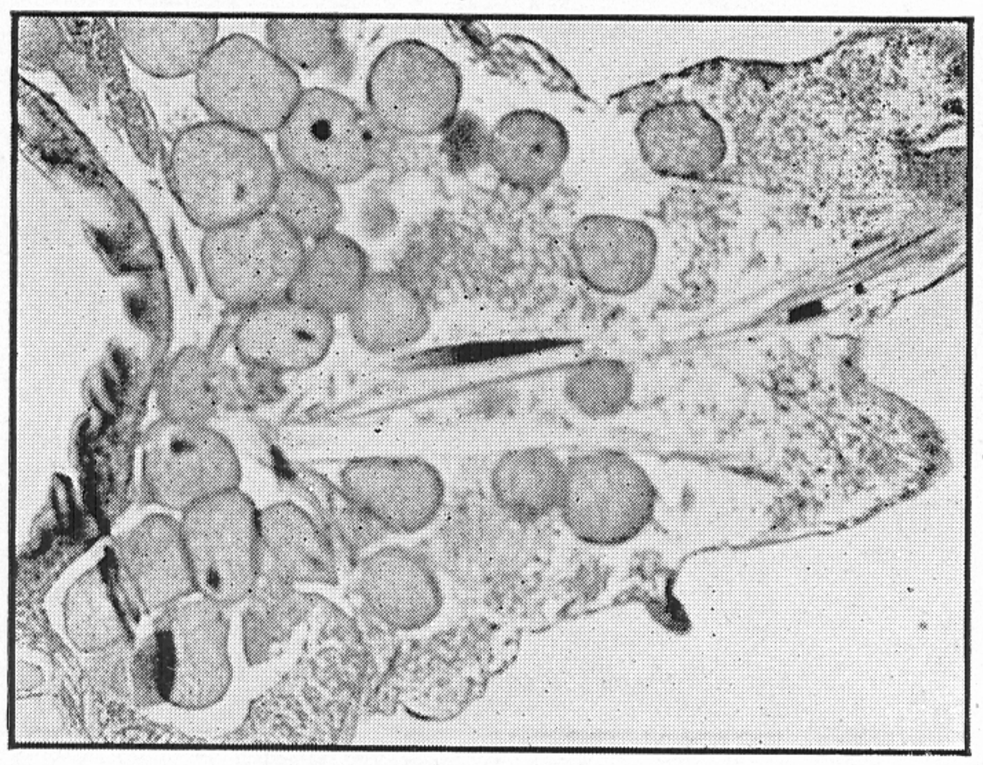

Fig. 1.

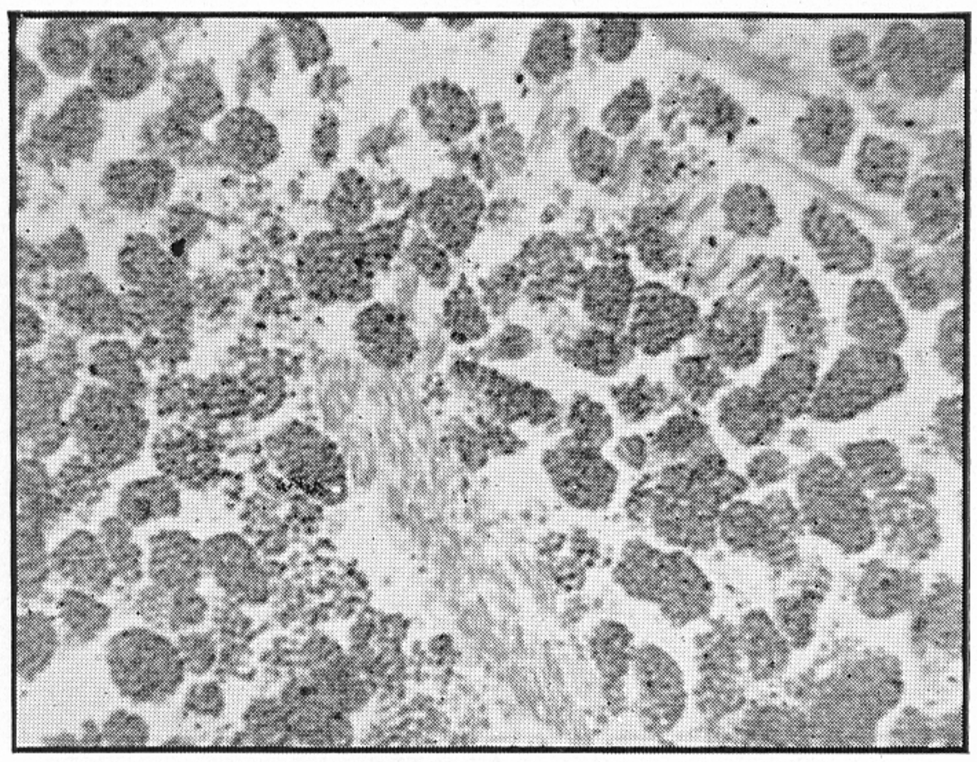

Fig. 2.

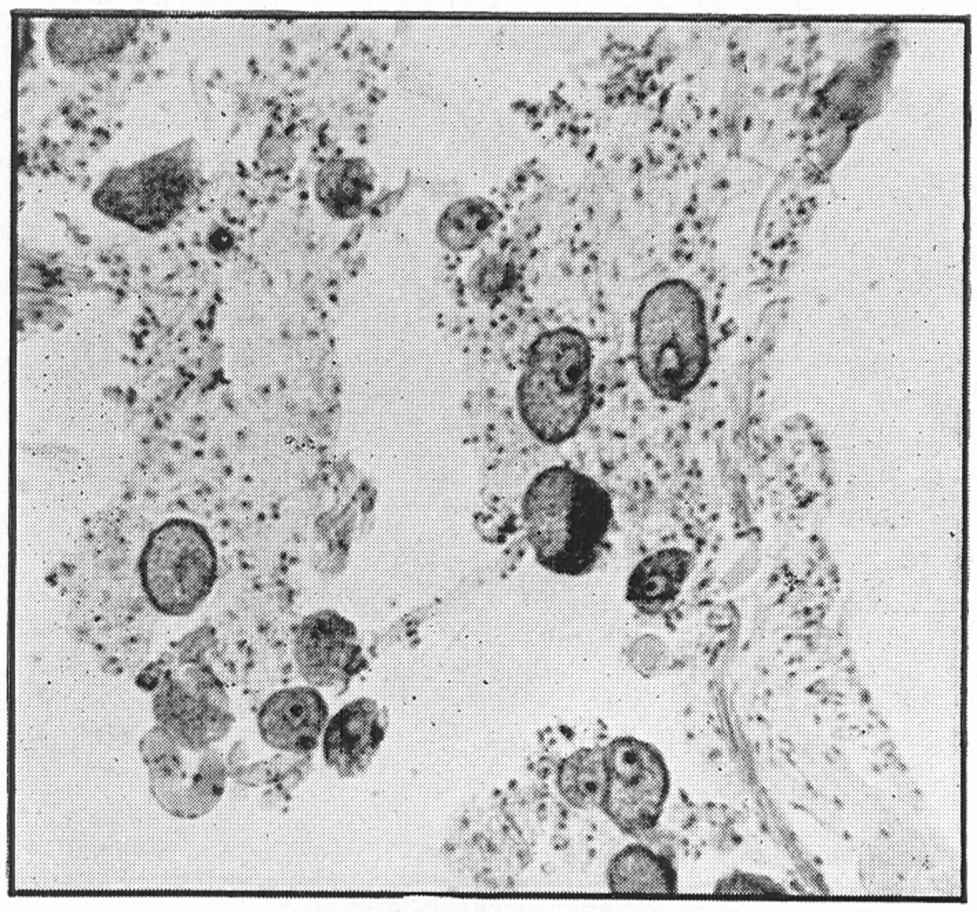

Fig. 3.

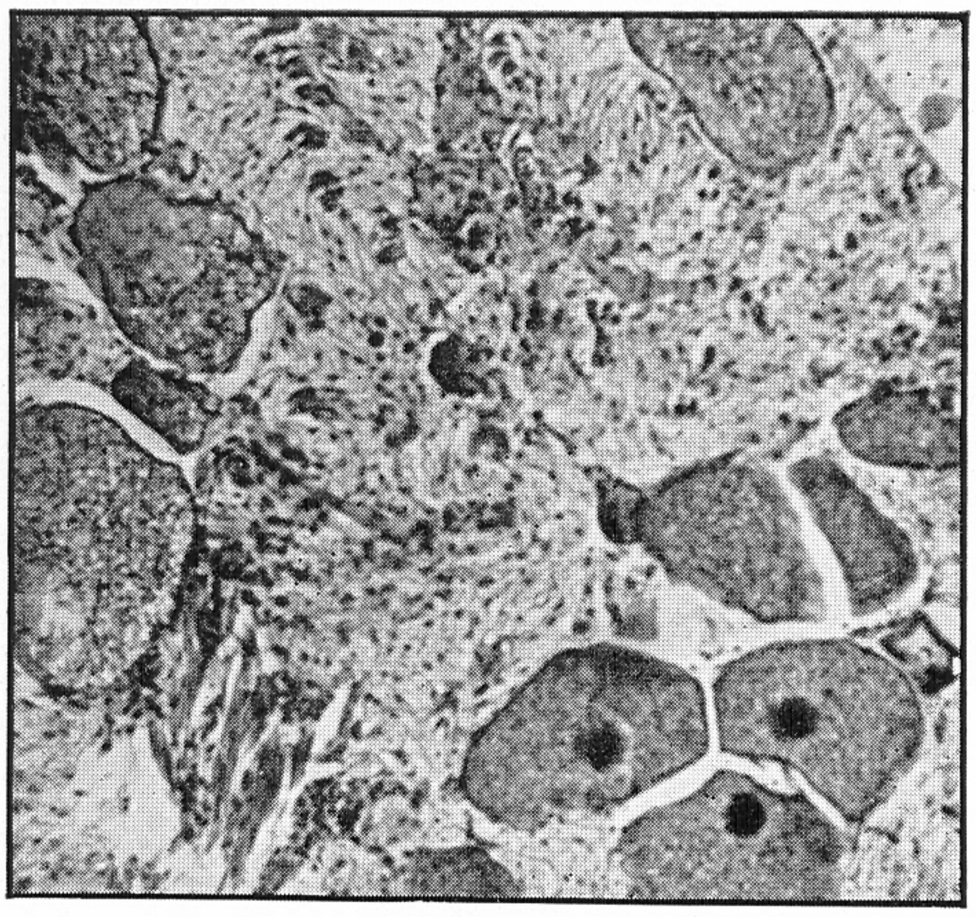

Fig. 4.

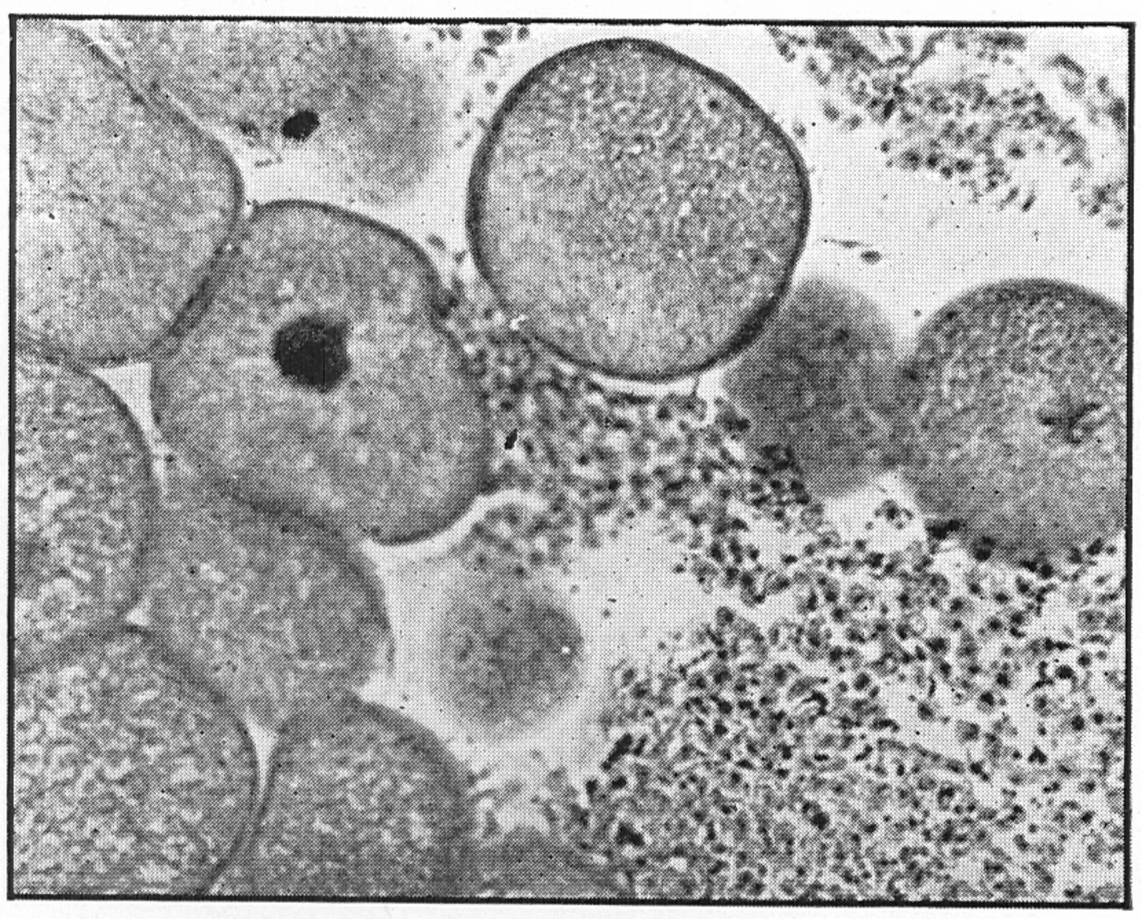

Fig. 5.

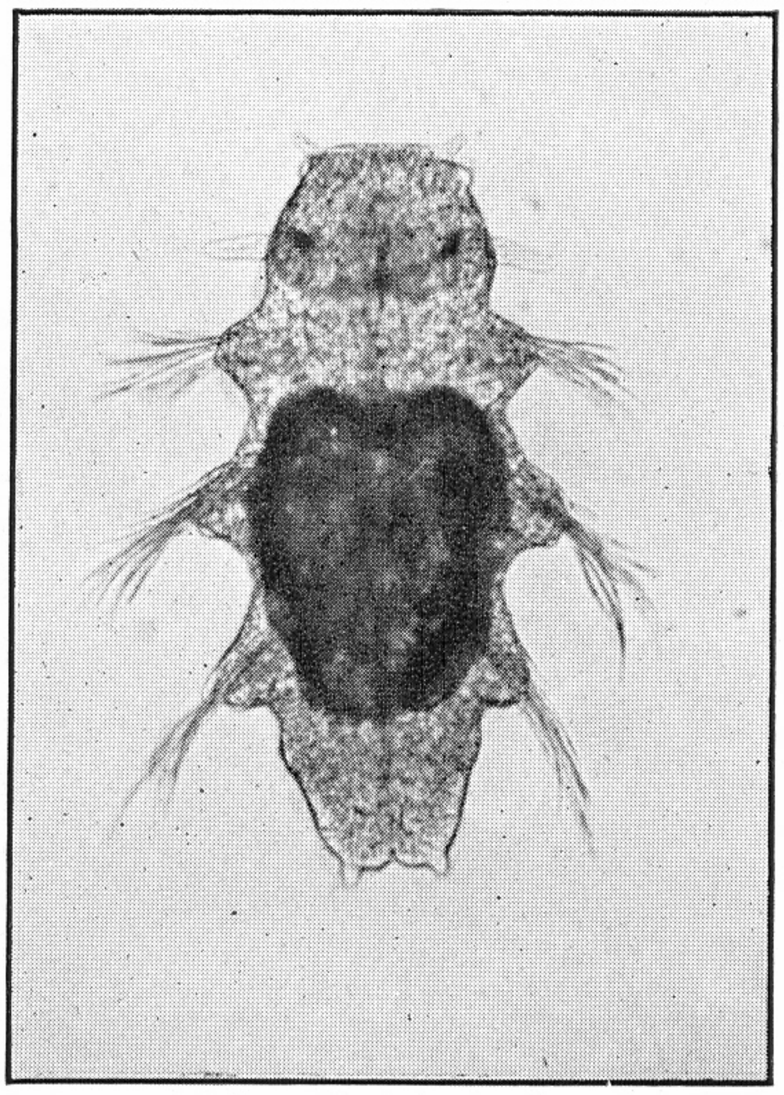

Fig. 6.

THE DISTRIBUTION OF *OCTOPUS VULGARIS* LAMARCK IN BRITISH WATERS

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British Museum (Natural History)

(With Plates I–III and Text-figs. 1–3)

CONTENTS

INTRODUCTION

Octopus vulgaris Lamarck is usually regarded as a Lusitanian member of our fauna. It is found on the south coast of England, and, as E. J. Allen noted (Marine Biol. Assoc., 1931, p. 278) 'generally only a few specimens are taken during the summer months, but it varies greatly in abundance in different years'. In 1899–1900 there was a great plague of *Octopus* all along the south coast of Devon and Cornwall, which served to accentuate the rarity of the species in other years. This phenomenon was the subject of a report by Garstang (1900). Another puzzling feature was the paucity of records of *Octopus* larvae and spawn in our inshore waters which at once suggested that the species rarely breeds on the English coast. If so, how was the population maintained from year to year and whence did the larvae or adults come? During the recent cruises of the M.Y. *Manihine* planktonic larvae of *O. vulgaris* have been found for the first time in fairly substantial numbers in the Channel. These yield much information on the early larval *Octopus*, and also I believe on its distribution in the Channel and southern North Sea.

In order to present as complete a picture as possible, I have thought it desirable to review earlier records for the south coast of England, the Channel Islands and the French coast, the southern North Sea and other British records.

Acknowledgements are due to Major H. W. Hall, M.C., whose interest in marine biology led to the very generous loan of the M.Y. *Manihine* for this and other investigations in the English Channel.

I am also especially indebted to Dr H. W. Parker for facilitating my work in various ways. I wish to thank: Mr D. W. Tucker for the care he took in the preservation of some of the larvae, Dr D. P. Wilson for the use of the photograph on Plate I, and Mr G. L. Wilkins for his admirable drawings. My thanks are also due to Mr H. O. Ricketts and Miss B. Skramovsky for technical assistance.

The Distribution of *Octopus vulgaris*

O. vulgaris has a wide distribution in the warmer waters of the Atlantic. It is found from the English Channel southwards as far as the Cape of Good Hope, in the Mediterranean, the Caribbean, at the Canaries, the Azores and Bermuda (Robson, 1929; Pickford, 1945). Farther afield it occurs at some places in the Indian Ocean and in Japanese waters (Sasaki, 1929). It is the common octopus of the Mediterranean where it is the object of fisheries at many places. It has been reported on many occasions from the Red Sea.

The English Side of the Channel

The species occurs in inshore waters along the whole of the south coast from Land's End to Dover, but except in some years it is seldom common. According to Forbes & Hanley (1853, p. 210) the first British record was from Dover; later in 1841 it was taken at Plymouth by Robert Ball. Lee (1875) mentions a specimen captured in a lobster pot at Eastbourne, one from Mevagissey and another from Brighton; all these were exhibited at the Brighton Aquarium in the days when *Octopus* was a star attraction. Other sporadic records indicate that the species is found along the whole coast.

In the years 1899–1900, as mentioned above, there was a plague of *Octopus* along the south coast of Devon and Cornwall. According to Garstang (1900), *Octopus*, which had been scarce in the neighbourhood of Plymouth since the opening of the Laboratory there, became more plentiful from January 1899 onwards. During 1900 the increase reached the dimensions of a plague which had a disastrous effect on the crab and lobster fisheries along the whole coast of Devon and Cornwall. Not only did the *Octopus* invade the crab pots, but they were so numerous, in September 1900, as to drive large crabs out of their normal haunts below low-water mark on to the intertidal region in Plymouth Sound. In the same year Allen & Todd found several *Octopus* 'nested' on the shore of Salcombe Estuary, and Garstang records a minute

Octopus larva in a tow-netting in the same estuary in August. Garstang was inclined to attribute the startling increase of *Octopus* to the warm summers and the mild winters experienced from 1893 onwards, these providing favourable conditions for a warm-water animal. This view is discussed in relation to distribution problems below (p. 374).

Minor plagues appear to have occurred at Brighton in 1913 and 1922 (Robson, 1929), and in the summer of 1948.

Lee (1875, p. 64) records an *Octopus* with its spawn taken in a dredge off Brighton in March 1874. Apart from occasional spawning under artificial conditions in public aquaria, and the two records mentioned, I can find no other records of spawning or of larvae in our inshore waters. Crawshay (1912), in his thorough report on the fauna of the Outer Eddystone, and F. S. Russell, in numerous plankton reports from the Plymouth area, mention neither spawn nor larvae.

Another interesting feature of *Octopus* distribution on the English coast is the absence of nested specimens at low water on the shore, except in plague years.

The Channel Islands and the North Coast of France

Octopus is fairly common on the shore at low water in the Channel Islands and has been reported on numerous occasions.

Dautzenberg & Fischer (1925, p. 1) state that the species is common on both west and north coasts of Finistère. In the Bay of St Malo, Dautzenberg & Durouchoux (1913, p. 7) record its occurrence in shallow water in the *Zostera* beds or lurking under large stones or in crevices of rocks, presumably on the shore. They say that its presence when nested is often indicated by masses of bivalve shells of molluscs on which it feeds.[1]

On the Normandy coast it is recorded for the north and east coasts of the Cherbourg peninsula by Kerville (1898, 1901). He found small specimens on the shore between tide marks on the beach at St Martin, to the west of Omonville la Rogue, as well as specimens in lobster pots. In this area the species is regarded as more or less common. On the east coast of the peninsula, Kerville states that it is very common in holes in rocks and under large stones in the region of Grandcamp-les-Bains. A large specimen was caught between tide marks on the Îles Saint-Marcouf.

Still further east, Loe & Raeymaekers (1885, p. 212) record *Octopus* from the Bay of the Somme, where it is sometimes thrown up on the beach after storms and frequently taken by fishermen in their nets.

Giard (1885, p. 302) also mentions *Octopus* in the eastern end of the Channel from Tour de Croy and Pointe à Zoie, Audresselles. It appears that it is very common under stones from April to September.

The plague year 1899, in particular, is mentioned by Kerville (1901). The

[1] Mr A. E. Salisbury informs me that in the Channel Islands these remains consist almost entirely of *Paphia rhomboides* (Pennant).

species was then very abundant in the region of Omonville la Rogue. Dautzenberg & Fischer (1925) also mention for Finistère that the species was very abundant in some years. Garstang gives additional information, derived mainly from newspaper reports, about the plague on the French coast in which *Octopus* appears to have been as abundant in 1899 as in 1900—unlike the situation on the English coast where the peak as regards numbers was reached in 1900. It appears that the infestation, if it may be so termed, affected the whole coast of Finistère and the Channel Islands, and extended eastwards at least as far as Omonville la Rogue. As on the English coast the lobster and crab fisheries were ruined for the time.[1]

Two features emerge from this survey. The species is normally found close inshore, even nesting at low water on the shore, a habit which occurred on the English coast during 1900. The abundance of *Octopus* reached the dimensions of a plague about a year earlier than it reached its peak on the English side. The significance of these points is discussed below (p. 375).

The Southern North Sea

Records of *Octopus* in the southern North Sea are few and the species appears to be rare. Robson (1929) mentions a specimen from the River Crouch, Essex: this is the only record that can be verified from the east coast of England. For the Belgian coast Adam (1933) has shown that many of the older records are not reliable, but quotes an early record by van Beneden (1883). Adam reported a specimen from Ostende and another taken between Blankenberghe and Orfordness. As Adam remarks, the capture of only two specimens during an intensive survey of the southern North Sea, between 50 and 53° N., is an indication of the rarity of the species in the area.

Tesch (1908), mainly quoting earlier records, mentions several specimens from the Dutch coast, but some of these need verifying. Only three specimens are known from the German coast. One, labelled 'Westerems (Rottum)', is in the Leipzig Museum, and another in the Berlin Museum is from Heligoland. The third was reported from the Borkum area by Hertling (1936).

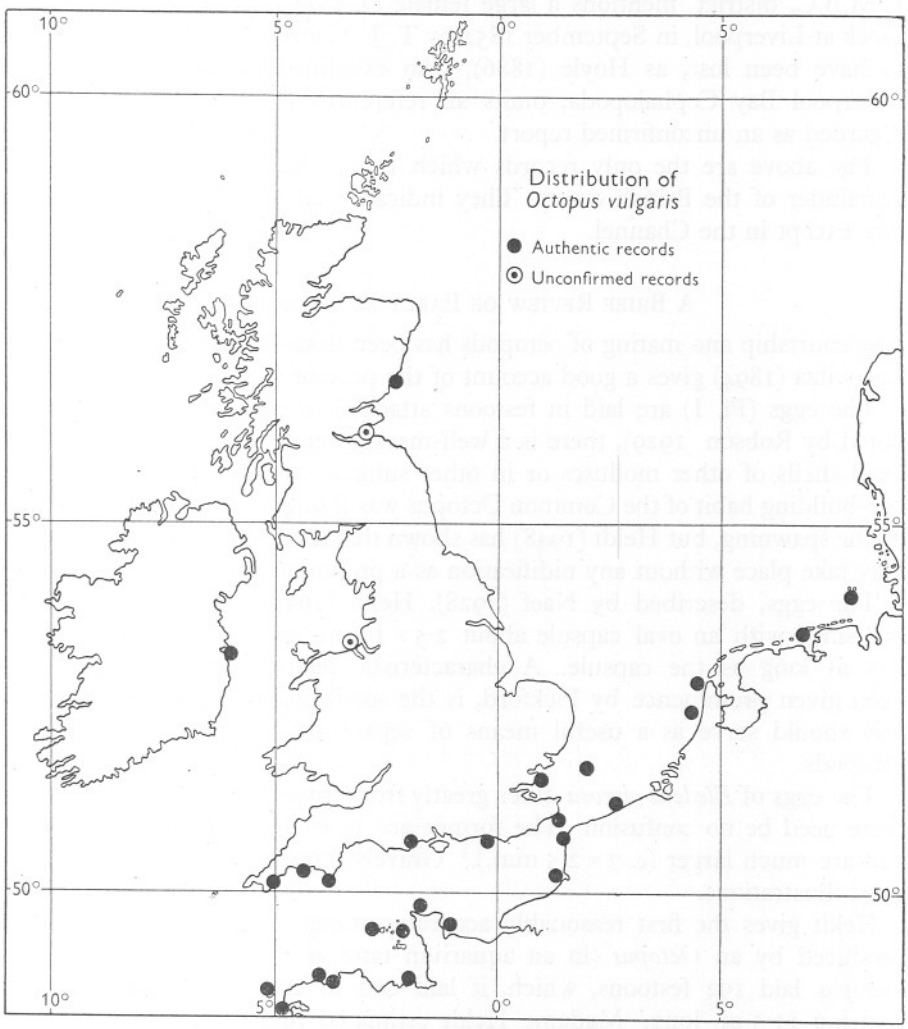
There are no records from the Danish, Swedish and Norwegian coasts.

Other British Coasts

Records of *Octopus* from other British coasts are few and most of them have been discounted by Grimpe (1925) and Robson (1929). The species has been confused with *Eledone cirrosa* which normally has a single row of suckers on

[1] Since this part of the paper was written, I have been privileged to examine a file of newspaper cuttings kept by Mr R. Winckworth. It appears that there was a plague of *Octopus* on the coast of Finistère in 1922 with the usual disastrous effect on the shell-fisheries (*The Times*, 27 March 1922). According to one report the crabs were seeking refuge on the shore in July of that year (*Daily Mail*, 11 August 1922).

each arm. In the latter the suckers may appear to be biserial, as in *Octopus*, particularly in contracted specimens. Occasionally an abnormal *Eledone* is found in which the suckers are irregularly biserial (Gravely, 1908).



Text-fig. 1. The distribution of *O. vulgaris* in North European waters. Token records only are given for the English Channel but all records (usually referring to one or two specimens each) are plotted for other areas.

Early records from the Firth of Forth cannot be verified, but Stephen (1937) confirms a record of a very juvenile specimen, of 1·5 cm. in mantle length, picked up on the beach at Montrose in 1893.

Nearly all of the old Irish records are also doubtful, but the specimens reported by Haddon (1886) from Dublin Bay are in the Museum of Trinity

College, Dublin. These were re-examined by Massy (1909, p. 6), who confirmed that they were *Octopus vulgaris*.

Darbisher (1886, p. 245), in his report on the molluscan fauna of the L.M.B.C. district, mentions a large female *O. vulgaris*, taken in the Albert Dock at Liverpool, in September 1854 by T. J. Moore. The specimen appears to have been lost, as Hoyle (1886), who examined the remainder of the Liverpool Bay Cephalopoda, omits all references to it. This can only be regarded as an unconfirmed report.

The above are the only records which I have been able to find for the remainder of the British coasts. They indicate that *O. vulgaris* is extremely rare except in the Channel.

A Brief Review of Early Development

The courtship and mating of octopods has been described for several species: Racovitza (1894) gives a good account of the present species.

The eggs (Pl. I) are laid in festoons attached to rocks or stones, and, as noted by Robson (1929), there is a well-marked tendency to deposit them in dead shells of other molluscs or in other suitable cavities. The 'nesting' or lair-building habit of the Common Octopus was thought to be an essential part of the spawning, but Heldt (1948) has shown that the laying of batches of eggs may take place without any nidification as a preliminary.

The eggs, described by Naef (1928), Heldt (1948) and Pickford (1950), are small with an oval capsule about $2{\cdot}5 \times 1$ mm. and the stalk is more or less as long as the capsule. A characteristic feature, which has recently been given prominence by Pickford, is the small oval swelling on the stalk; this should serve as a useful means of separating the species from other octopods.

The eggs of *Eledone cirrosa* differ greatly from those of *Octopus*, with which there need be no confusion. The former are pear-shaped with a short stalk and are much larger (*c.* $7 \times 2{\cdot}5$ mm.).[1] Gravely (1908, Pl. II, figs. 7, 8) gives good illustrations.

Heldt gives the first reasonably accurate estimate of the number of eggs produced by an *Octopus* (in an aquarium tank at Salammbô, Tunis). The *Octopus* laid 192 festoons, which, if laid end to end, would have formed a string 11·5 m. long. Madame Heldt estimated that there was a total of 150,000 eggs.

At Naples, Lo Bianco (1909, p. 654) records that spawning in the aquarium takes place from May to September, and Heldt mentions October as the time of spawning of her specimen. Tandy's eggs from Florida were found in August, and Pickford (1950) mentions eggs laid in March and August from the same locality. In the Channel, as already stated, Lee (1875) records an *Octopus*

[1] Naef (1928) gives 6–9 mm. as the length of *Eledone* eggs.

with its eggs in March 1874, while Garstang's larva from Salcombe was found in August and must have come from eggs laid not later than June or July. Portmann (1933), working at Banyuls, found eggs in various phases of development and concluded that they had been developing for about 8 days. They hatched on 4 September, about 18 days after spawning. On the other hand, Naef (1928), working at Naples, found that the larva took 28 days to develop. Portmann attributed the rapid development of his larvae to the high temperature of his aquarium (24–25° C.). In view of much lower temperatures in the Channel, development there may be expected to take at least a month, possibly even longer, and in breeding areas larvae are probably hatched from April or May until the end of September.

According to Lee (1875): 'At this early stage of its existence the young *Octopus* seeks and enjoys the light.' But Portmann states that in his larvae phototropism was less marked than in *Loligo*. This author admits a great mortality among the developing eggs, but assumes it to be due to the absence of the parent, and to the inadequate aeration of some of the eggs.

The early development of the larva within the egg has often been studied. Naef (1928) and Portmann (1933) sum up our knowledge of this development, and the latter states that the fully developed larva possesses a small external vitelline sac at its birth, its contents being absorbed soon after, or sometimes even before, hatching.

Even before hatching the minute *Octopus* is provided with numerous groups of small bristles (Köllikersche Bundel), scattered over the whole outer surface, and Naef considers that their function is to assist the larva to leave the egg. He states: 'These spines or bristles are used when the egg hatches, as seen by me in *Octopus vulgaris*. The hatching occurs with the posterior end in front, as is usual in dibranchiate cephalopods, the opening is rather small, and is situated on the thicker end of the egg capsule; the exit is the same place through which the spermatophores entered, that is, the micropyle. Through this small opening the animal has to liberate itself, this process being helped by the spines which act as hooks. Sometimes the embryo is wrongly placed in the egg capsule, that is, with the oral end towards the opening, in which case it becomes impossible for it to leave the egg capsule and it dies, as it is impossible for it to turn round inside the egg and the spines are now directed in such a way as to face the opening, and so prevent the animal from leaving the capsule.' Portmann disputes these conclusions and points out that in some larvae (7 hr. after liberation) the bundles were still hidden beneath the skin. Querner (1926), on the other hand, considers that these structures indicate that the ancestors of cephalopods were provided with bristles similar to those of annelids. Whatever purpose these bristles serve during liberation, it appears that they help to keep the animal afloat and later develop into the warts which are so characteristic of the skin of the *Octopus*.

The post-embryonic life of the larva has been little studied. Naef (1923,

text-figs. 400, 409) gives a thumb-nail sketch of the newly emerged *Octopus*, of about 1·5 mm. in ventral mantle length, and of some slightly older larvae of about 1·8 mm. in ventral mantle length. He records that larvae of this size are fairly common in the plankton in the Gulf of Naples during the summer and autumn. Naef further remarks that older juvenile stages are not found in the plankton and assumes that they settle on the sea floor, undergoing metamorphosis buried in the sand or detritus, and are found again when they are much larger and have assumed the shape of the adult.

The Channel Larvae

Naef's view of a very brief plankton stage in the life of an *Octopus* has been generally accepted for this species, and Portmann, for example, remarks: 'Il se peut donc que la vie d'*Octopus* ne comprenne pas une première étape pélagique et que la larve mène déjà la vie de la pieuvre adulte.' It was therefore quite unexpected that *Octopus* larvae should be found in the plankton in the middle of the Channel and that they should still be planktonic at a much larger size than mentioned by Naef.

Octopus larvae were found at the stations enumerated below. These are shown in the map in Text-fig. 2 as black circles.

Stations at which Larvae were Found

St. 47. 31. viii. 48. 49° 55′ 20″ N., 02° 08′ W. Sounding 109 m.; N 100 B, 90–0 m. Four larvae.

St. 48. 31. viii. 48. 49° 52′ 10″ N., 02° 10′ 10″ W. Sounding 78 m.; N 100 B, 73–0 m. Seven larvae.

St. 49. 31. viii. 48. 49° 50′ N., 02° 08′ 45″ W. Sounding 73 m.; N 100 B, 69–0 m. Five larvae.

St. 50. 31. viii. 48. 49° 49′ N., 02° 28′ 45″ W. Sounding 127 m.; N 100 B, 100–0 m. Four larvae.

St. 51. 31. viii. 48. 49° 50′ 20″ N., 02° 31′ 40″ W. Sounding 155 m.; N 100 B, 93–0 m. Four larvae.

St. 60. 20. viii. 49. 50° N., 1° 54′ W. Sounding 75 m.; N 100 B, 46–0 m. Seven larvae.

St. 61. 21. viii. 49. 50° 04′ N., 1° 57′ W. Sounding 60 m.; N 100 B, 46–0 m. Thirteen larvae.

St. 62. 21. viii. 49. 50° 06′ 30″ N., 1° 49′ 30″. W. Sounding 57 m.; N 100 B, 43–0 m. Ten larvae.

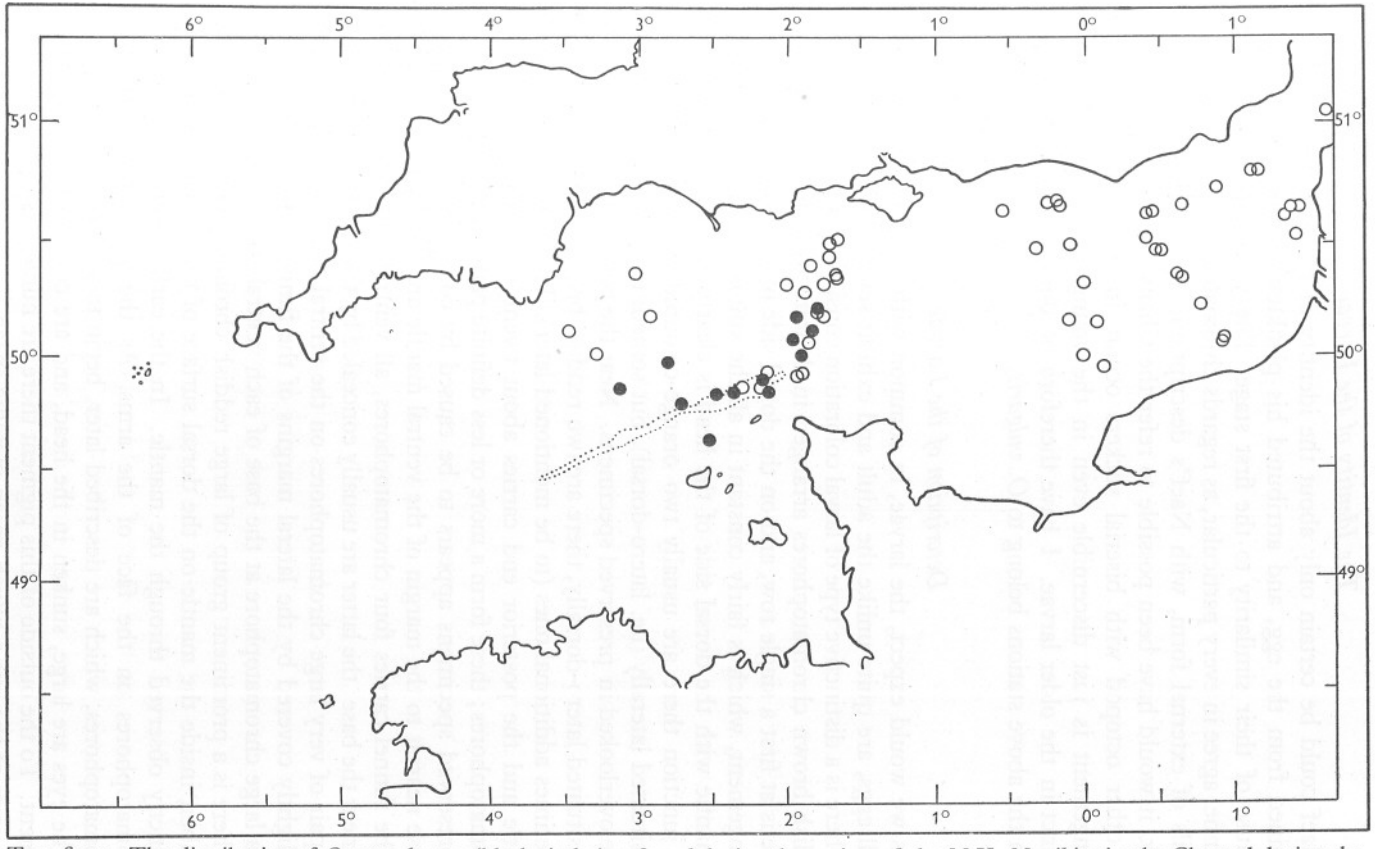
St. 63. 21. viii. 49. 50° 10′ 30″ N., 1° 55′ W. Sounding 55 m.; N 100 B, 53–0 m. Two larvae.

St. 64. 21. viii. 49. 50° 12′ 30″ N., 1° 47′ 30″ W. Sounding 55 m.; N 100 B, 51–0 m. One larva.

St. 71. 30. viii. 49. 49° 58′ 0″ N., 2° 48′ 30″ W. Sounding 66 m.; N 100 B, 29–0 m. Three larvae.

St. 72. 30. viii. 49. 49° 47′ N., 2° 42′ 20″ W. Sounding 124 m.; N. 100 B, 56–0 m. Seven larvae.

St. 73. 30. viii. 49. 49° 37′ N., 2° 30′ 30″ W. Sounding 64 m.; N 100 B, 26–0 m. Two larvae.



Text-fig. 2. The distribution of *Octopus* larvae (black circles) as found during the cruises of the M.Y. *Manihine* in the Channel during the summers of 1948 and 1949. Negative stations (open circles) are also plotted to show the areas worked during the investigations.

The Identity of the Larvae

Naef could be certain only about the identity of his first stage, which he obtained from the egg, and attributed his planktonic larvae to *O. vulgaris* because of their similarity to the first stage. The youngest larvae from the Channel agree in every particular, as regards chromatophore pattern and other details of external form, with Naef's description. Quite apart from Naef's work, it would have been possible to refer the Channel larvae to *O. vulgaris*. No other octopod with biserial suckers occurs in the Channel, and this arrangement is just discernible even in the youngest larvae, and is quite distinct in the older larvae. I have therefore no doubt that the larval series from the above stations belong to *O. vulgaris*.

Description of the Larvae

As we would expect, the larvae, in common with other Octopodinae with small eggs, are quite unlike the adult and exhibit several characteristics.

There is a distinctive type of larval coloration consisting of large, prominent, reddish brown chromatophores arranged in definite patterns. On the arms, there is at first a single row, and on the dorsal side of the head a symmetrical arrangement, which is fairly constant in all the younger stages. The junction of mantle with the dorsal side of the head is clearly visible, and just behind this junction there are usually two orange-coloured chromatophores; these are situated laterally (i.e. latero-dorsal), but sometimes they are faint and apt to be overlooked in preserved specimens. Near the posterior end of the body, also situated latero-dorsally, there are two reddish brown chromatophores and sometimes additional ones (to be mentioned later). The ventral surface of the mantle and the posterior end carries about twenty distinct reddish brown chromatophores; these form a more or less definite pattern, but its irregularity in preserved specimens appears to be caused by contraction of the mantle. Those nearest to the margin of the ventral mantle are usually in a row of six.

The funnel carries four chromatophores, all ventral, two near the tip and two near the base; the latter are usually concealed by the mantle margin. There is a pair of very large chromatophores on the ventral head, one on either side or slightly covered by the lateral margins of the funnel, and there is also an extra large chromatophore at the base of each ventral arm.

There is a prominent group of large reddish chromatophores, six to ten in number, inside the mantle on the dorsal surface of the viscera; these can be distinctly observed through the mantle. In the earliest stages there are no chromatophores on the face of the arms. As the larva grows, additional chromatophores, which are described later, begin to appear.

The eyes are large, sunken in the head, and are covered with dark brown pigment. To the outside of this pigment there are numerous iridocytes, which give parts of the eye a bluish-green metallic sheen.

The arms are quite short in early stages (Pl. II, figs. 1, 2). They are all about the same length and have a thin whip-like terminal portion.

The youngest Channel larvae were provided with three or four primary uniserial suckers, each with a diameter of 0·175–0·2 mm. Larvae of 2·25–3·45 mm. (mantle length) had primary suckers of 0·25–0·3 mm. in diameter. In larger larvae of 3·75–6·0 mm. the diameter of primary suckers reached 0·35–0·55 mm. and those of the first part of biserial suckers, 0·25–0·5 mm.

The web is poorly developed, showing no sign of differentiation in depth. Only the rims of the jaws appear to be chitinized.

The newly hatched *Octopus* is covered on head, mantle and arms with numerous groups of bristles; but in the preserved specimens the latter are not easily seen, because they tend to disappear in formalin. They are believed, apart from whatever role they may play in the release of the larvae from the egg, to have some significance in the planktonic life of the animal (Naef, 1928; Adam, 1937). In the Channel larvae they are present at all stages up to the largest of 6 mm. in ventral mantle-length. In the latter, they appear to be in process of being transformed into the warts of the adult.

In the youngest larvae the mantle width is frequently greater than the mantle length. Between 1·8 and 2·4 mm. (that is, in ventral mantle length) the length overtakes the width, and beyond this size the mantle length is always greater than the width. This is clearly indicated in Text-fig. 3, where the mantle width is expressed as a percentage of the mantle length. There is a suggestion too that the mantle is more elongated during its growth between 3 and 4·5 mm. than when it grows beyond this stage. Unfortunately the number of larvae of this size are too few to give adequate results and it must be remembered that the mantle itself is capable of much variation.[1]

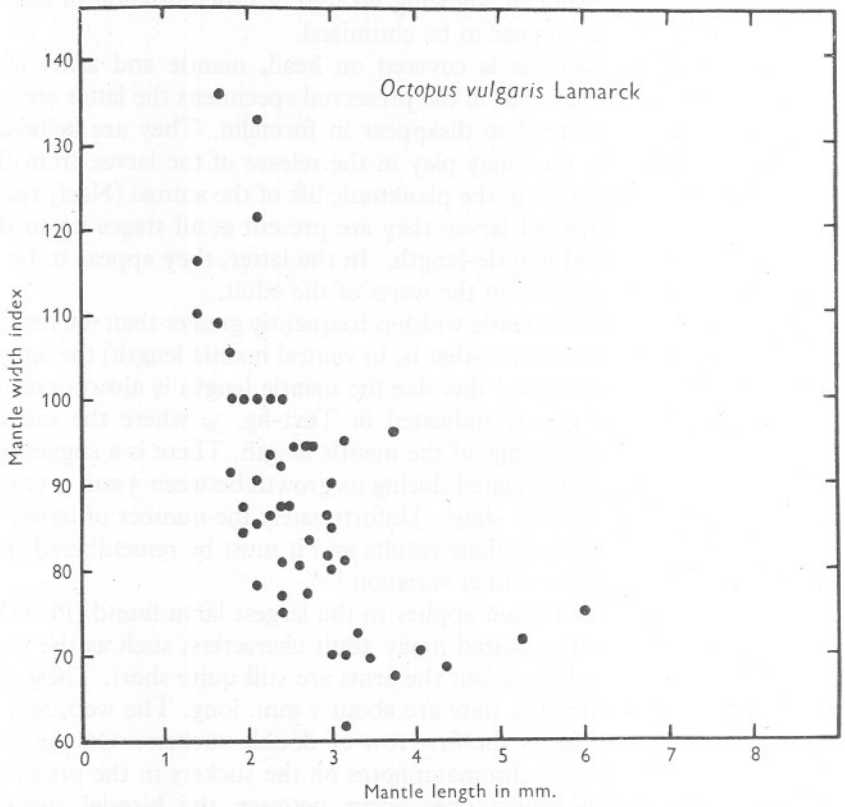
The following brief description applies to the largest larva found (Pl. III). This specimen has already acquired many adult characters, such as the proportions of the mantle and head, but the arms are still quite short. These are subequal, and in the contracted state are about 7 mm. long. The web, too, is subequal and reaches as far as the first row of double suckers. On the oral face of the arms there are no chromatophores on the suckers in the proximal web region, but reddish brown ones occur between the biserial suckers beginning with the first pair (Pl. III, fig. 8). Some suckers on the arms are also developing chromatophores around their rim, in the same way as illustrated by Adam (1937, fig. 30H) for his *Octopus* larva from the coast of Brazil.

The outer surfaces of the arms carry a double row of evenly spaced chromatophores, and, in addition to these, two further rows are developing, one on either side of the arms; those on the dorsal and dorso-lateral arms are

[1] The ventral mantle length is used by all workers on Cephalopoda and is regarded as a more reliable measurement than those of the head, arms and funnel. It is for this reason that I have refrained from giving measurements of the head and arms, but the proportions in larvae at different stages can be seen from the drawings.

better developed than those on the ventral arms. There are also light orange-coloured chromatophores developing in the surface skin of the head and web. Some on the former are difficult to see because they are situated over the more deep-seated chromatophores of the head region. In this specimen there are also four reddish brown surface chromatophores on the surface of the mantle, at its junction with the head.

Intermediate younger stages are illustrated in Pl. I.



Text-fig. 3. The relation of mantle length to mantle width in the Channel larvae. The mantle width is expressed as a percentage of the mantle length.

The Source of the *Octopus* Population in British Waters

The Rarity of Spawn and Larvae in Inshore Waters

It has already been indicated that the eggs of *Octopus* have been found only on one occasion on our coast. This alone is insufficient proof of absence of regular breeding, because the eggs of *Eledone* are almost equally scarce and both species probably lay their eggs in places which are almost inaccessible to the ordinary dredge or trawl. The absence of any report of planktonic larvae,

except in the abnormal year 1900, during the whole existence of the Plymouth Laboratory is much more significant and may be regarded as reasonable proof that the species breeds here only under abnormal conditions. *Eledone*, as is well known, breeds all round our coast but its larvae are rarely found in the plankton for a very different reason, so I believe. Its eggs are large, 6–9 mm. in length, so that the embryo is able to complete its larval development before hatching. As Naef (1923) has shown, the young *Eledone* already possesses all the characteristics of the adult form, and so on liberation is nearly ready to settle down to a benthic existence.

It is therefore extremely doubtful whether the *Octopus* is able to maintain a breeding stock on the English side of the Channel, and the most likely explanation is that the population is an immigrant one, maintained each year by an influx of young from the south, reinforced in exceptional years by limited local breeding.

The Dispersal of Larvae by Water Movements

The duration of the planktonic life of the young *Octopus* is certainly not short as assumed by Naef. Judging from my larvae the period could not be less than 1 month and might even be 3 months, under exceptional circumstances. This moderately long planktonic life enables us to consider dispersal by currents and other water movements. In this connexion, the work of Carruthers (1927) with drift bottles in the English Channel proves very interesting, especially as many of his bottles were released in approximately the area in which the larvae were found. Most of the larvae appear to have been taken in the mid-water and surface layers with open nets.

Although the larvae are not strictly comparable to either surface or bottom bottles, the experiments of Carruthers are of sufficient interest to indicate in a broad way the future movements of larvae. I have not considered the movements of surface bottles very closely, because they may have been unduly influenced by wind drift, and the bottom bottles are probably more reliable for our purpose.

There is an easterly set along the north coast of Finistère which impinges on the Manche coast and swings northwards past the Channel Islands. This is borne out by both surface and bottom bottles. To the north of the Channel Islands, as Carruthers states, 'there seems to be in longitude 2° W. (approximately) a parting of the ways in respect of the movements of the bottom water. To the north of 50° N. latitude there appears to be a west-going bottom set, whereas south of this parallel there is a set going in an easterly direction'. This is the very area in which the *Octopus* larvae occur; many of the latter are obviously recently hatched, some being no longer in mantle length than specimens just released from the egg. The hydrographic conditions indicate that they come from the south, that is, the Channel Islands, the Manche coast, and possibly also the north coast of Finistère. These areas are undoubtedly

important, if not the main, breeding grounds of *Octopus* in the Channel, and from them the species is distributed westwards to Lyme Bay and beyond, and eastwards to Dover and also occasionally into the North Sea. It is also possible that Lyme Bay may draw some of its *Octopus* from a more south-westerly source, as may Cornwall and the Plymouth area. We do not know whether *Octopus* reaches Cornwall from the east in 'Channel water', or from across the Channel, in one of the bodies of water known to penetrate into the Channel occasionally from Ushant and the Biscay region (see Russell, 1939). As far as I am aware, no larvae have been taken in this outer part of the Channel, and it may be that they become benthic at some distance from our coast. Winckworth (1928), discussing the scarcity of male specimens, states 'the scanty evidence available points to the probability that mating takes place in deeper water after which the females migrate towards the shore to spawn'.

There may also be subsidiary breeding areas along the French coast between the Cherbourg Peninsula and Boulogne, but available evidence indicates that *Octopus* is much less abundant there than it is to the west of the Peninsula.

The conditions found by Carruthers (1927) were those existing in July 1924, and as Russell has shown (1939) the water circulation in the Channel is very variable. These fluctuations will regulate the number of larvae distributed to various points of our coastal areas, so that Brighton, for instance, may have a dearth of *Octopus* during a year when they are fairly common in Lyme Bay.

I am inclined to regard the easterly set along the north coast of Finistère, carrying larvae to the coast of the Manche and the Channel Islands, as a very important factor in maintaining the stock of *Octopus* in the Channel, as the larvae would reinforce the local stock at this northern limit for breeding. As temperature is undoubtedly the most important factor controlling breeding in this area, a succession of years of low sea temperature would mean that few larvae would hatch out and reach maturity. These reinforcements would help to maintain the stocks.

The Plague Years

The plague years 1899 and 1900 were probably due to a combination of factors, all favourable to the multiplication and spread of the species in the Channel.

As already mentioned, temperature is undoubtedly a controlling factor and, as Garstang believed, the abnormal conditions probably began in 1893, an exceptional year, during which 'Under the influence of the great heat the temperature of the Channel waters rose continuously until in August it had attained a point unprecedented for a quarter of a century.... In June the tow-nets were crowded with Salps, while towards the latter end of August they were almost choked by masses of living Radiolaria.... Even the bottom fauna was influenced, as was shown by the extraordinary abundance in the Sound....'

(Garstang, 1894). The French coast, too, was influenced by the exceptional conditions, as there was a heavy fall of oyster spat in that year (Herdman, 1893). Later (1900) Garstang adds: 'The warm summers and mild winters which we have experienced during the past few years (i.e. since 1893) have also provided the conditions most suitable to a warm water animal and have favoured its residence in our inshore waters.'

The fauna of the north-west coast of France and the Channel Islands is much richer in southern species than the corresponding coast of Britain. This may be partly accounted for by a slightly higher temperature, but the hydrographic conditions undoubtedly play a big part. Unfortunately, we know so little about the penetration of various bodies of water, from the mouth of the Channel and the Biscay area, along the south side of the Channel. The relative abundance of the commoner littoral forms on the two sides of the Channel, has been the subject of a report by Fischer-Piette (1936).

On the French side of the Channel there appears to have been a gradual building up of stocks during these years, culminating in the plague of 1899. It is also possible that there may have been large-scale immigration of larvae from the west coast of France, in the years immediately prior to 1899. The crab and shell-fisheries were ruined by the hordes of hungry *Octopus* and fishermen were forced to seek alternative employment. On the English side there was no indication of a building up of the population before 1899, but from January of that year the species became increasingly plentiful, reaching its greatest abundance in 1900, causing widespread damage to the shell-fisheries by the end of the year. Garstang thought that the plague on the English coast was caused by dearth of food on the French side, resulting in 'migrations outwards from the overcrowded centres of multiplication'. This view is probably correct because a great many of the *Octopus* were large, reaching a span of 7 ft. from tip to tip of outstretched arms. These could not be less than 3 or 4 years old, and before 1899 there was no indication of an increase in the *Octopus* population.

The abundance of *Octopus* at Brighton in 1913 appears to be the outcome of favourable hydrographic conditions concentrating numerous larvae in the area in an earlier year. This was likely to be the year 1911 when a warm fine summer was experienced. I have no information on the prevalence of the species in Brittany and the Channel Islands for these years.

The second minor plague at Brighton, late in 1922, was obviously similar and probably linked with the more serious plague on the coast of Finistère in 1922.

In May 1948 a plague of young *Octopus* was reported at Brighton by the Press. These appear to have been mostly small specimens and may reasonably be regarded as brood of 1947, another favourable year for breeding.

Quite recently, January 1950, an increase of *Octopus* was reported from the Channel Islands, with the usual complaint from fishermen that they were

devouring the shellfish.[1] The exceptionally warm summers we have experienced in recent years have undoubtedly favoured the increase of *Octopus*.

The finding of a young *Octopus* on the beach at Montrose in Scotland can probably be attributed to the exceptional hydrographic conditions in the year 1893. In order to reach this point, the larva must have had an extended planktonic life in the North Sea. This raises the question whether benthic cephalopods with planktonic larvae are able to prolong their life in the plankton, in the same way as annelids, when the factors which induce 'settlement' are absent. It is possible that the Dublin Bay specimens were also carried beyond their normal range because of some unusual hydrographic conditions.

Summary

In Britain *Octopus vulgaris* occurs on the Channel coast and only very rarely on other coasts. In Brittany and the Channel Islands it frequently makes its lair at low water, but on the English side of the Channel it does not come so close inshore except in abnormal years of high sea temperatures.

The discovery of *Octopus* larvae of various sizes, from newly hatched to 6·0 mm. (mantle length), in plankton hauls taken to the north of the Channel Islands, proves that the species has a much longer planktonic life than hitherto supposed.

The water circulation in the English Channel, as indicated by drift bottles, is admirably suited to the dispersal of larvae to our shores from breeding centres on the coasts of Brittany and the Channel Islands.

Thus our *Octopus* population is believed to be an immigrant one maintained each year by an influx of larvae, and the vagaries of the water movements each year would account for the fluctuations in the abundance of the species.

Periodic plagues of *Octopus* appear to be due to good weather conditions over a succession of years causing a higher sea temperature, ensuring better breeding conditions for a warm water animal at the northern limit of its breeding range.

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[1] *Daily Telegraph*, 19 January 1950.

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EXPLANATION OF PLATES

PLATE I

Eggs of the Common Octopus (*Octopus vulgaris* Lamarck) spawned in an aquarium tank at Plymouth, March 1947. The strings of eggs hang from the roof of a small cave just large enough to contain the octopus. They were found and photographed when the tank was drained for cleaning.

PLATE II

Figs. 1–4. *O. vulgaris* Lamarck; larvae from the English Channel; del G.L.W. Fig. 1. Dorsal view of larva of 2·4 mm. in ventral mantle length. Fig. 2. Ventral view of same specimen. Fig. 3. Dorsal view of larva of 3·15 mm. in ventral mantle length. Fig. 4. Lateral view of larva of 3·75 mm. in ventral mantle length.

PLATE III

Figs. 5–8. *O. vulgaris* Lamarck; the largest larva, St. 72, 30. viii. 49; del G.L.W. Fig. 5. Dorsal view. Fig. 6. Oral face of web and tentacles. Fig. 7. Ventral view. Fig. 8. Enlarged view of arm suckers.

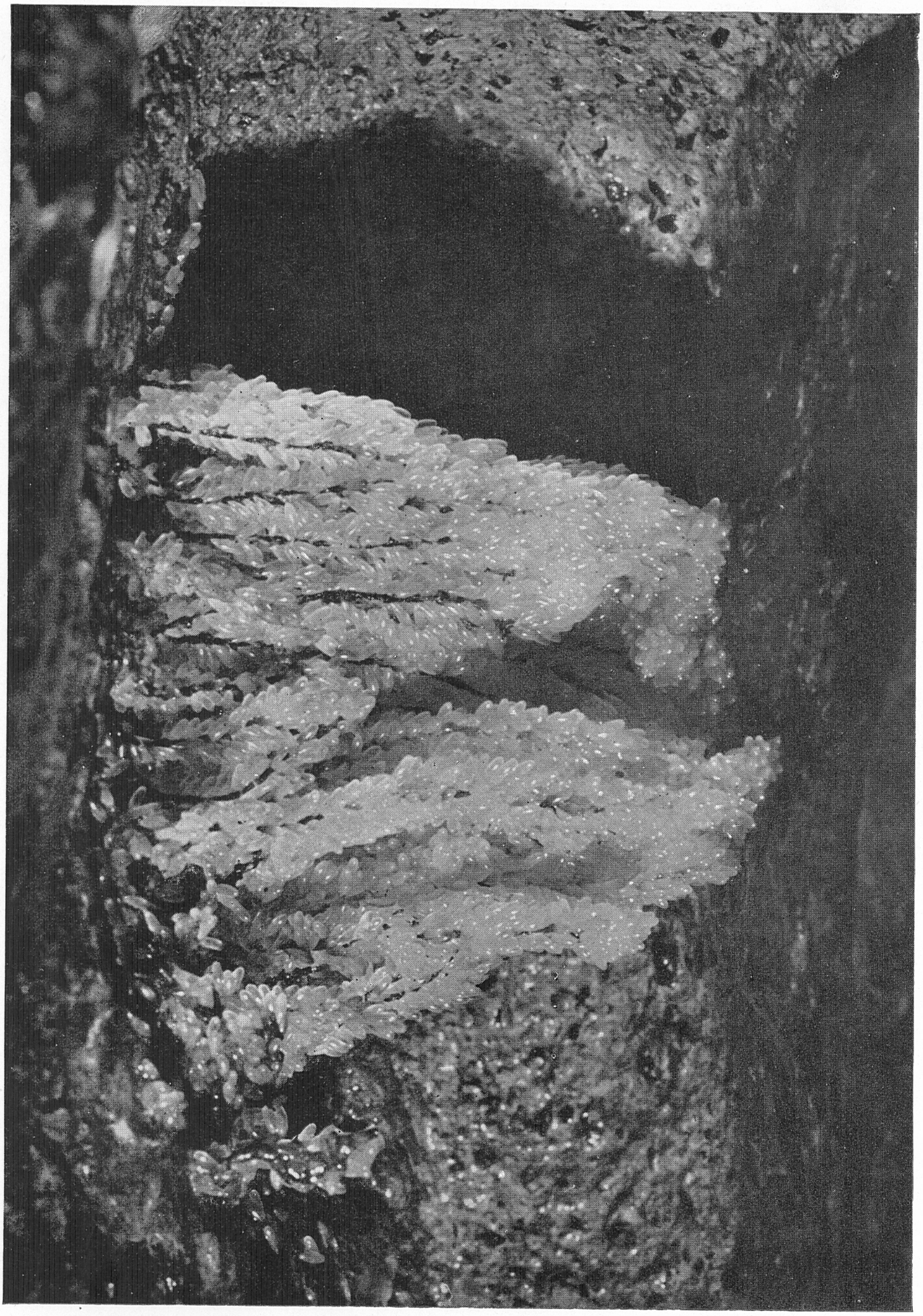
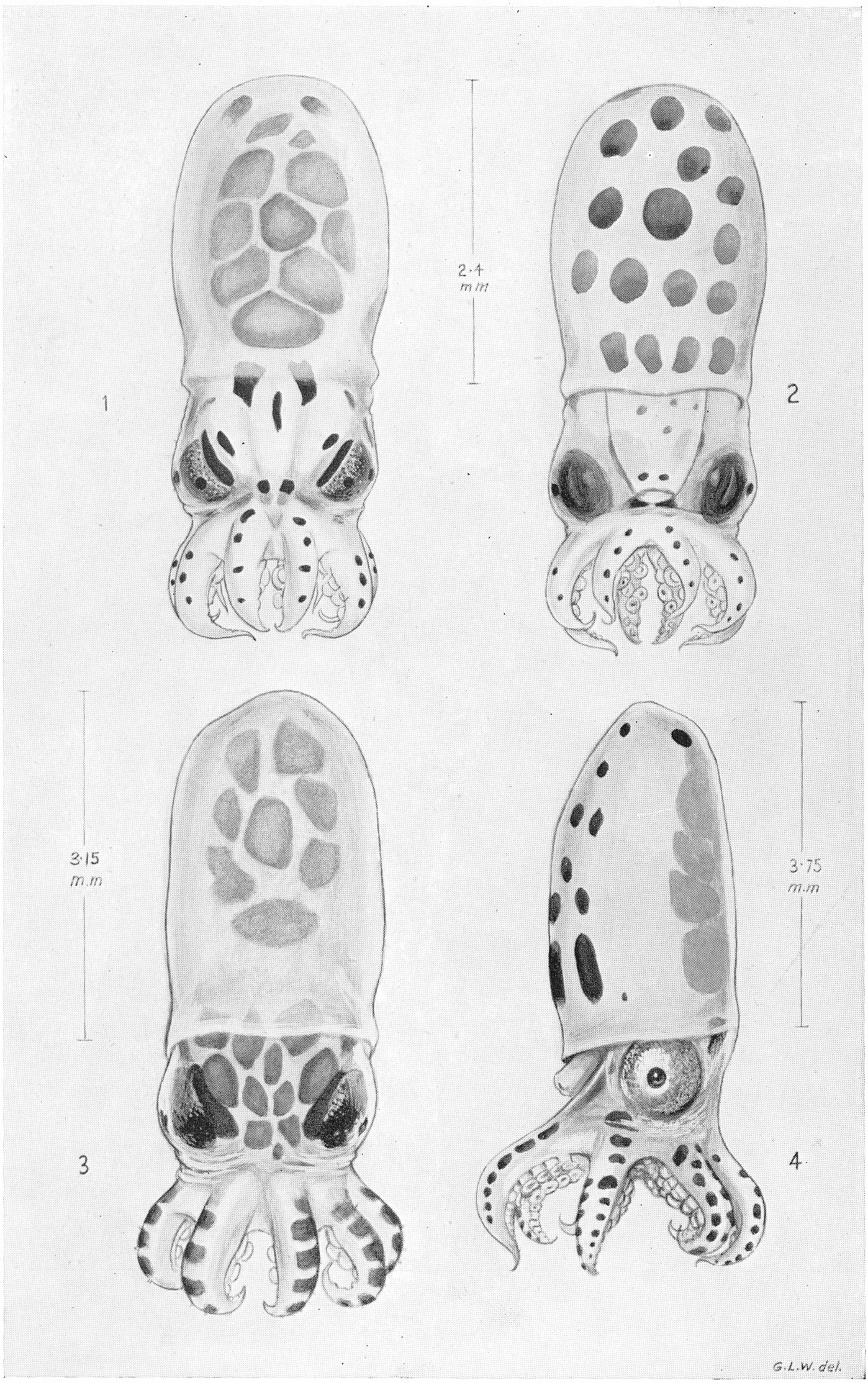
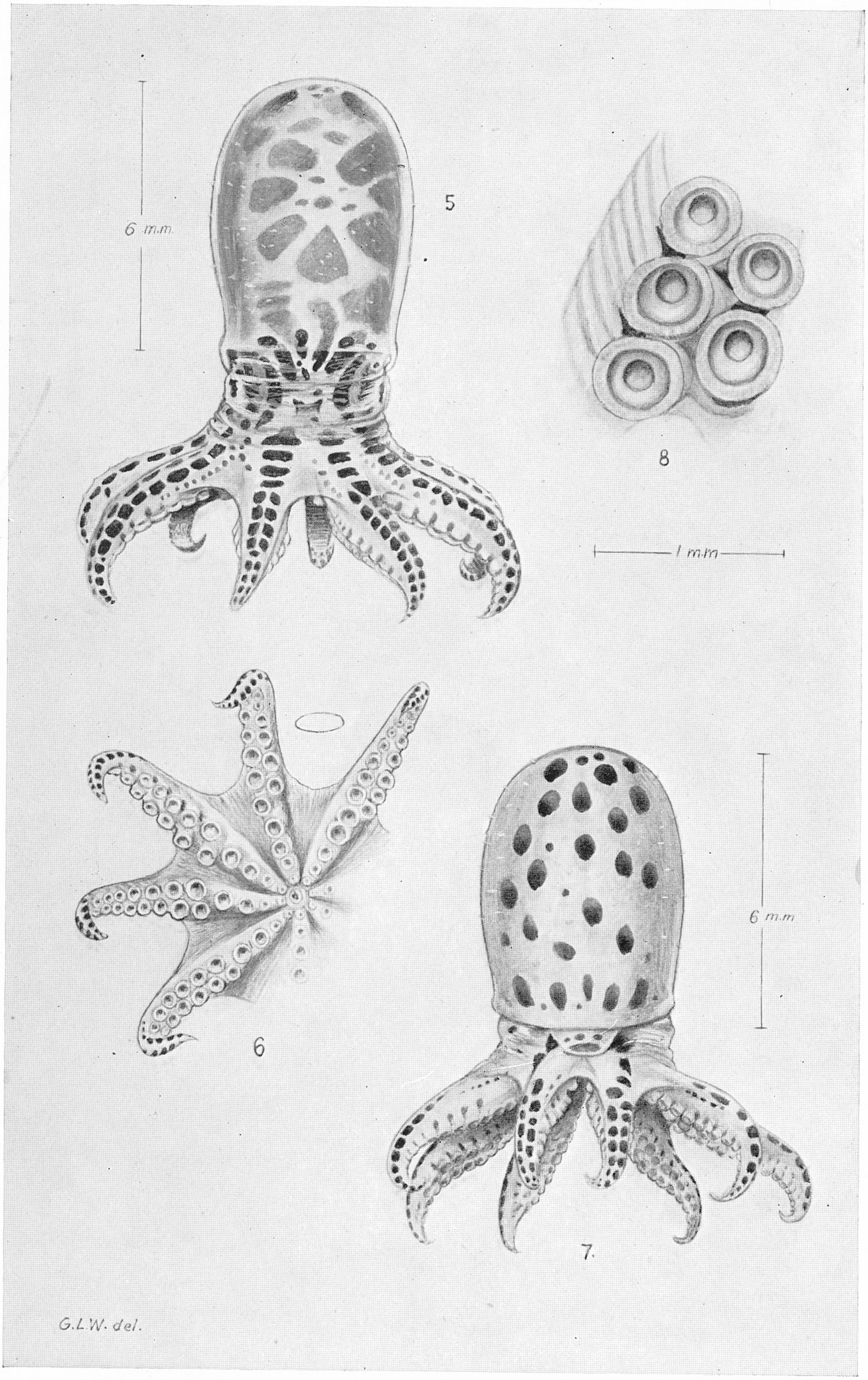


Photo by D. P. Wilson



Figs. 1–4.



Figs. 5–8.

THE SEASONAL VARIATION IN THE CELLULOSE CONTENT OF THE COMMON SCOTTISH LAMINARIACEAE AND FUCACEAE

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(Text-figs. 1–6)

Introduction

Algal cellulose appears to have been relatively little studied and there is no information as to its seasonal variation in the brown marine algae. A study of the literature reveals numerous contradictions. In 1884, Stanford indicated in a report on alginic acid that he had obtained pure cellulose representing 10–15% of the air-dried plant.

Kylin (1915) showed that algal cellulose gave the characteristic colour reaction with iodine and sulphuric acid. He boiled the material in turn with 1·25% sulphuric acid and 1·25% sodium hydroxide and called the insoluble residue cellulose.

In 1926, Atsuki & Tomodo obtained a crude fibre figure of 6% for *Laminaria saccharina*, but stated that the greater part of the crude fibre of the laminarias consisted of the hemicelluloses and that there was so far no evidence of the normal cellulose.

Ricard (1931) removed the alginic acid with sodium carbonate, then treated the residue with dilute boiling solutions of sulphuric acid and potassium hydroxide. The hydrolysis of the residual material with sulphuric acid gave only traces of reducing sugars, and the author did not regard it as cellulose but called it algulose. *L. flexicaulis* contained 4·3–7·6% of this material and *L. saccharina* 2·8–10·9%.

Dillon & O'Tuama (1935), however, isolated cellulose from the brown algae. The residue after the removal of alginic acid with dilute ammonia was treated with dilute hydrochloric acid and then several times with boiling 5% sodium hydroxide. It was finally washed with alcohol and ether, and was shown to have the properties of cellulose. On hydrolysis with hydrochloric acid it gave glucose characterized by the isolation of the glucosazone, and with carbon disulphide it formed a viscose resembling the viscose from ordinary cellulose. They also prepared acetylated and methylated compounds with properties similar to those of the corresponding derivatives of ordinary cellulose.

Russel-Wells (1934) determined the crude fibre content of various algae and showed by its solubility in cuprammonium hydroxide and by its acetate that this fibre was cellulose.

Viel (1939) carried out a systematic study of the celluloses from *Fucus vesiculosus* (2·10%), *F. serratus* (2·81%), *Laminaria saccharina* (6·9%) and *L. cloustoni* (5·04%). Analysis showed the carbon-hydrogen percentages to be remarkably similar and in agreement with $(C_6H_{10}O_5)_n$. Hydrolysis gave 90% glucose, while thermal fractionation of the products of pyrogenation gave graphs comparable with those of previously studied vegetable celluloses.

Recent work by Percival & Ross (1949) has shown conclusively that algal cellulose is essentially the same as cotton cellulose. Hydrolysis with 72% sulphuric acid gave only D-glucose. Cellobiose octa-acetate was prepared by acetolysis indicating the presence of 1:4-β-linkages. Determinations by periodate oxidations indicated a chain length of 160 units, but the original cellulose was no doubt degraded during isolation. Finally, X-ray diagrams of algal cellulose showed the characteristic pattern of normal cellulose.

Experimental

The samples analysed were those taken in 1946 and previously reported by the writer (1948*a*,*b*, 1949). The cellulose was estimated as follows.

Ground seaweed (2 g.) was boiled under reflux with sulphuric acid (200 ml., 1·25%) for 30 min., filtered by suction through a 1 × 2 Gallenkamp sintered glass crucible, washed free from acid with water, and the residue boiled with sodium hydroxide (200 ml., 1·25%). After boiling in this way for 30 min., the solution was filtered through the 1 × 2 crucible and washed with water. The residue was removed from the crucible and kept overnight in chlorine water (100 ml. saturated), filtered on a weighed hardened paper, washed free from chlorine and washed on the filter with hot sodium hydroxide solution (50 ml. N/10). The residue was washed with water until free from alkali and finally with alcohol and ether, and then dried at 50° for 10 min. to give a white product which was weighed.

When applied to *Fucus* spp. the residue after treatment with boiling sodium hydroxide and chlorine water was often slimy and difficult to filter, and separation by centrifuging was necessary.

The results are given in Figs. 1–6.

Discussion of Results

General

Very little is known regarding the structure of the cell wall of the Phaeophyceae. Fritsch (1945) concludes that it consists of pectic substances with a layer giving the reactions of cellulose adjacent to the protoplast. In the brown algae the pectic substance is no doubt alginic acid which, with its long

chain structure, will give flexibility to the plant. To withstand wave-action such a structure is probably reinforced with cellulose, and the results of this investigation show that the cellulose content increases with the depth of immersion, when additional strength is required by the plant.

Very little is known, also, regarding the metabolism of the brown algae, but in the absence of any reducing sugars, it would appear that mannitol is probably the primary product of photosynthesis. In 1933, Khouvine showed that cellulose could be synthesized from mannitol by *Acetobacter xylinum*, and quite independently Barsha & Hibbert (1934) obtained the same results and showed that the cellulose membranes were chemically identical with cotton cellulose. In the brown algae, therefore, mannitol is probably the precursor of the cellulose.

The Laminariaceae

Laminaria cloustoni

In Fig. 1 the graphs for the stipe, the frond and the whole plant show that the cellulose content on the anhydrous basis exhibits two maxima and two minima in the year. Similar graphs have been obtained for several of the other constituents (Black, 1948*a*,*b*, 1949) and for the diatom periodicity, and sometimes there is a correlation with the nutrient content of the water and the periods of rapid and slow growth (Black & Dewar, 1949).

In March, when the new frond is forming, the cellulose is at a maximum of 5·76% in the frond and 10·27% in the stipe. From March to June/July a period of rapid growth occurs with an increase in the mannitol content while the cellulose content decreases. This may be due to the accumulation of mannitol in the whole plant or to elongation during rapid growth. From June to August/September during the period of slow growth, when the nutrients are absent from the sea water, the cellulose content increases again, while at the same time laminarin is also increasing (Black, 1948*a*). In September, when the nutrients are again regenerated in the sea water, there is probably a second period of growth and a decrease in the cellulose content occurs. It would appear, therefore, that when the results are expressed on the anhydrous basis a correlation exists between the cellulose content and the periods of rapid and slow growth. When the results, however, are calculated on the wet basis (Fig. 2) two maxima are again recorded, one in February/March and the other from September to November. On the dry basis the cellulose content begins to fall in April and continues to fall until June; on the wet basis it is constant and at a minimum from April to June, due to the dry weight increasing with a rapid increase in mannitol. From June to November the cellulose on the wet basis increases while on the dry basis it begins to decrease in September, the increase in dry-weight content now being due to an increase in laminarin. A rapid decrease then occurs in December, the period of sporogenesis of this species, and this is probably accompanied by an increase in the uptake of water, as there is a considerable decrease in the dry-matter content both in

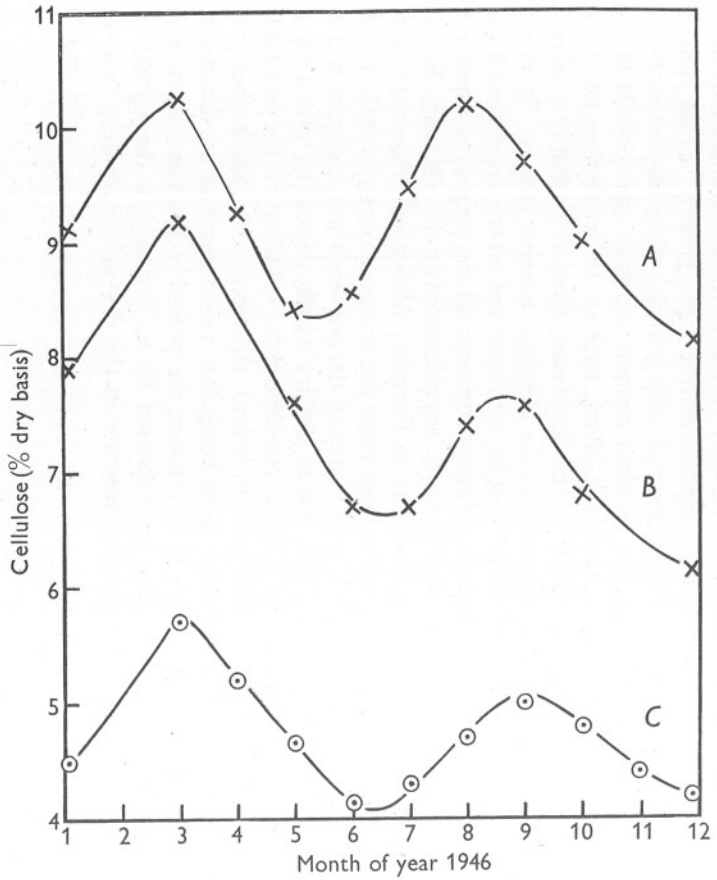

Fig. 1. Seasonal variation in the cellulose content of *Laminaria cloustoni* (dry basis): (*A*) in the stipes; (*B*) in the whole plant; (*C*) in the fronds.

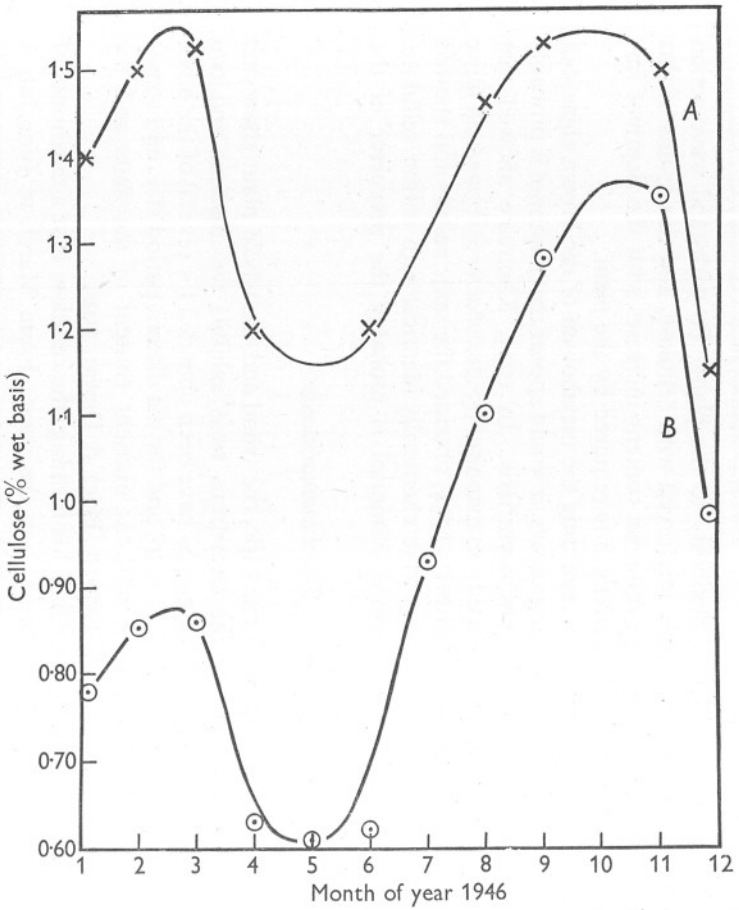

Fig. 2. Seasonal variation in the cellulose content of *Laminaria cloustoni* (wet basis): (*A*) in the stipes; (*B*) in the fronds.

stipe and frond, which explains the rapid decrease on the wet basis while there is little change on the dry basis. On the wet basis, therefore, there would appear to be a correlation between the cellulose content and the reproductive cycle of the plant.

Laminaria saccharina

In this species the cellulose content (dry basis) of the frond (4–5%, Fig. 3) is of the same order of magnitude as that of *L. cloustoni* frond (Fig. 1), but the stipes contain less cellulose (7–8%) than those of *L. cloustoni* (8·5–10%). Considerably less seasonal variation occurs in this species, but despite this the two maxima are apparent in the year and occur at approximately the same time as those of *L. cloustoni*.

Laminaria digitata.

The cellulose content of this species (Fig. 4) undergoes a similar seasonal variation to that of *L. saccharina*, with the exception of the loch frond samples in which the variation is between 3 and 5%. In general, however, the graphs are very similar and exhibit two maxima in the year and a distinct minimum in July.

The cellulose graphs on a wet basis for *L. saccharina* and *L. digitata* have been omitted. The only outstanding feature in both species is that the graphs for the open-sea samples show less seasonal variation (0·5–0·7%) than those for the loch samples (0·5–1·0%). This is due to the marked seasonal variation in dry matter which occurs in the loch samples as the result of the accumulation of laminarin. This is in agreement, to a certain extent, with the theory that the cellulose content can be correlated with the periods of growth. At Atlantic Bridge the *L. digitata* frond grows to a length of 7–8 ft. (213–244 cm.), growth appears to continue throughout the summer and there is very little laminarin formed. The dry weight shows little change and there is no marked variation in the cellulose content. On the other hand, in Loch Melfort, the *L. digitata* frond only grows to a length of about 2–3 ft. (61–91 cm.), laminarin accumulates and there is a marked increase in the dry-matter content. It appears, therefore, that laminarin is formed when photosynthesis can proceed, but some other factor is limiting growth.

The Fucaceae

With the exception of *Fucus spiralis*, which contains approximately 4·5% of cellulose (dry basis) throughout the year, there appears to be a correlation between the cellulose content of the Fucaceae and the depth of immersion of the species, the cellulose increasing from about 1% in *Pelvetia canaliculata* to 2–2·5% in *Fucus serratus* and *F. vesiculosus*. On the anhydrous basis the cellulose content of *Pelvetia canaliculata*, *Ascophyllum nodosum* and *Fucus spiralis* remains relatively constant throughout the year (Fig. 5). But when the results

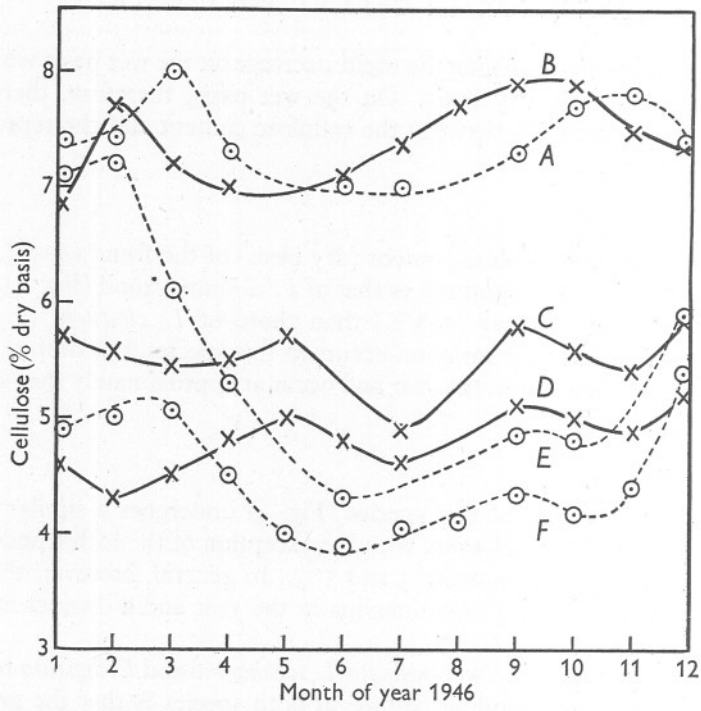

Fig. 3. Seasonal variation in the cellulose content of *Laminaria saccharina* (dry basis): (*A*) in the open-sea stipes; (*B*) in the loch stipes; (*C*) in the loch whole plants; (*D*) in the loch fronds; (*E*) in the open-sea whole plants; (*F*) in the open-sea fronds.

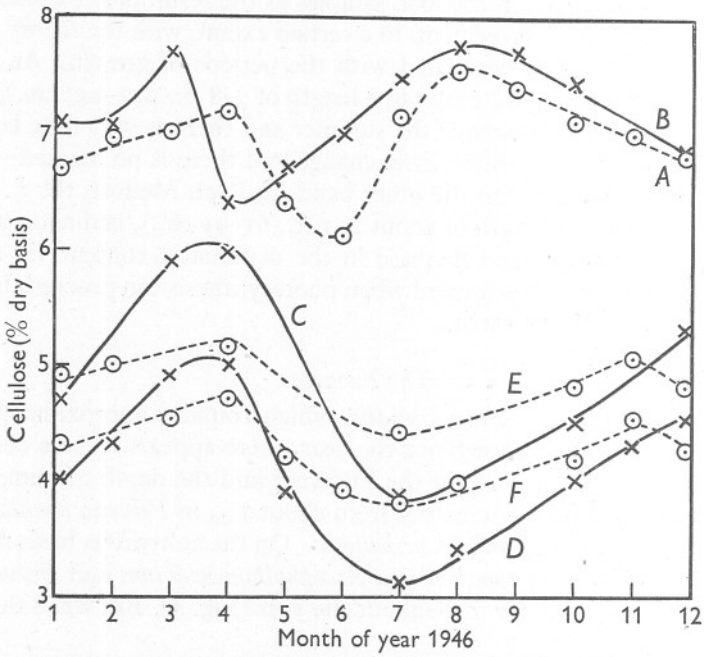

Fig. 4. Seasonal variation in the cellulose content of *Laminaria digitata* (dry basis): (*A*) in the open-sea stipes; (*B*) in the loch stipes; (*C*) in the loch whole plants; (*D*) in the loch fronds; (*E*) in the open-sea whole plants; (*F*) in the open-sea fronds.

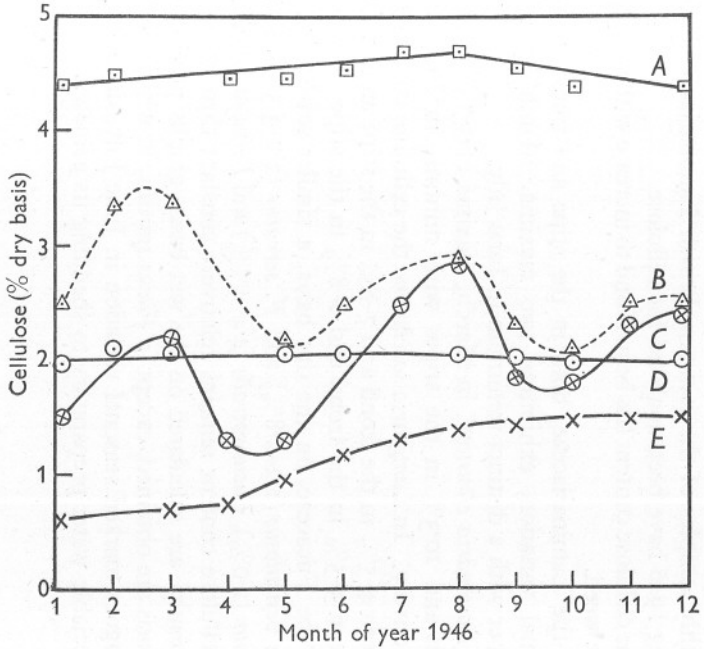

Fig. 5. Seasonal variation in the cellulose content of the Fucaceae (dry basis): (*A*) *Fucus spiralis*; (*B*) *F. serratus*; (*C*) *F. vesiculosus*; (*D*) *Ascophyllum nodosum*; (*E*) *Pelvetia canaliculata*.

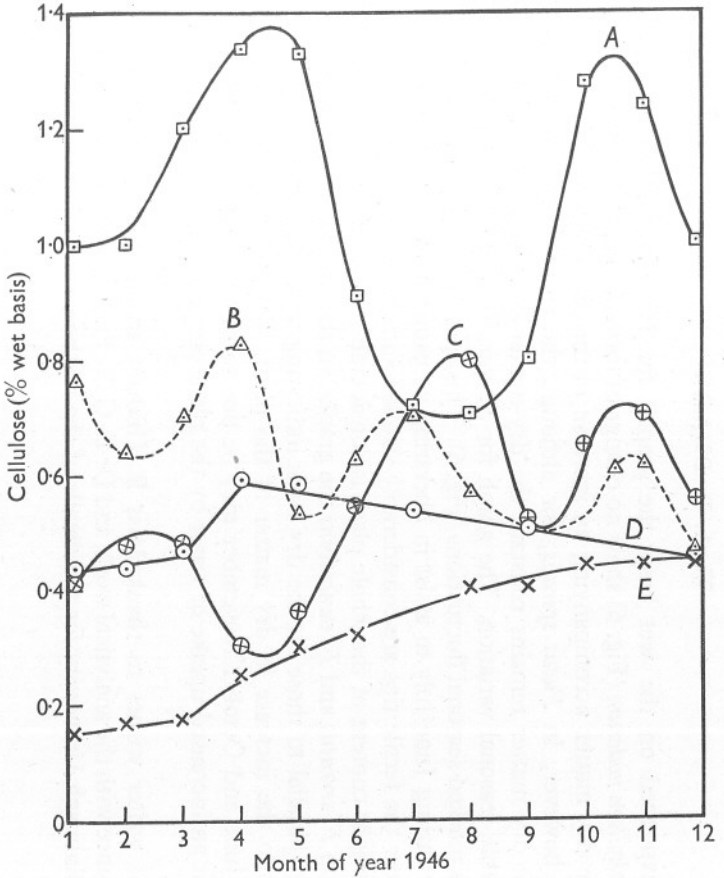

Fig. 6. Seasonal variation in the cellulose content of the Fucaceae (wet basis): (*A*) *Fucus spiralis*; (*B*) *F. serratus*; (*C*) *F. vesiculosus*; (*D*) *Ascophyllum nodosum*; (*E*) *Pelvetia canaliculata*.

are expressed on the wet basis the graphs for *Pelvetia canaliculata* and *Ascophyllum nodosum* (Fig. 6) show no change of form, an increase in cellulose in the dry matter accompanying an increase in the dry weight. This is not true, however, in *Fucus spiralis*, for although the proportion of cellulose in the dry matter remains constant the dry-matter content undergoes considerable seasonal variation. The graph for *F. spiralis* (wet basis), therefore, shows marked seasonal fluctuations (Fig. 6). This species takes in a quantity of water during June/July to assist in liberating its gametes, and at this time of the year the fertile tips are considerably swollen and full of mucilage and the dry-weight content of the whole plant is considerably reduced.

With *F. serratus* and *F. vesiculosus* the graphs on the wet basis are approximately parallel to those for the dry basis indicating that the cellulose contributes to the increase in dry matter of the plant. The minima obtained in May/June and October/November may be due to rapid growth at that time and/or an increased uptake of water by the plant preparatory to sporing.

The writer wishes to thank Miss B. Graham and Mr W. Cornhill for assistance with the analytical work, and Dr E. G. V. Percival and Dr A. G. Ross of Edinburgh University for the details of the method.

Summary

Monthly samples of the common British Laminariaceae and Fucaceae taken during 1946 have been analysed for cellulose.

The cellulose content has been found to increase with the depth of immersion of the weed.

In the Laminariaceae, both in the stipe and frond it undergoes marked seasonal variation, exhibiting two maxima, March/April and September/October with a distinct minimum in June/July.

In *Laminaria cloustoni*, in March, maxima of 5·7 (dry basis) occur in the fronds and 10·3% in the stipes with minima, in June, of 4·1 and 8·4% respectively. In *Laminaria saccharina* the cellulose content (dry basis) varies between 4–5% in the frond and 7–8% in the stipe and in *Laminaria digitata* between 3–5% in the frond and 6–8% in the stipe.

In the Fucaceae, on the dry basis, a similar seasonal variation occurs in *Fucus vesiculosus* (1·2–2·8%) and *F. serratus* (2·1–3·5%), but in *Ascophyllum nodosum* (2·0%), *Fucus spiralis* (4·4–4·7%) and *Pelvetia canaliculata* (0·6–1·5%) the cellulose content remains relatively constant throughout the year. When the results are calculated on the wet basis, graphs parallel to those for the dry basis are obtained, except in *Fucus spiralis*, in which the cellulose content undergoes marked seasonal variation in June/July, since this species takes in appreciable water preparatory to shedding its gametes.

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LISSOCLINUM ARGYLLENSE N.SP., A NEW ASCIDIAN FROM SCOTLAND

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(Text-fig. 1)

In the summer of 1949 a compound ascidian was collected from the shore of Seil Island, Argyll. This proved to be a new species of the family Didemnidae. It is proposed to name it *Lissoclinum argyllense*, the specific name indicating the area in which it was first found. No species of *Lissoclinum* has hitherto been included in the British fauna.

Occurrence. Colonies have been found round the shores of Seil Island, Argyll, and on the shore at Salen in the Isle of Mull, Argyll. All colonies were on the under sides of stones in the intertidal zone. They were not common, except locally, where several colonies sometimes occurred within a few yards of each other.

The colony (Fig. 1A) is usually pure white but is sometimes tinged with pink or buff. It forms encrusting sheets up to 50 mm. in diameter and about 2 mm. thick. The colony is rather flaccid and the upper layer of the test can be easily torn away from the lower layer. The oral openings (Fig. 1A, *Or.op.*), which are scattered evenly over the surface, are round and more conspicuous than those on the colony of *Didemnum maculosum* (Edwards), with which the present species might be confused. Cloacal openings (Fig. 1A, *Cl.op.*) are also conspicuous and are round or elliptical. The cloacal cavities are very greatly developed within the colony and leave little more than a thin upper and lower layer of test between which the zooids are stretched. In these upper and lower layers spicules are densely packed, giving the colony its white appearance. The zooids are arranged in the colony in irregular rows.

The spicules (Fig. 1B) are of a very characteristic shape, which at once distinguishes them from those of *Didemnum*. In optical section they show four to six rays, which are not conical and pointed as in *D. maculosum*, but have instead a broad end with two or three rounded prominences. The spicules are 0·03–0·05 mm. in diameter. They somewhat resemble the spicules of *D. perforatum* (Giard).

The zooid (Fig. 1C) is about 1·8 mm. long. The oral siphon has six short pointed equal lobes. There is no atrial siphon. The atrial opening, which is without a languet, is very large and extends round the thorax to near the endostyle, so exposing nearly the whole branchial sac. The tentacles number

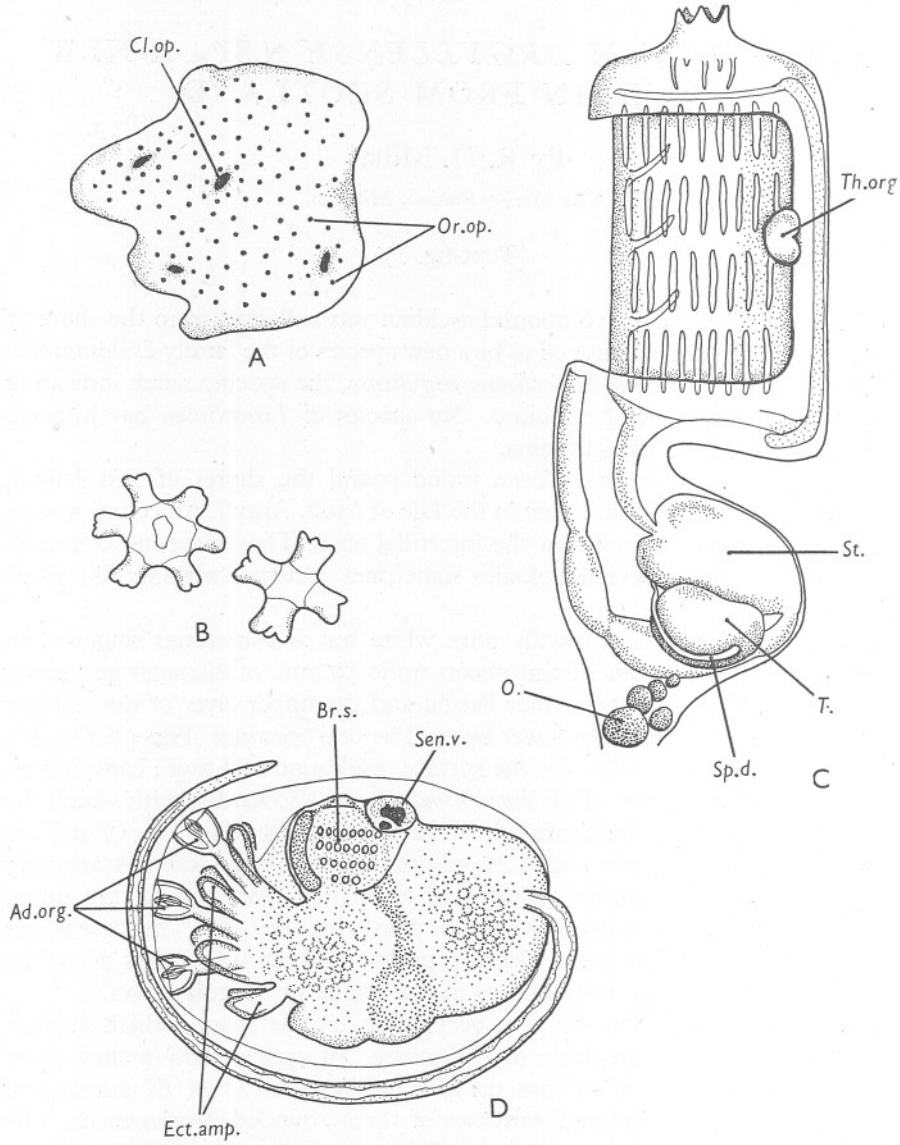

Fig. 1. *Lissoclinum argyllense* n.sp. A, colony; B, spicules; C, zooid, seen from the right; D, larva, seen from the left. *Ad.org.*, anterior adhesive organs; *Br.s.*, rudiment of the branchial sac; *Cl.op.*, cloacal opening; *Ect.amp.*, ectodermal ampullae; *O.*, ovary; *Or.op.*, oral openings; *Sen.v.*, sensory vesicle; *Sp.d.*, sperm duct; *St.*, stomach; *T.*, testis; *Th.org.*, lateral thoracic organ.

up to 24 and alternate in size. There are four rows of stigmata in the branchial sac, each row having eight or nine stigmata. The three dorsal languets of the pharynx are quite large. A lateral thoracic organ (Fig. 1 C, *Th.org.*) is present on each side of the body, on the ventral margin of the atrial opening, between the second and third rows of stigmata. Beside each thoracic organ is a large mass of spicules. The abdomen is shorter than the thorax and contains the slightly curved oesophagus, the ovoid smooth-walled stomach (Fig. 1 C, *St.*), the intestine divided into three long chambers, and the rectum extending to the level of the fourth row of stigmata. In the intestinal loop is a single large round testis (Fig. 1 C, *T.*). The sperm duct (Fig. 1 C, *Sp.d.*) is not spirally coiled but passes round in a half circle to the lower side of the testis, where its origin is marked by a slight thickening. The ovary (Fig. 1 C, *O.*) has a string of ova extending from the lower part of the intestinal loop down into the common test below the abdomen. Apparently the ova in development pass down into the lower layer of common test, where the larvae are found. Asexual reproduction is by pyloric budding as in other didemnids.

Larvae (Fig. 1 D) were found in colonies collected in August and November, but may have been present in other months when no colonies were examined. The larvae were embedded in the lower layer of the common test. In general organization the larva of *Lissoclinum argyllense* resembles the larva of other didemnids. It measures 0·6 mm. from the end of the adhesive organs to the base of the tail. The sensory vesicle (Fig. 1 D, *Sen.v.*) has a small ovoid static organ on the floor and a larger ocellus on the posterodorsal wall. The rudiment of the branchial sac (Fig. 1 D, *Br.s.*) has four horizontal rows of stigmata and a vertical endostyle. At the anterior end of the larva there are eight ectodermal ampullae (Fig. 1 D, *Ect.amp.*) and a vertical row of three adhesive organs (Fig. 1 D, *Ad.org.*).

Systematic position. This new species shows the common characteristics of the family Didemnidae, into which it falls naturally. The genera of this family are divisible into two groups identified thus:

(*a*) The proximal part of the sperm duct always spirally coiled; the common cloacal cavities generally not greatly developed.

(*b*) The proximal part of the sperm duct never spirally coiled; the common cloacal cavities often greatly developed.

The second group contains *Diplosoma* (Macdonald), *Lissoclinum* (Verrill), and *Echinoclinum* (Van Name), and to it the new species belongs. It is excluded from *Diplosoma* by the possession of spicules, and from *Echinoclinum* by the shape of the spicules. It agrees closely with *Lissoclinum* in all features examined except in its undivided testis. All species of *Lissoclinum* hitherto described have two or more testis follicles. Thus *L. aureum* Verrill has five to ten follicles, most species have two follicles, and *Echinoclinum*, which Van Name (1945) is inclined to regard as a subgenus of *Lissoclinum*, has the testis only partially divided into two by a deep groove. *L. argyllense*, with its undivided

testis, appears to stand at one end of this series. By including the new species in *Lissoclinum* we expand the definition of that genus to include forms with an undivided testis.

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THE BIOLOGY OF THE SMALL PLANKTONIC COPEPODS OF PLYMOUTH

By P. S. B. Digby, M.A.

From the Marine Laboratory, Plymouth

(Text-figs. 1–13)

CONTENTS

Introduction

The following paper describes investigations carried out on the life histories of the smaller plankton copepods in the Plymouth area during 1947. A large number of investigations have been carried out on the life history of *Calanus*, but our knowledge of the other species is meagre. What knowledge exists is mainly due to the work of Fish (1936*a–c*) in the Gulf of Maine, Wiborg (1940, 1944) in Oslo Fjord and the Nordåsvatn, a partly enclosed body of water near Bergen, and Marshall (1949) in Loch Striven. The differences in hydrography and other conditions made it desirable that a similar study should be carried out at Plymouth.

The species considered are: *Paracalanus parvus* (Claus), *Pseudocalanus elongatus* Boeck, *Centropages typicus* Krøyer, *Temora longicornis* (O. F. Müller), *Oithona similis* Claus, *O. nana* Giesbrecht, *Oncaea venusta* Philippi, and *Corycaeus anglicus* Lubbock.

All but the last three (*Oithona nana*, *Oncaea* and *Corycaeus*) were most abundant in the spring and summer; the last three were abundant at the end of

the year, accompanied by the harpacticid *Euterpina acutifrons* (Dana). Only very small numbers of species other than the above were taken.

This work was carried out at the Marine Laboratory, Plymouth, during the tenure of a grant from the Development Commission. I wish to record my thanks to Mr F. S. Russell, F.R.S., for his inspiration and encouragement in this work, and for making freely available all the facilities of the laboratory, to Dr H. W. Harvey, F.R.S., for loan of measuring nets, and to Capt. W. H. Creese and the crew of the '*Sabella*' for their care in taking my samples in all weathers.

Material and Methods

Area. The bulk of the samples were taken at the Station L 4, 5 miles from Plymouth breakwater, where there is an average depth of a little over 50 m. A few samples were taken a mile or two outside the breakwater (Table I), and in addition three short cruises were undertaken to investigate the state of the copepod population in the surrounding waters.

Nets used. Most of the samples were taken with Harvey measuring nets fitted with a silk net of 200 meshes to the inch (Harvey, 1934, 1935). Additional hauls were made with various tow nets and with a Clarke-Bumpus plankton sampler (Clarke & Bumpus, 1940). All hauls at L 4 (except those with the plankton sampler) were made vertically, fishing through all but the lower 1 or 2 m. of the water column. Normally between 1 and 3 m.^{3} of water were passed through the net. In the cruises, the hauls were made vertically from 50 m. to the surface. The quantitative results are based on samples taken with the later model of the Harvey net (Harvey, 1935) until 6 August, when the instrument was unfortunately lost. After that date the earlier net (Harvey, 1934) was used, and later the calibration was checked and found identical to the original calibration made by Harvey (1934). The calibration of the net used first was never checked, but as the meter was in good order it is probable that it had not altered more than a small amount. Two quantitative samples are utilized that were taken with the Clarke-Bumpus sampler. For these, the published calibration was used. Thus all counts for quantitative purposes were based on known volumes of filtered water.

Subsampling. Samples were subsampled by an adaptation of the method described by Russell (1931). During the spring and summer months when the small stages were very numerous it was necessary to divide the samples into coarse and fine fractions by passing through sieves, subsampling to deal with a small amount of the fine fraction and a larger amount of the coarser fraction. The exact degree of subsampling for each catch and each species is given in Table I. The species and stages were counted and measured on a squared slide under a microscope fitted with a mechanical stage and micrometer eyepiece, of which one division represented 17·7 μ. Measurements are comparable with those of Marshall (1949), representing length of cephalothorax.

Identification of stages. Full use was made of the papers by Oberg (1906) and Kraefft (1910) for distinguishing the nauplii and copepodite stages respectively. *Microcalanus* was not present in any number at Plymouth, so the distinction between the nauplii of *Paracalanus* and *Pseudocalanus* was easy to make on size alone.

A certain number of *Centropages hamatus* occurred. No distinction was drawn between the nauplii of these two species, but in view of the numerical superiority of *typicus* all the *Centropages* nauplii are lumped as belonging to that species, whereas some were undoubtedly *hamatus* nauplii.

The nauplii of *Oithona similis* and *O. nana* were confused in the early part of the year, when few *nana* were present, but in the later part of the year the distinction became obvious and the nauplii were separated. The nauplii of *nana* were smaller and altogether more slender than those of *similis*.

There appears to be no account of the stages of *Oncaea* or *Corycaeus*, and here these two species are separated into males, females and juvenile individuals. They were accompanied by large numbers of nauplii which were counted *in toto*: they probably comprised nauplii of these two species together with possibly *Euterpina* and other harpacticids. *Metridia lucens* was encountered in a cruise to the west of Plymouth, although it was not met with at Plymouth. The stages were worked out, and found to agree with the usual pattern.

Presentation of Data

With most of the species under consideration, all stages from nauplii to adults were found throughout the year. Conclusions as to number of generations passed through therefore rest on the comparative abundance of the different stages, the percentage distribution of the stages, and the sizes of the adults. Each of these methods has its disadvantages, and it is necessary to draw conclusions from all three lines of evidence together.

Absolute numbers, presented as abundance graphs, suffer from the disadvantage that if the water is patchy, with rich and poor areas, an abundance of nauplii encountered during one week does not necessarily give rise to the expected abundance of adults a few weeks later. They have the advantage, however, of showing the stock as it actually occurs.

Percentages of stages reveal the state of affairs in patchy water to a much better degree than do abundance figures. However, if the nauplii vary in number from one sample to another over a wide range, the percentage figures of the adults bear little relation to their numbers, but reflect the changes in the numbers of nauplii. Thus a peak of nauplii will apparently be followed by an increase in adults, while in actual fact the numbers of adults may decline, to a lesser extent, with the numbers of nauplii.

Size-groups of adults possibly present the most reliable evidence of separate generations, where such differences in size exist. Size differences do not

always occur, however; in the later part of the year successive generations of adults would appear to have arisen, in some species, with little difference in size, generations being separable on other grounds.

Conclusions as to number of generations must therefore be drawn from all these sources. In the diagrams given, the percentage and size-group graphs are mounted beneath the abundance graphs, and the interpretation that appears most probable is placed below them all.

In the abundance graphs, the nauplii are illustrated in a scale which is one-tenth of that of the copepodites. In the percentage figures, the divisions are taken as: nauplii, copepodites I–III, IV–V, and VI. This is the grouping used by Fish (1936 *a*, *b*, *c*) and is sufficient to show the main features.

The size-group graphs are reproduced in such a way that one individual measurement is reproduced as one unit on the figure, the numbers not being reduced to percentages. This has the advantage that use can be made of small numbers, such as occur, for instance, in *Temora* and *Acartia* in winter, which are concrete evidence but are not plentiful enough to make into percentage figures. The vertical scales are varied for convenience according to the species.

The method of suggested interpretation is adapted from Russell (1935). The different levels of the parts of the diagram representing adults of different size; the mid-line of a particular adult block is more or less the average size of the group concerned, and is a very rough replica of the adult figure of the abundance graph. The successive generations of nauplii in the interpretation are a rough replica of the naupliar peaks in the abundance graph.

Hydrography and Phytoplankton

The hydrographic conditions and phytoplankton of the area around L4 have been made the subject of many publications. For phytoplankton conditions, see Harvey, Cooper, Lebour & Russell (1935), and Mare (1940). No phytoplankton counts or pigment assessments have been made in connexion with this study. Temperatures were taken at 1 and 30 m. with an insulated water-bottle, supplemented on occasion by surface temperatures taken by bucket from further in-shore (Table I).

To compare the temperatures for 1947 (Fig. 1) with those in 1934, when the combined study was made on the various aspects of the phyto-zooplankton relationships (Harvey *et al.*, 1935) we may note the following differences. In 1947, the winter minimum temperatures at the beginning of the year were roughly 5·5° C., or two degrees lower; the summer maximum was roughly 16·5° at 30 m., or two and a half degrees higher. Stratification set in towards the end of March, about 2 weeks earlier than in 1934, but broke up at about the same time, at the end of September. In 1947, the temperature at 30 m. had not attained its full value until the end of August; after which a slow

decrease occurred until the end of October, when it became more rapid. In 1934, however, the highest values were reached a month earlier.

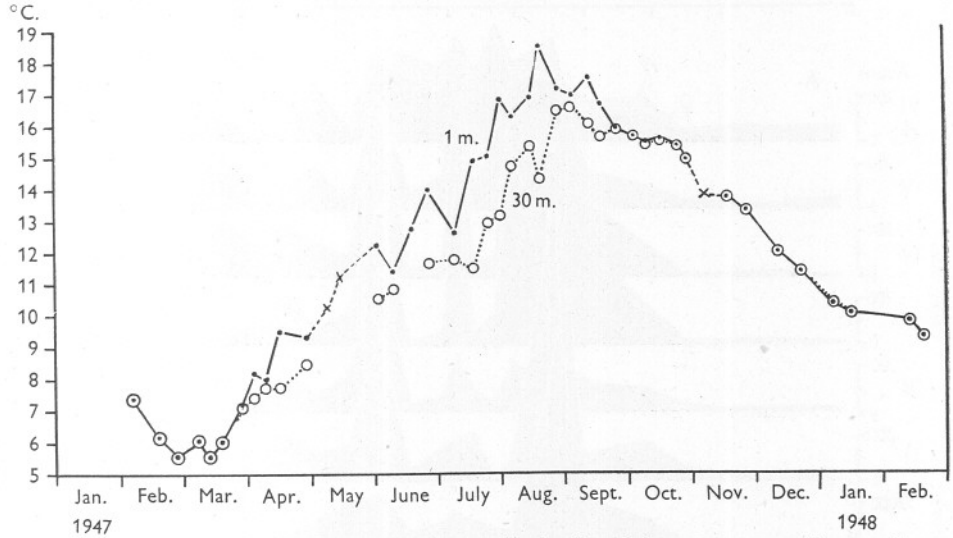

Fig. 1. Temperature of the water at 1 and 30 m. depth at L4 during 1947. ×, surface readings from closer in-shore

Abundance and Reproduction near Plymouth

Pseudocalanus elongatus (Fig. 2, Table II)

Abundant from March to October, greatest numbers from April to August.

The adult *Pseudocalanus* found early in the year (January and February) were of small size. Size-groups reveal that this population persisted until the end of March, when it died out. This population is here called the '0' generation. It was joined at the end of February by a population of adults of larger body size. This population received increments at progressively larger size, the early arrivals at the end of February being small and dying out in early April, the later members appearing in late March and early April and dying out by June. This '1' group appears to have been responsible for the large group of nauplii in May, which can be followed through the later developmental stages to adults in June. These adults were of a clearly different size, smaller than the adults '1' and are called adults '2'. The peaks in the abundance graph at mid-June and at the end of June were composed of individuals similar in size, and together they gave rise to the middle peak of abundance of nauplii at the end of June and beginning of July. It therefore seems most reasonable to consider this as one generation, although the abundance of late stages and percentages present a rather confused picture.

After this the generations became more merged, and large variations occurred in the total stock. It would appear from the percentage graph that

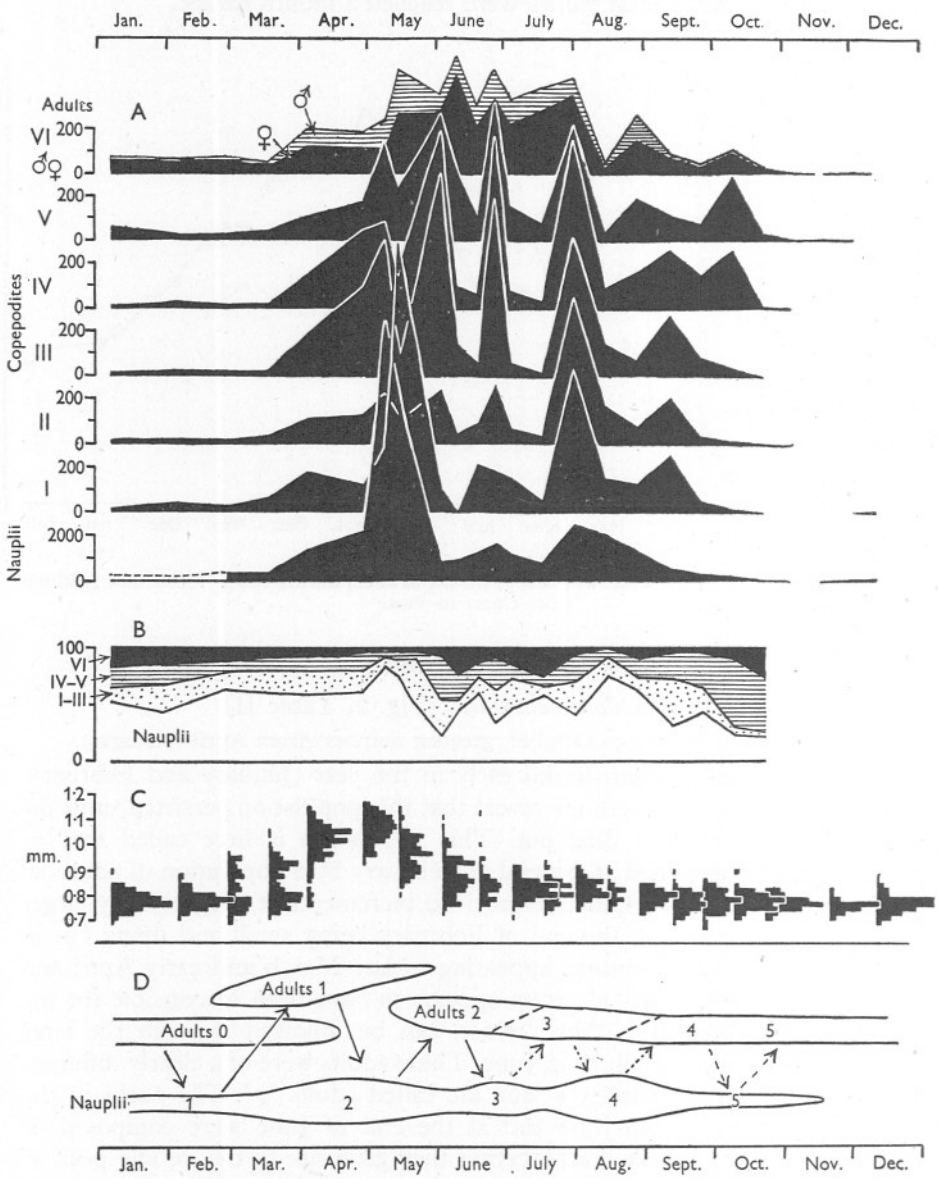

Fig. 2. *Pseudocalanus elongatus*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, suggested interpretation.

these nauplii gave rise to adults '3' in July. These were not separable from the adults '2' on size. These adults were responsible for the third period of abundance of nauplii (nauplii '4' in the interpretation) during July and August, and these nauplii in turn gave rise to adults '4' in late August and September, of slightly smaller size than adults '3'.

Now the abundance figure for nauplii '4' here indicates only one extended period of abundance, but from consideration of the stages from copepodites 1 to adults, it is obvious that a further group developed from nauplii in early September to adults in October, and these nauplii appeared shortly after the development of adults of group '4'. This would appear therefore to make a fifth and last generation, apparent also from the percentage figure. The adults of this generation, however, are not obviously distinguishable from those of the previous generation by size.

In Loch Striven (Marshall, 1949) the course of generations was similar up to nauplii '2', when in the latter locality breeding became continuous to such an extent that individual generations could not be followed.

Paracalanus parvus (Fig. 3, Table III)

Abundant from end of April to December, greatest numbers from May to June and August to October.

Paracalanus showed a considerable degree of similarity to *Pseudocalanus*, the size-groups revealing populations of adults replacing each other in time with those of *Pseudocalanus*. It differed in that the size differences between adults of groups '2' and '3' were much more clearly marked, and the existence of a fifth group of adults is more certain. It would appear that an extra generation was passed through at the end of the year, when *Pseudocalanus* had ceased breeding. The march of the generations from the '0' group adults as far as nauplii '3' was clear, but after this the broods were less well defined. In the abundance diagram, there is no clear transition from the nauplii '3' to adults of smaller size in August. It may be that the June nauplii did not survive, the eventual adult stock developing from the smaller numbers of nauplii present in July. It may be, on the other hand, that in June a different body of water moved over the station, water in which the development was at a slightly different stage. This delay in production of the next generation, whatever its cause, has been suggested in the interpretation by showing the adults '3' as not developing directly from nauplii '3'. The adults present during August, September and October were the adults '3' and '4', distinguishable in size groups. Adults '3' were smaller than those of generations '2' or '4'. Adults '3' and '4' gave rise to nauplii '4' and '5' in August and September. The nauplii present in November and December constitute yet another brood, the nauplii '6', which arose from an ill-defined group of adults '5'. This group was not distinguishable on size from adults '4', but its development can be traced through the copepodite stages on the abundance graph.

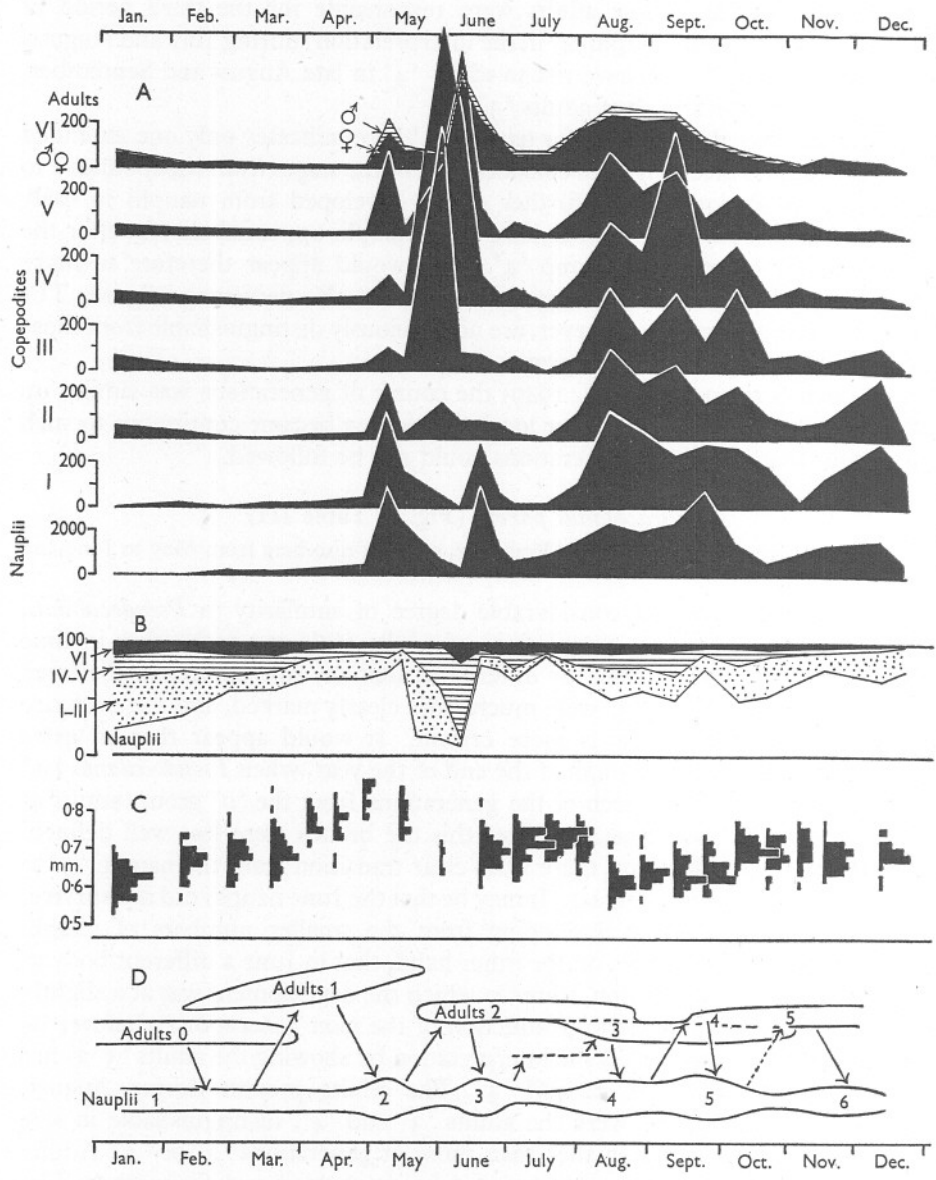

Fig. 3. *Paracalanus parvus*, A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, suggested interpretation

Centropages typicus (Fig. 4, Table IV)

Few specimens of the genus *Centropages* were taken, most of them being *C. typicus*. Specific distinction between the nauplii of *typicus* and *hamatus* was not made, and because of its numerical superiority all the nauplii are included here as *typicus*. Although the numbers are small, the data are sufficient

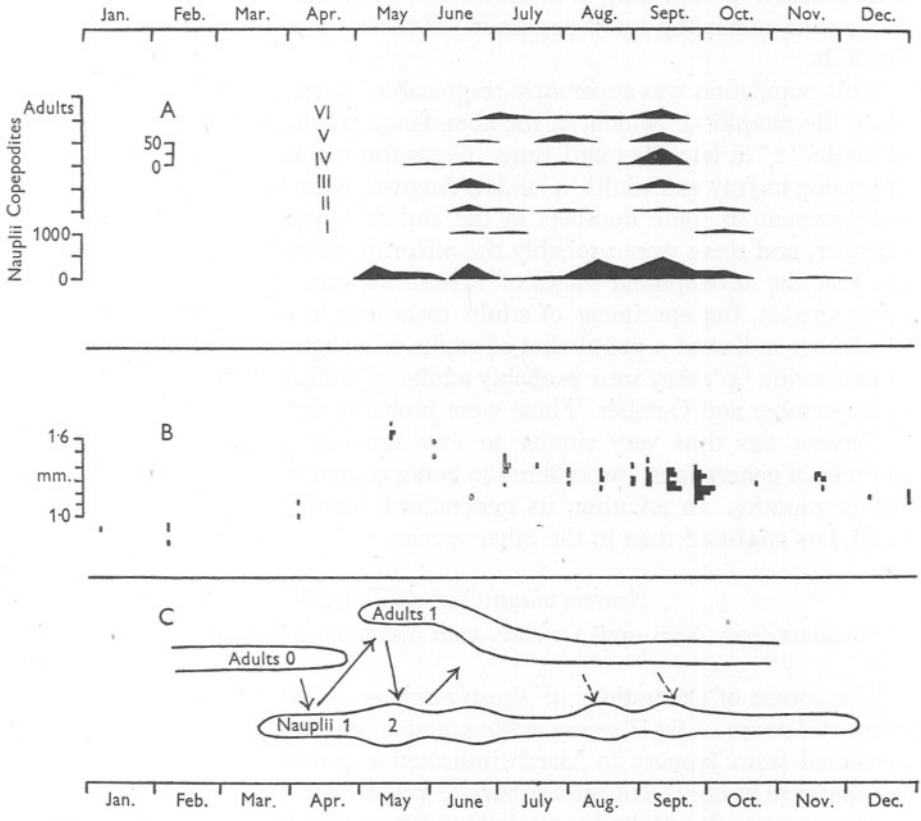

Fig. 4. *Centropages typicus*. A, abundance of stages; B, size-groups of adult females; C, suggested interpretation.

to show that *Centropages* nauplii were present from April to November, and the copepodite stages and adults were most abundant from June to September. The seasonal change in size was, so far as can be seen, similar to that in the other species, and groups of adults '0', '1' and '2' are suggested. The data are not sufficient to separate other generations, but the general similarity between the fragmentary picture obtained in this manner and the clearer pictures for *Temora* and *Acartia*, suggest the occurrence and course of generations to be somewhat similar.

Temora longicornis (Fig. 5, Table V)

Abundant from April until September, with a first maximum in May and June and a second in August and September.

The adult and copepodite stages of *Temora* were very scarce early in the year. Nauplii, however, were found in the plankton from February onwards. Because of the scarcity, the evidence as to size early in the year is scanty, but it is sufficient to show that, as in the other species, the size-groups change early in the year, indicating a new population of adults '1' appearing from February onwards.

This population was apparently responsible for the large peak of nauplii in May, the nauplii '2' which, in the abundance graph, can be seen developing to adults '2' in late May and June. Generations followed clearly, adults '3' appearing in July and adults '4' in late August. Nauplii and early copepodites were present in some numbers at the end of September and beginning of October, and these were probably the offspring of adults '4'. At this time of the year the development stages of *Temora* became swamped in numbers by other species, but specimens of adults measured in October, November and December indicated a population of adults of a slightly larger size than those of generation '4'; they were probably adults '5' which developed from nauplii in September and October. These were probably the overwintering adults.

Temora was thus very similar to *Pseudocalanus* and *Paracalanus* in the number of generations, but differed in being comparatively more scarce in the winter months. In addition, its generations were more clear-cut, breeding being less confused than in the other species.

Acartia clausi (Fig. 6, Table VI)

Abundant from April until October, with maximum numbers in May, June and July.

The course of generations of *Acartia* appears to have been very similar to those of *Temora*. Like *Temora*, it was scarce in the winter months. Specimens measured from January to March indicated a group of adults of small size, too sparse to be noticed in the abundance graph. These were joined in April by a larger group, the adults '1', and these latter were responsible for the large group of nauplii, the nauplii '2', at the end of April and beginning of May. These developed to adults '2' early in June. Generation '3' followed, with nauplii in June and adults in July and August. Generation '4', with nauplii in early August, developed to adults, distinguishable by size from those of '3', in late August and September. A further period of abundance of nauplii in September, the nauplii '5', cannot be seen to develop. All stages were present in small numbers in late November and December, and although there is no evidence for it here, it would appear possible, by comparison with *Temora*, that adults '5' arising from nauplii '5' might give rise to nauplii '6' in November.

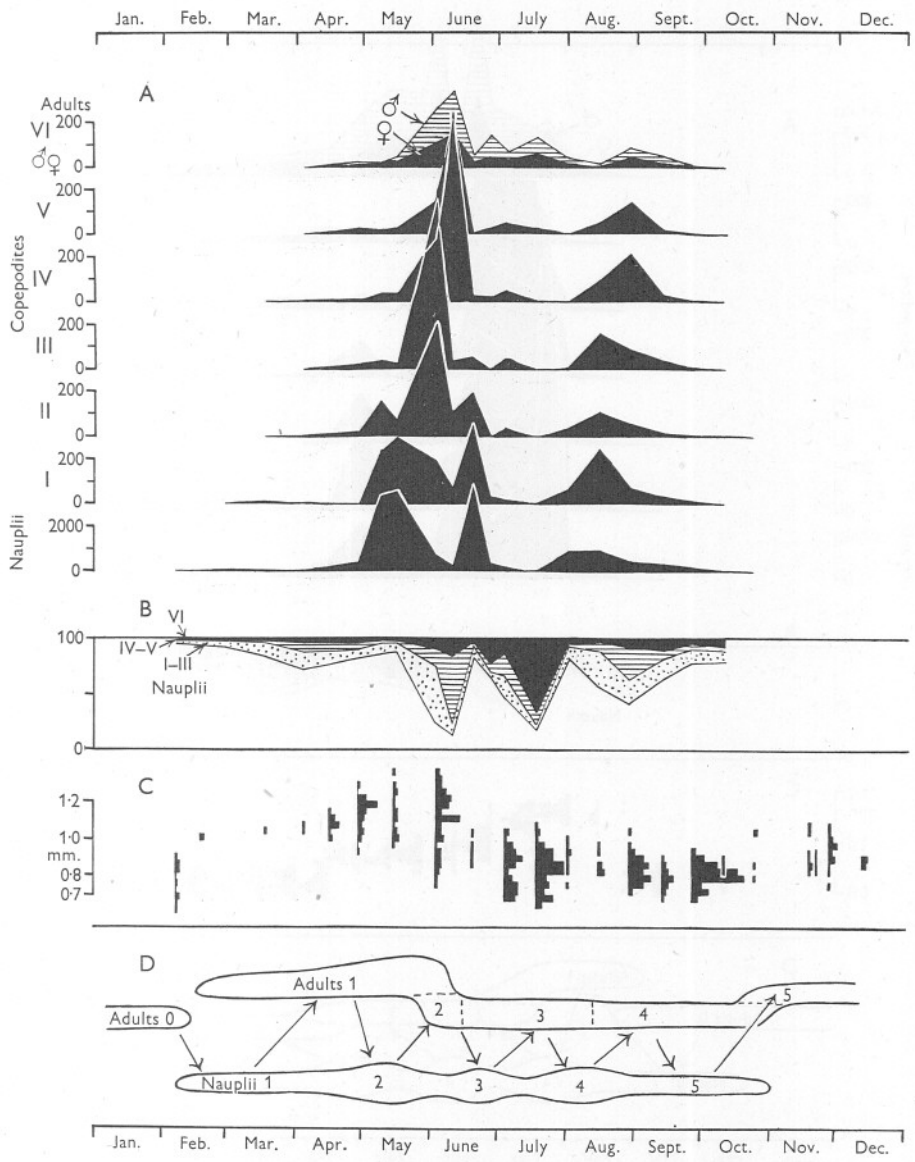

Fig. 5. *Temora longicornis*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

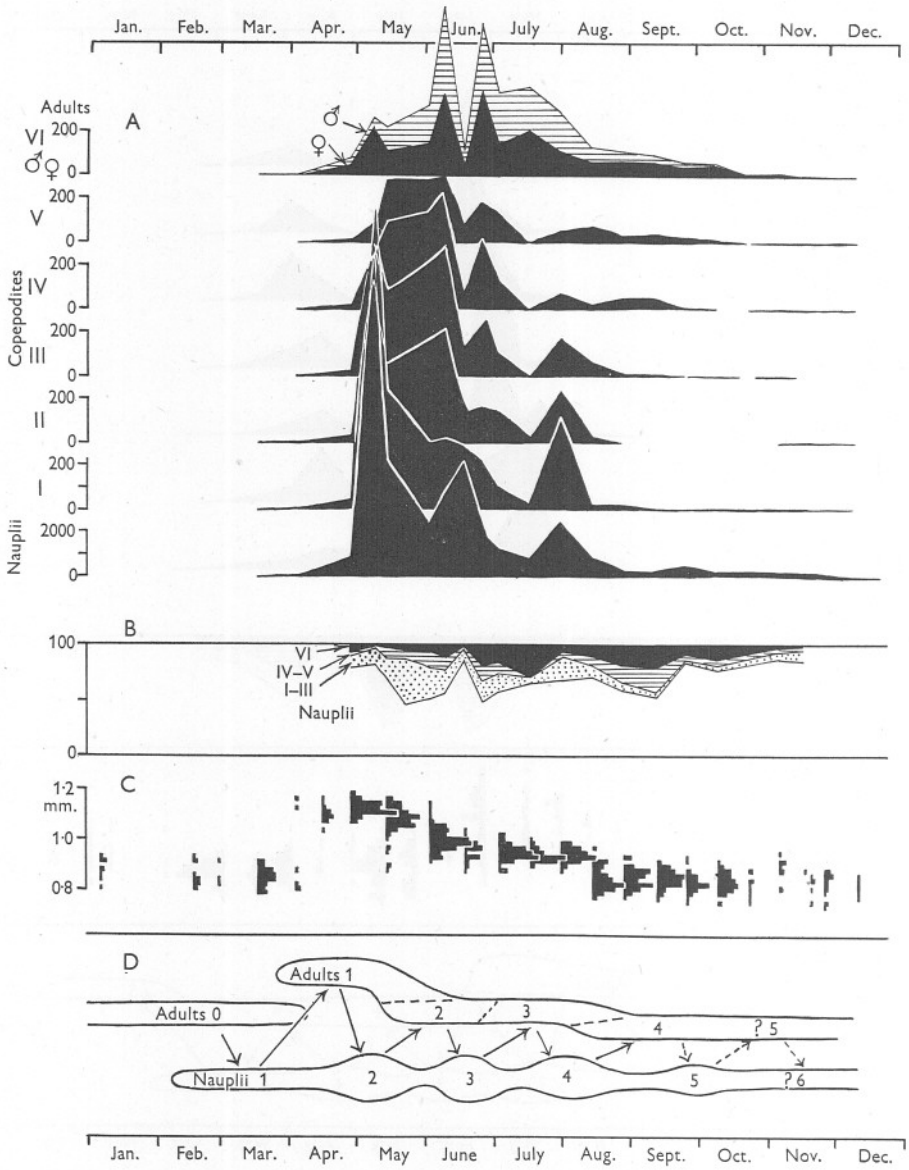

Fig. 6. *Acartia clausi*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

Oithona similis (Fig 7, Table VII)

Abundant from April until October, with maxima in early May, late July and mid September.

There was again striking similarity to *Pseudocalanus*, but breeding was more diffuse. Generations can be traced as follows. Small adults '0' early in the year gave rise to nauplii, which developed to larger adults '1' in March, April and May. The nauplii '2' developed to adults '2', of smaller size, in June. The next group, adults '3', appeared in August and were smaller still. From here, the picture is obscure owing to continuous breeding with subsequent broods of adults appearing at the same size, but on the basis of the abundance and percentage graphs, together with comparison with other species, it would appear that adults occurring in September and October were adults '4' and those in November and December might be adults '5'.

Oithona nana (Fig. 8, Table VIII)

Abundant from September until December.

A few appeared early in the year, but were not counted. Those appearing after July were recorded and the nauplii counted. Nauplii appeared in August, and the first adults in considerable numbers in September. Inspection of the graphs reveals that probably a succession of generations occurred with adults in August, September, October, November and, it seems, in January when observations had ceased.

Oncaea venusta (Fig. 9, Table IX)

Abundant from September until December.

Oncaea was separated into copepodites and adults. As with *Oithona nana*, this species did not appear in numbers until August, after which it became plentiful. Separate generations were indicated coming to maturity in early September, September to October, November and possibly January. The numbers measured, although small, suggest size distinction between the generations.

Corycaeus anglicus (Fig. 10, Table IX)

Abundant from September until December.

Corycaeus anglicus was treated like *Oncaea* for similar reasons. It was similar to *Oithona nana* and *Oncaea* in its occurrence. Generations came to maturity in early September, and October to November. Another generation probably came to maturity in January, while the '0' group was possibly present in very small numbers in July. Separation of generations '2' and '3' was not possible on size.

Other Species

Calanus finmarchicus (Gunnerus) occurred in the samples, but in small numbers. As the last stages no doubt escaped the net, it was not counted.

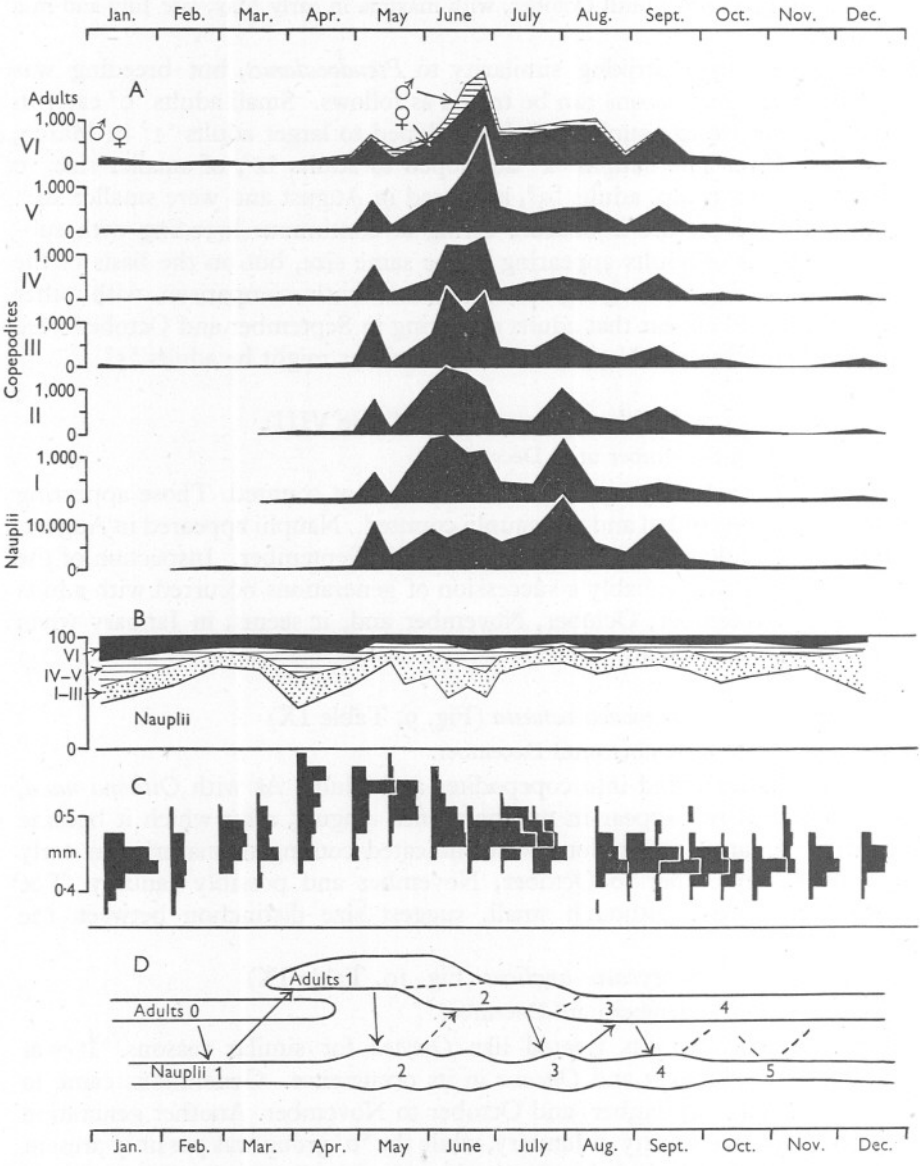

Fig. 7. *Oithona similis*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

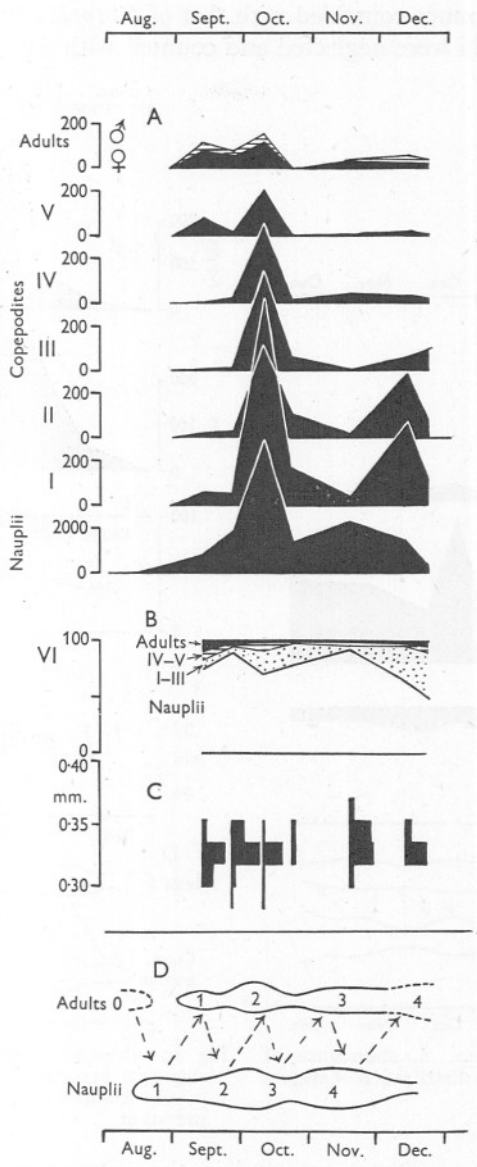

Fig. 8. *Oithona nana*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

Centropages hamatus (Lilljeborg) occurred in small numbers in the summer months. Its appearance coincided with that of *C. typicus*. Owing to its small numbers, its nauplii were neglected and counted with those of *C. typicus*.

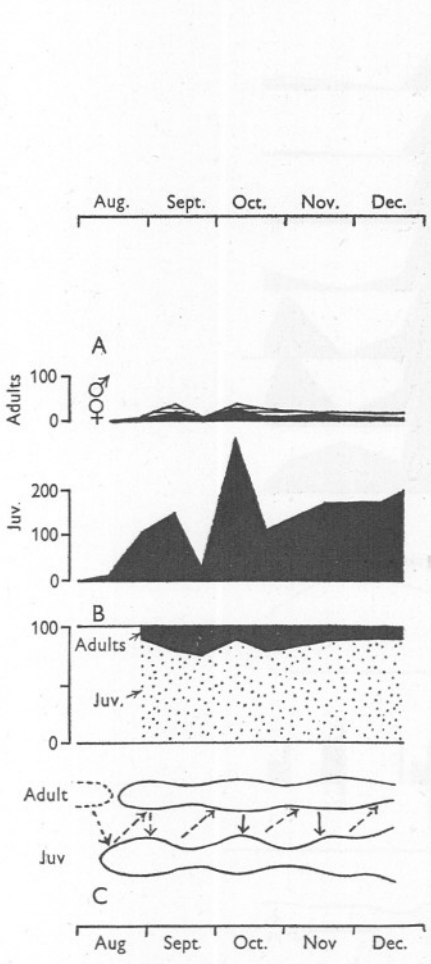

Fig. 9. *Oncaea venusta*. A, abundance of stages; B, percentage distribution of stages; C, interpretation.

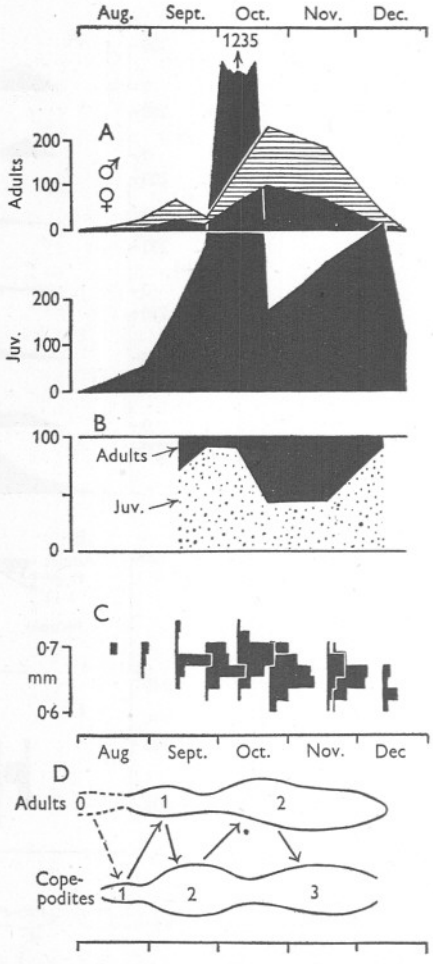

Fig. 10. *Corycaeus anglicus*. A, abundance of stages; B, percentage distribution of stages; C, size-groups of adult females; D, interpretation.

Euterpina acutifrons (Dana) occurred in the autumn at the same time as *Corycaeus* and *Oncaea*.

At the same time that the water was populated with *Oncaea*, *Corycaeus* and *Euterpina*, there appeared large numbers of nauplii of a type not previously encountered. These presumably belonged to these three species, and have been indicated as such in Fig. 13 (p. 414).

Size Near Plymouth

Pseudocalanus (Fig. 11, Table X) was present throughout the whole year. Sizes as a whole rose to a peak in April and then declined towards the end of the year. As in Loch Striven (Marshall, 1949) the adult female was larger than the adult male, and the Stage V female larger than the Stage V male, Stage IV being more nearly equal, with the female slightly larger until May, after which both sexes were about the same size.

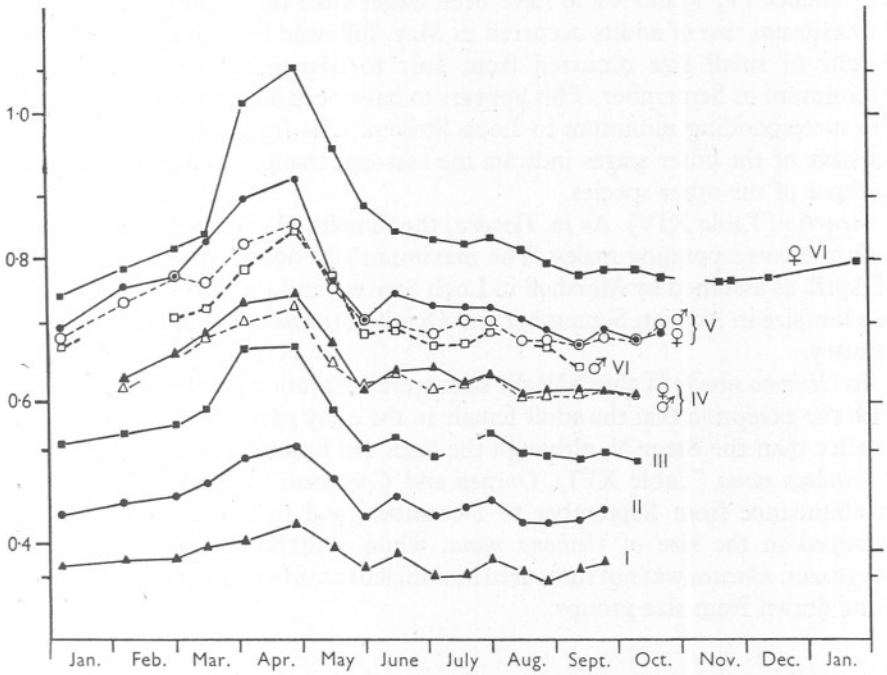

Fig. 11. *Pseudocalanus elongatus*. Median sizes of copepodites throughout the year

In Loch Striven, Marshall found that after May the male IV was slightly but distinctly larger than the female IV, while at Plymouth there appears to have been little difference. The only striking differences between the sizes at Plymouth and Loch Striven are that at Plymouth the median sizes of the IV, V and adult females were more widely separated than they were at Loch Striven, and no large variations in size of the Stage V occurred as did at Loch Striven. The changes in size of the adults were inadequate for separating broods at the end of the year.

Paracalanus was present (Table XI) throughout the whole year, and behaved in a similar manner to *Pseudocalanus*. Marshall found it present in numbers in Loch Striven only in the later part of the year. The relative sizes of the stages were similar to those found by Kraefft (1910) and Marshall (1949) in that the males of Stages IV, V and VI were larger than the corresponding female, the

male V being as large or larger than the adult female. The seasonal changes of size were similar to those of *Pseudocalanus*, but the adults differed in that the fluctuations in size from June to December were greater than those in *Pseudocalanus* and can be used with greater confidence for distinguishing the different generations. The increase in size of *Paracalanus* in October appears to have had no counterpart in *Pseudocalanus*.

In *Temora* (Table XIII), although few were measured, the sizes indicate the females IV, V and VI to have been larger than the corresponding males. A maximum size of adults occurred in May, followed by a sharp drop in size. Adults of small size occurred from July to September or October, with a minimum in September. This appears to have been about a month later than the corresponding minimum in Loch Striven. The fragmentary observations on sizes of the other stages indicate the seasonal changes to have been similar to those of the other species.

Acartia (Table XIV). As in *Temora*, the females IV, V and VI were larger than the corresponding males. The maximum size occurred in the latter half of April, as assumed by Marshall in Loch Striven, and thereafter sizes declined to a low size in August, September and October, to rise again in December and January.

In *Oithona similis* (Table XV) the sizes were very much as found by Marshall, with the exception that the adult female in the early part of the year was never smaller than the Stage V, although the sizes did become closely similar.

Oithona nana (Table XVI), *Oncaea* and *Corycaeus* (Table XVII) appeared in abundance from September to December, and in that time no changes occurred in the size of *Oithona nana*, while a slight decrease occurred in *Corycaeus*. *Oncaea* was not measured in sufficient numbers to enable conclusions to be drawn from size groups.

Distribution and Size in Adjacent Waters

The interpretation as to generations which has been placed on the changes observed at L 4 depends upon the changes being true changes with time, and not changes due to sampling different populations of copepods distributed in a localized manner in the water which passed Plymouth in the course of the year. In order to obtain information on the populations of copepods in adjacent waters, a few cruises were accomplished as follows:

January 1947—to the south-west of Plymouth and west of Penzance (Table XVIII).

June 1947—to the south-west of Plymouth (Table XIX).

August 1947—south and south-east of Plymouth (Table XX).

Hauls were made with a measuring net at the various stations and the samples were analysed to give numbers per cubic metre, and median sizes of adults.

In the January cruise, the noteworthy points were the existence of numbers of *Calanus finmarchicus* and *Metridia lucens*, at the stations off the coast of France and off Land's End, and the great increase in size of *Oithona* and *Pseudocalanus* off Land's End. The increased size might be suspected to have been due to a burst of phytoplankton during the previous November or December in this region. *Pseudocalanus* and *Paracalanus* were most abundant off the English coast and *Oithona* off the French coast.

In the June cruise, all species, with the exception of *Centropages hamatus* and *Calanus finmarchicus*, were most plentiful at stations 1–3. The size of *Pseudocalanus* was particularly great at station 4, at which it was least abundant. The figures for *Calanus* are probably low, as the large individuals no doubt escaped the net.

In the August cruise, the English side of the Channel seemed to be richer in all species except *Centropages typicus*, which was most common on the French side. The sizes of *Pseudocalanus* were similar with the exception of one station, no. 4, off Ushant, in which the median size was much higher than in the others. Again, it might be suspected that this marked the site of a transitory flowering of phytoplankton just at the time when these were coming to maturity.

In considering the significance of these regional variations, it would appear that, as far as these somewhat inadequate samples tell us, at most times a drift of water from 40 miles offshore over L4 would not unduly affect the general picture given of the total abundance of stock at these times. In some species such as *Temora*, however, the results might be seriously disturbed.

Discussion

Examination of the size-groups of adults has shown that a given group, appearing at a certain size, can be traced in subsequent samples until the members disappear. Meanwhile they are often replaced by other groups of adults appearing at a larger or smaller size. Thus while the median size can show a steady rise or fall, the size-groups can indicate a bimodal group with one population replacing another. When, as often, a new population, separable in the adults as being of different size, can be traced from the nauplii through the preceding samples, proof is offered that a new generation has arisen and that the change in size is not due to the sampling of different bodies of water. If the old brood of adults dies out slowly while the new brood is appearing, as in *Oithona*, the resulting median curve exhibits a gradual rise or fall, while if the new brood is produced suddenly in superior numbers, as in *Temora*, the curve will be step-like in form. The size-groups for *Pseudocalanus*, Stages I–III and females IV–VI, are given in Fig. 12. These show that although the adults may form bimodal groups, the younger stages rarely do so. This is because, although the adults may survive for a considerable time at a given

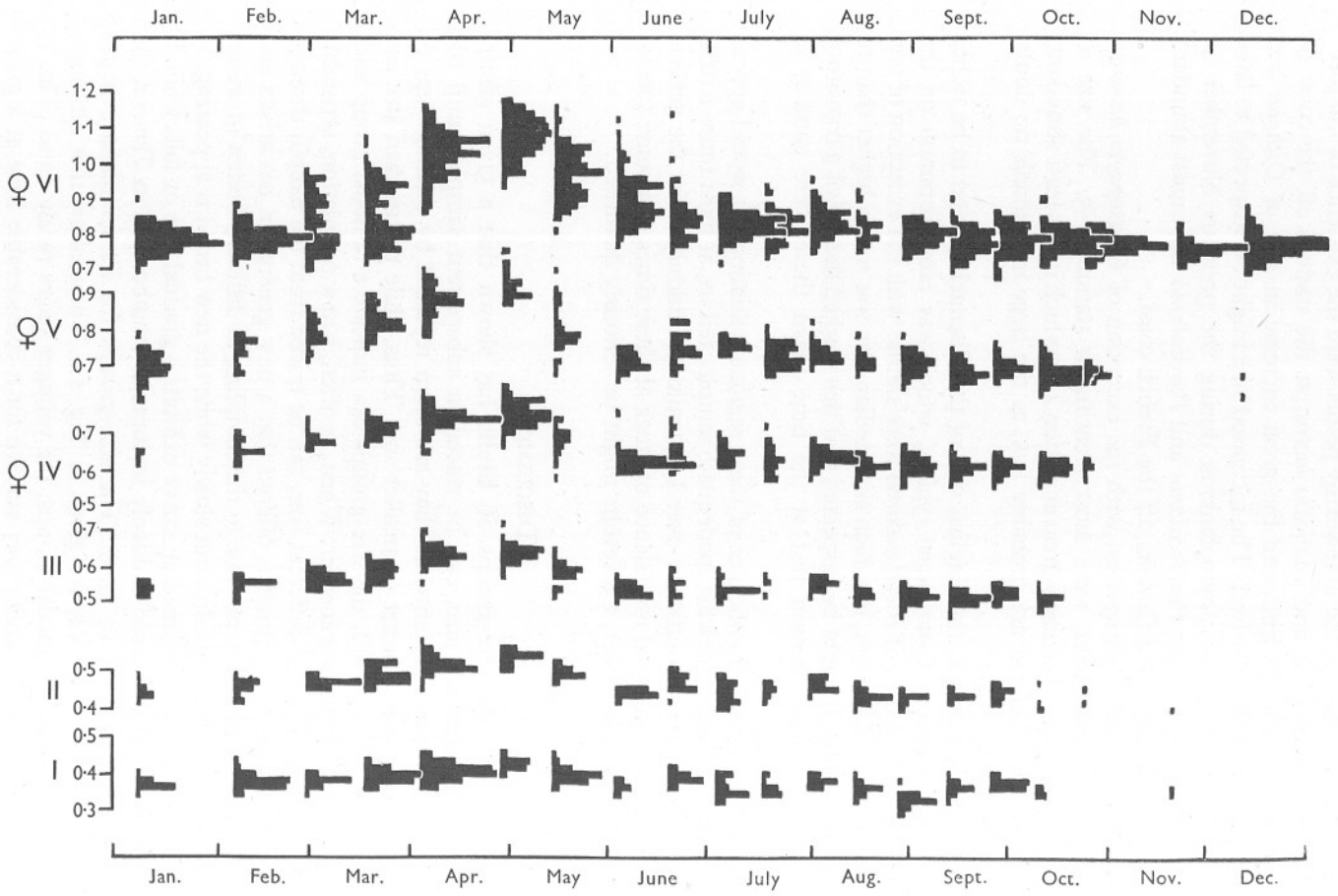

Fig. 12. *Pseudocalanus elongatus*. Size-groups of copepodites I–III and females IV–VI.

size, the developmental stages are transitory. The sizes of the adults are the result of the varied conditions for possibly some weeks preceding sampling; not to exclude the effect of the size of the previous stages, as suggested by Ussing (1938). The sizes of the younger developmental stages are a reflexion of conditions immediately preceding sampling, and bimodal groups exist only if conditions change very rapidly. It is noteworthy that all the stages change size in unison. Ussing (1938) obtained evidence to show that in Greenland the size of *Calanus* was partly dependent upon the size of the preceding stage, and partly on the state of nutrition before moulting. If that were so at Plymouth it would be evident from a rise in size, of, say, Stages I or II being followed by a rise of Stages IV or V in the next sample 2 weeks later. The absence of this effect may be due to the surplus of food which we know to be available (Harvey *et al.*, 1935) in Plymouth waters. The total densities per cubic metre of the various species of copepods throughout the year are illustrated in Fig. 13. All have been drawn to the same scale. Copepods are marked solid black, the nauplii are added as a continuous line and the eggs as dotted line. No nauplii are indicated for *Oncaea* and *Corycaeus*, but the group of nauplii belonging to these two species and to *Euterpina* is figured separately.

The totals indicated here represent the majority of specimens present in the plankton off Plymouth, for *Calanus finmarchicus*, although representing on occasions a large part of the plankton by bulk, was numerically poor compared with these smaller species.

The appearance of the graphs for *Paracalanus* indicates a delay of about 3 weeks in the development of the generation at the end of June. Attention was drawn to it in the interpretation for *Paracalanus* (Fig. 3). It can also be seen in *Temora*. It would be expected that if this was due to poor phytoplankton, this effect would be visible in all the species. But this was not so. In *Pseudocalanus*, *Acartia* and *Oithona*, there was a repetition at the end of June of the conditions $2\frac{1}{2}$ weeks earlier, evident as a bimodal peak of abundance of adults and late stages in *Pseudocalanus* and *Acartia*, and of early stages in *Oithona*, and as a lengthened peak of abundance of adults in *Oithona*. Fish (1936*a*, *b*), found a difference in the stage of development of a population according to the time of flowering of the spring phytoplankton. It might be expected that a similar phenomenon might be encountered in these waters. The effects noted above would be entirely in accord with the drifting over L 4 in mid-June of water in which the spring increases had set in some $2\frac{1}{2}$ weeks earlier. Over the whole year, the water was characterized by *Sagitta setosa* (Mr. P. G. Corbin, personal communication).

The occurrence of the various species has been summarized by Marshall (1949) and reference may be made to that paper for comparison. The course of generations in Loch Striven and at Plymouth would appear to be similar in very broad outline. The time of development from nauplius to adult in the different species can be seen to range from about 4 to 6 weeks, while the periods

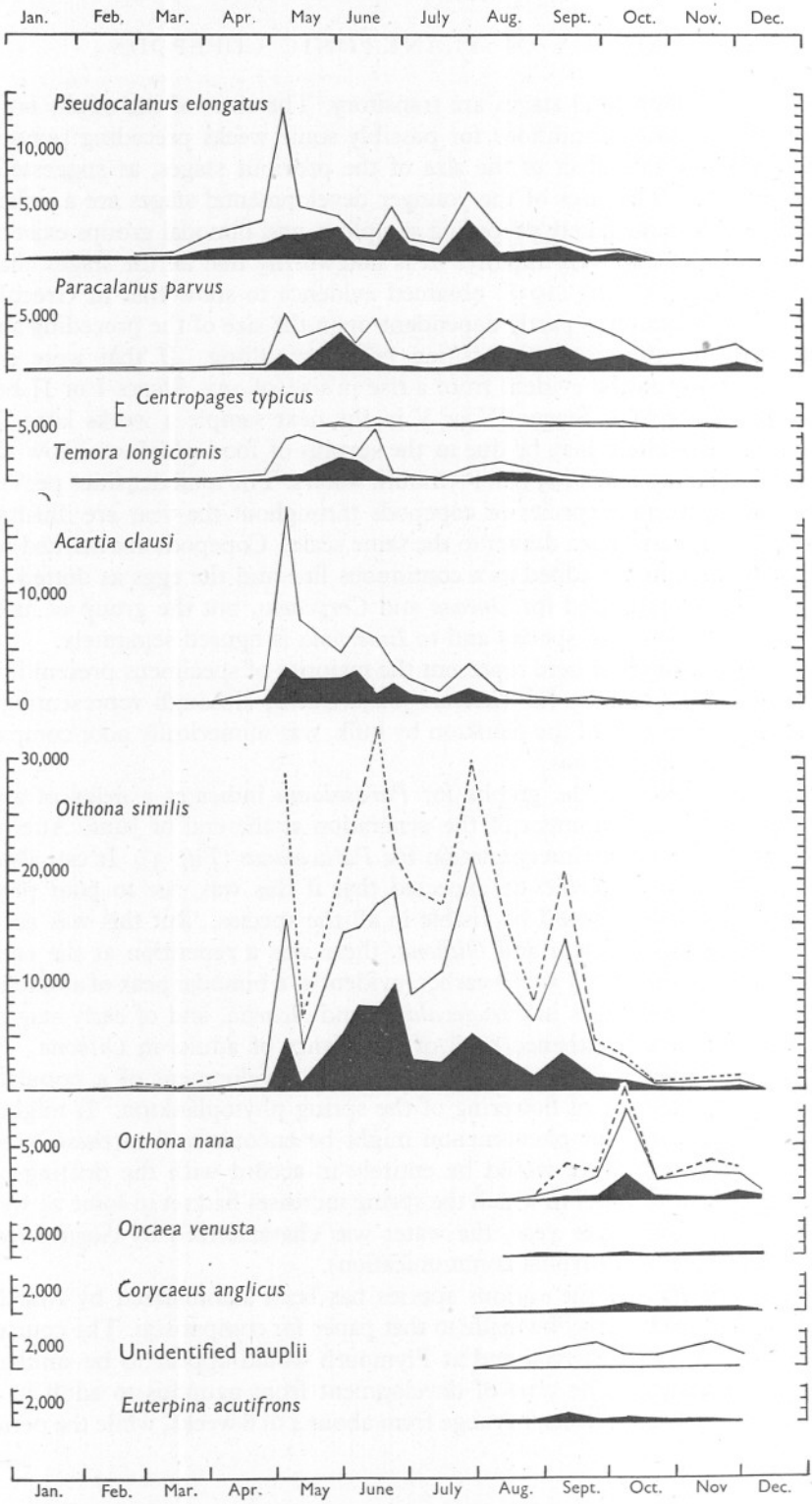

Fig. 13. Numbers per cubic metre of the smaller copepods throughout the year, all to same scale. Solid black, copepodites and adults. Continuous line, all stages including nauplii. Dotted line, total plus eggs.

between successive broods of adults were from 6 weeks to 2 months. These results are therefore closely comparable to those of Fish (1936*a*, *b*) who found generations of *Pseudocalanus* and *Oithona* in the Gulf of Maine to occur with the same developmental periods.

There was a great similarity in the behaviour of the different species, as found also by Marshall (1949) in Loch Striven.

It may be possible that the dynamic relationships which exist between the phytoplankton and the zooplankton serve to keep the generations of the different species more or less in step, as the conditions which cause the production of a good brood of nauplii in general appear to affect all the species alike. Thus it may well be that these species may have quite different development times if reared in the laboratory, whereas in the sea their generations appear to keep in step. Laboratory work on the factors relating phytoplankton and copepod populations is needed to elucidate these processes, and to give the final answer concerning the development time in species which breed continuously in the sea.

Summary

The life histories of the small planktonic copepods of Plymouth were studied during 1947. The samples were taken at Station L4 with Harvey measuring nets, and are thus truly quantitative.

The main species concerned were *Pseudocalanus elongatus*, *Paracalanus parvus*, *Centropages typicus*, *Temora longicornis*, *Acartia clausi*, *Oithona similis*, *O. nana*, *Oncaea venusta* and *Corycaeus anglicus*.

The species common in summer—all but the last three of the above—behaved in a very similar way, producing probably five generations in the course of the year, but differing from each other in the relative and absolute abundance of the different stages at different times of the year.

The species restricted to autumn and winter—*Oithona nana*, *Oncaea* and *Corycaeus*—resembled each other in appearing in countable numbers as nauplii in August and producing three broods in the late months of the year.

The Stages I–VI of the various species were measured throughout the year, and the variations in size found to be similar to those of the copepods of Loch Striven as found by Marshall.

The distribution of copepods in adjacent waters during January, June and August were investigated. It is concluded that a drift of water from the south-west of up to 40 miles would be unlikely to disturb severely the picture of the seasonal variations in total numbers of the copepod population as obtained from samples taken at L4.

The observed changes in size and abundance are discussed, with reference to possible water movements.

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APPENDIX

Table I. Stations, Temperature and Degree of Subsampling

Date	Station	Temperatures 1 m.	Temperatures 30 m.	Water fished (litres)	Volumes examined for various stages (litres): *Pseudocalanus*	*Paracalanus*	*Centropages*	*Temora*	*Acartia*	*Oithona similis*	*O. nana*	*Oncaea*	*Corycaeus*	*Euterpina*	Unidentified nauplii
6. i. 47	L 4	..	..	437	437 with all species										
5. ii	L 4	7·4	7·4	2760	1000 with all species										
17. ii	L 4	6·0	6·2	..											
27. ii	L 4	5·57	5·59	2350	1000 with all species										
7. iii	L 4	6·10	6·12	..											
12. iii	L 4	5·55	5·55	..											
17. iii	L 4	6·04	6·00	1900	N. 1000, I–IV 1500. All species										
28. iii	L 4	7·2	7·2	..											
3. iv	L 4	8·2	7·4	1950	N. 400 I–III 1000 IV–VI 1500	N. 400 I–III 1000 IV–VI 2000	N. 400 I–VI 1000	N. 400 I–III 1000 IV–VI 2000	..	..	..	..	..	..	..
8. iv	L 4	8·0	7·7	..											
15. iv	L 4	9·51	7·76	..											
28. iv	L 4	9·35 (surface)	8·43	2250	N. 200 I–VI 400 } with all species										
8. v	3½ miles outside breakwater	10·3	..	604	N. 25 I–VI 50 } with all species										
14. v	2 miles outside breakwater	11·2	..	332	N. 50 I–VI 300 } with all species										
		(1 m.)													
2. vi	L 4	12·27	10·52	2250	N. 100 I–VI 100 } with all species except adults of *Temora*, *Centropages*, *Acartia* (600)										
9. vi	L 4	11·40	10·81	2030	501 with all species										
18. vi	L 4	12·75	..	625	N. 50 I–V 250 VI 500	N. 50 I–V 250 VI 500	N. 50 I–III 250 IV–VI 500	N. 50 I–IV 250 V–VI 500	N. 50 I–IV 250 V–VI 500	50	50	..	..	..	..
26. vi	L 4	14·00	11·64	1800	N. 50 I–VI 100	N. 50 I–VI 100	N. 50 I–VI 100	N. 50 I–III IV–VI 250	N. 50 I–VI 100	50	..	..	..	..	..
3. vii	L 4	16·62	11·79	1650	N. 100 I–VI 500 } with all except *Oithona* (100)										
17. vii	L 4	14·90	11·50	1300	N. 100 I–III 250 IV–VI 1050	N. 100 I–IV 250 V–VI 1050	N. 100 I–III 250 IV–VI 1050	N. 100 I–II 250 III–VI 1050	N. 100 I–II 250 III–V 1050 VI 450	N. 50 I–II 100 III–VI 250	400	200	..	..	..
24. vii	L 4	15·00	12·95	..											
31. vii	L 4	16·82	13·13	900	N. 50 I–VI 200	N. 50 I–VI 200	N. 50 I–II 200 III–VI 500	N. 50 I–III 200 IV–VI 500	N. 50 I–III 200 IV–VI 500	N. 50 I–III 50 IV–VI 200	50	..	..	..	..

5. viii	L 4	16·33	14·70	..	..	..	..	..	..	..	..	..	..	..	..
14. viii	L 4	16·86	15·39	1480	N. 100 I–II 200 III–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–VI 200	N. 100 I–VI 200	100	Juv. 200	Juv. 200 Adults 1000	1000	100
19. viii	L 4	18·43	14·30	..	..	..	..	..	..	..	..	..	..	..	..
28. viii	L 4	17·14	16·42	1800	N. 200 I–II 200 III 500 IV–VI 1000	N. 200 I–III 200 IV 500 V, VI 1000	N. 200 I–II 200 III–VI 1000	N. 200 I–II 200 III 500 IV–VI 1000	N. 200 I–II 200 III–VI 1000	N. 200 I–IV 200 V–VI 500	200	Juv. 200	500	200	200
4. ix	L 4	16·99	16·60	..											
12. ix	L 4	17·50	16·01	1550	N. 100 I–III 200 IV–VI 1000	N. 100 I–IV 200 V–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–III 200 IV–VI 1000	N. 100 I–VI 200	N. 100 I–IV 200	200	Juv. 200 Adults 1000	200	100
17. ix	L 4	16·70	15·65	..	..	..	..	..	..	..	..	..	..	..	..
25. ix	L 4	15·90	15·85	1210	N. 200 I–III 500 IV–VI 1000	N. 200 I–IV 500 V–VI 1000	N. 200 I–IV 500 V–VI 1000	N. 200 I–VI 1000	N. 200 I–II 500 III–VI 1000	N. 150 I 200 II–VI 500	N. 200 I–II 200 III–VI 500	Juv. 500 Adults 1000	Juv. 200 Adults 1000	500	50 50
2. x	L 4	15·65	15·10	..	..	..	..	..	..	..	..	..	..	..	..
9. x	L 4	15·45	15·39	1520	N. 200 I–II 200 III–VI 1000	N. 200 I–II 200 III–IV 500 V–VI 1000	N. 200 I–II 500 III–VI 1000	N. 200 I–II 200 III–VI 1000	N. 200 I 200 II–III 500 IV–VI 1000	N. 200 I–IV 200 V–VI 500	N. 150 I–VI 200	200	Juv. 200 Adults 1000	200	50
15. x	L 4	15·59	15·54	..	..	..	..	..	..	..	..	..	..	..	..
23. x	L 4	15·35	15·38	1400	N. 250 I–III 500 IV–VI 1000	N. 250 I–III 500 IV–VI 1000	N. 250 I–III 500 IV–VI 1000	N. 500 I–III 500 IV–VI 500	N. 250 I–III 500 IV–VI 1000	N. 250 I–III 500 IV–VI 1000	N. 100 I–III 500 IV–VI 1000	500	Juv. 500 Adults 1000	500	50
28. x	L 4	14·89	14·90	..	..	..	..	..	..	..	..	..	..	..	..
6. xi	1 mile outside breakwater	13·8 (surface)	..	..	..	..	..	..	..	..	..	..	..	..	..
17. xi	L 4	13·78 (1 m.)	13·79	3140	N. 500 I–III 500 IV–VI 1000	N. 500 I–IV 500 V–VI 1000	N. 500	N. 500	N. 500 I–III 500 IV–VI 1000	N. 500 I–VI 500	N. 500 I–VI 500	500	Juv. 500 Adults 1000	500	500
26. xi	L 4	13·35	13·36	..	..	..	..	..	..	..	..	..	..	..	..
11. xii	L 4	11·97	12·00	2740	N. 200 IV–VI 2500	N. 200 IV–VI 1000	N. 200	N. 200	N. 200 I–VI 1000	N. 200 I–VI 200	N. 200 I–VI 200	Juv. 200 Adults 1000	Juv. 200 Adults 1000	200	200
22. xii	L 4	11·40	11·65	2540	N. 200 I–III 200 IV–VI 1000	N. 200 I–III 200 IV–VI 1000	N. 200	N. 200	N. 200	N. 200 I–VI 200	N. 200 I–VI 200	200	200		
7. i. 48	L 4	10·32	10·40	..	..	..	..	..	..	..	..	..	..	..	..
16. i	L 4	10·00	10·62	..	..	..	..	..	..	..	..	..	..	..	..
13. ii	L 4	9·80	9·82	..	..	..	..	..	..	..	..	..	..	..	..
19. ii	L 4	9·29	9·29	..	..	..	..	..	..	..	..	..	..	..	..

Note. N. is used as abbreviation for nauplii; and Roman numerals for copepodite stages.

TABLE II. *PSEUDOCALANUS ELONGATUS*. ABUNDANCE

	Number per cubic metre									Percentages			
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	220	18	16	14	14	62	66	7	417	53·8	9·0	12·3	24·9
5. ii	166	47	20	23	36	30	57	3	382	71·3	12·8	9·4	6·5
27. ii	349	34	21	23	19	34	63	8	551	62·6	15·0	9·6	12·8
17. iii	357	69	38	22	20	43	35	15	601	59·4	21·4	10·8	8·3
3. iv	1,348	182	112	181	147	108	126	76	2280	59·0	20·8	11·2	8·8
28. iv	2,145	125	130	398	341	178	120	68	3,505	61·5	18·7	14·8	5·3
8. v	11,440	280	220	600	380	440	120	120	13,600	83·8	8·1	6·0	1·8
14. v	7,720	1,180	110	93	144	230	270	193	9,940	77·5	14·0	3·8	4·6
22. v	..	..	..	..	..	..	..	..	..	49·7	39·8	6·4	4·0
2. vi	858	102	249	895	784	572	277	74	3,811	22·5	32·7	35·6	9·2
9. vi	940	..	40	140	100	320	440	80	2,060	45·6	8·7	20·4	25·2
18. vi	1,260	212	92	60	64	108	218	80	2,094	62·2	17·4	8·2	14·4
26. vi	1,680	180	260	780	750	610	330	130	4,720	35·6	25·8	28·8	9·1
3. vii	1,150	152	70	60	80	156	224	98	1,990	57·7	14·2	11·9	16·3
7. vii	830	56	36	16	33	80	287	91	1,429	58·2	7·6	7·9	26·5
31. vii	2,500	620	635	600	740	495	350	70	6,010	41·7	30·9	20·5	7·0
14. viii	2,060	155	175	139	94	42	32	8	2,705	76·1	17·7	5·0	1·5
28. viii	1,325	130	80	70	163	195	155	89	2,184	60·7	12·8	15·3	11·2
12. ix	570	255	205	270	262	115	75	11	1,773	32·1	41·2	21·8	4·8
25. ix	340	54	34	84	148	74	34	4	772	44·0	22·3	28·7	4·9
9. x	215	15	15	39	257	287	94	8	930	23·1	7·4	58·5	11·0
23. x	20	..	4	..	10	31	23	2	90	22·2	4·4	45·5	27·8
17. xi	10	..	..	..	1	5	1	..	17	..	..	..	..
11. xii	100	..	..	..	1	4	10	1	115	..	..	..	..
22. xii	130	10	..	..	..	..	..	..	140	..	..	..	..

TABLE III. *PARACALANUS PARVUS*. ABUNDANCE.

	Number per cubic metre									Percentages			
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	..	2	55	62	41	41	69	7	121	24·1	43·6	20·6	11·7
5. ii	..	26	33	24	30	28	22	..	173	35·4	38·6	20·7	5·2
27. ii	128	7	3	16	21	21	25	1	222	57·7	12·0	19·0	11·3
17. iii	95	18	4	2	4	20	18	..	161	59·0	14·9	14·9	11·2
3. iv	208	25	18	12	18	8	12	2	303	68·6	18·1	8·6	4·6
28. iv	345	48	23	28	28	13	15	..	500	69·0	19·8	8·2	3·0
8. v	3760	400	240	100	120	360	160	40	5180	72·5	14·3	9·3	3·9
14. v	2460	170	37	57	47	30	83	17	2901	84·9	9·1	2·6	3·5
22. v	..	..	..	..	..	..	..	..	..	19·5	64·8	12·8	2·8
2. vi	636	55	166	1540	1226	332	74	..	4029	15·8	43·6	38·6	1·8
9. vi	240	..	80	80	840	820	400	20	2480	9·7	6·4	66·9	16·9
18. vi	3840	276	80	72	124	120	218	28	4758	80·6	9·0	5·1	5·2
26. vi	1300	70	70	30	40	10	140	..	1660	78·3	10·2	3·0	8·4
3. vii	700	18	26	66	70	60	62	22	1024	68·3	10·7	12·7	8·2
7. vii	940	24	4	..	..	12	65	13	1058	89·0	2·6	1·1	7·4
31. vii	1540	110	120	65	135	125	180	..	2275	67·7	13·0	11·4	7·9
14. viii	2360	415	390	370	354	372	232	53	4546	51·9	25·8	16·0	6·3
28. viii	2025	335	240	160	230	201	227	42	3460	58·5	21·2	12·4	7·8
12. ix	2350	230	320	355	760	300	236	19	4570	51·4	19·8	23·2	5·6
25. ix	3270	276	160	136	124	89	125	6	4186	78·1	13·7	5·1	3·1
9. x	1460	270	235	372	260	195	77	18	2887	50·6	30·4	15·8	3·3
23. x	544	180	106	56	30	43	43	4	1006	54·1	34·0	7·3	4·7
17. xi	1294	130	82	32	42	29	58	2	1669	77·5	14·6	4·3	3·6
11. xii	1570	285	275	105	44	39	34	2	2354	66·7	28·2	3·5	1·5
22. xii	645	160	20	15	8	3	2	..	853	75·6	22·8	1·3	0·2

TABLE IV. *CENTROPAGES TYPICUS*. ABUNDANCE

Number per cubic metre

Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total
6. i	..	..	..	..	..	..	2	..	2
5. ii	8	..	..	..	..	..	..	..	8
27. ii	7	..	..	..	..	..	..	..	7
17. iii	7	..	..	..	1	..	..	..	8
3. iv	14	..	1	..	..	..	2	..	17
28. iv	10	..	..	..	..	..	..	..	10
8. v	..	..	..	..	..	..	..	..	..
14. v	..	..	..	..	..	3	3	..	6
2. vi	230	10	..	..	10	..	2	1	253
9. vi	20	..	..	..	..	..	..	..	20
18. vi	640	16	32	44	14	10	..	2	758
26. vi	220	..	10	20	10	10	..	10	280
3. vii	40	8	10	2	2	4	12	12	90
7. vii	80	5	..	..	2	3	1	6	97
31. vii	220	..	5	6	18	36	6	6	297
14. viii	830	..	..	..	3	3	5	4	845
28. viii	440	..	..	4	7	5	5	2	463
12. ix	920	..	10	35	79	46	18	24	1132
25. ix	360	..	2	2	..	3	1	1	368
9. x	315	22	18	2	5	2	..	..	364
23. x	12	..	..	..	1	..	..	..	13
17. xi	90	..	..	..	..	..	..	..	90
11. xii	10	..	..	..	..	..	..	..	10
22. xii	..	..	..	..	..	..	..	..	..

TABLE V. *TEMORA LONGICORNIS*. ABUNDANCE

	Number per cubic metre									Percentages			
Date	Nauplii	I	I	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	16	..	2	2	..	..	..	..	20	..	..	..	..
5. ii	54	2	..	1	..	1	..	..	58	96·4	2·4	0·6	0·6
27. ii	74	2	1	1	..	..	1	..	79	93·4	5·7	..	0·9
17. iii	82	11	2	..	2	..	1	..	98	83·8	13·3	2·0	1·0
3. iv	68	6	6	3	5	4	1	2	95	71·5	15·8	9·5	3·2
28. iv	455	3	23	25	10	23	13	5	557	81·6	9·2	5·9	3·2
8. v	3400	240	160	40	40	20	20	..	3920	86·7	11·2	1·5	0·5
14. v	3600	300	77	23	37	27	27	17	4108	87·7	9·7	1·6	1·1
22. v	..	..	..	..	..	..	..	..	..	36·2	56·9	5·8	1·0
2. vi	729	194	507	747	295	147	115	158	2892	25·2	50·0	15·3	9·5
9. vi	320	80	120	40	860	520	160	180	2280	14·0	10·5	60·5	14·9
18. vi	3840	356	196	56	32	6	24	32	4542	84·6	13·4	0·8	1·2
26. vi	440	30	..	..	24	28	48	96	666	66·1	4·5	7·8	21·6
3. vii	260	22	38	48	54	54	40	36	552	47·1	19·6	19·6	13·8
7. vii	40	4	..	1	1	21	65	75	207	19·6	2·4	10·6	67·6
31. vii	940	70	40	10	..	8	18	24	1110	84·7	10·8	0·7	3·8
14. viii	980	250	115	165	97	57	7	10	1681	58·3	31·5	9·2	1·0
28. viii	505	80	60	88	214	144	48	42	1181	42·8	19·3	30·3	7·6
12. ix	340	40	15	35	25	21	17	34	527	64·5	17·1	8·7	9·7
25. ix	185	15	10	6	6	4	3	5	234	79·0	13·2	4·3	3·4
9. x	60	..	5	2	1	2	3	3	76	78·9	9·2	3·9	7·9
23. x	16	4	..	..	..	..	1	..	21	..	..	..	..
17. xi	32	..	..	..	..	..	..	..	32	..	..	..	..
11. xii	45	..	..	..	..	..	..	..	45	..	..	..	..
22. xii	10	..	..	..	..	..	..	..	10	..	..	..	..

TABLE VI. *ACARTIA CLAUSI*. ABUNDANCE

	Number per cubic metre									Percentages			
Date	Nauplii	I	II	III	IV	V	VI♀	VI♂	Total	N.	I–III	IV–V	VI
6. i	..	..	..	..	..	..	5	..	5	..	..	..	..
5. ii	..	..	..	1	2	2	1	..	6	..	..	..	..
27. ii	25	..	..	..	..	..	..	..	25	..	..	..	..
17. iii	23	..	1	1	1	1	3	..	30	..	..	..	..
3. iv	45	7	8	2	3	3	3	1	72	..	..	..	..
28. iv	875	48	40	28	23	18	45	33	1,110	79·0	10·4	3·7	7·0
8. v	14,280	1,340	740	580	240	100	220	40	17,540	81·2	15·2	1·9	1·5
14. v	5,320	547	353	390	394	287	110	107	7,508	70·7	17·2	9·1	2·9
22. v	..	..	..	..	..	..	..	..	..	45·9	38·4	9·8	5·9
2. vi	2,350	304	461	516	434	286	141	173	4,665	50·4	27·5	15·4	6·7
9. vi	3,800	320	520	580	520	300	360	400	6,800	55·9	20·9	12·0	11·2
18. vi	5,060	288	144	136	72	84	44	70	5,898	86·9	9·6	2·6	1·9
26. vi	1,740	230	170	260	310	100	380	310	3,508	48·6	18·4	13·7	19·3
3. vii	1,290	108	146	108	132	82	142	230	2,238	57·7	16·4	9·6	16·6
7. vii	880	28	28	6	5	2	204	193	1,346	65·5	4·6	0·5	29·5
31. vii	2,460	410	240	170	78	56	180	174	3,696	66·9	21·6	3·6	7·7
14. viii	830	25	35	70	25	75	60	65	1,185	70·0	11·0	8·4	10·5
28. viii	335	25	..	19	56	31	62	46	574	58·4	7·7	15·1	18·9
12. ix	230	5	..	15	57	39	58	32	436	52·6	4·6	22·0	20·6
25. ix	505	6	2	2	12	25	34	18	604	83·6	1·6	6·1	8·6
9. x	285	10	6	2	7	12	46	5	373	76·4	4·8	5·1	13·7
23. x	..	8	4	..	..	..	4	..	16	..	..	..	..
17. xi	218	12	10	2	7	3	1	3	256	85·1	9·4	3·9	1·6
11. xii	10	2	4	1	..	..	..	..	17	..	..	..	..
22. xii	..	..	..	..	..	..	..	..	..	..	..	..	..

TABLE VII. *OITHONA SIMILIS*. ABUNDANCE

Date	Number per cubic metre: Eggs	Nauplii	I	II	III	IV	V	VI ♀	VI ♂	Total excl. eggs	Percentages: N.	I–III	IV–V	VI	Eggs per egg-sac
6. i	} Lost through		} 9	16	30	18	66	156	27	..	40·9	15·9	22·6	20·9	..
5. ii	} net mesh		} 9	15	27	27	24	29	3	..	57·1	17·9	12·2	12·8	..
27. ii	272	254	19	9	12	6	11	28	52	451	74·0	11·5	5·0	9·5	6·3
17. iii	80	156	16	8	4	8	8	22	2	224	69·7	12·5	7·1	10·7	8·9
3. iv	835	183	39	48	43	57	64	45	14	493	37·2	26·4	24·6	12·0	12·8
28. iv	?	630	80	63	63	45	55	140	25	1,101	57·0	18·7	9·1	14·9	..
8. v	13,240	10,560	700	800	1,040	740	720	580	130	15,320	68·8	16·6	9·5	5·0	13·8
14. v	2,780	3,000	130	130	103	130	157	147	50	3,847	78·0	9·4	7·4	5·1	13·9
22. v	..	..	..	..	..	..	..	..	..	..	58·0	28·2	7·9	5·8	..
2. vi	5,750	8,990	1,410	1,190	728	434	701	508	101	14,062	64·0	23·8	8·1	4·9	9·7
9. vi	10,280	6,960	1,500	1,480	1,760	1,200	820	780	180	14,680	47·4	32·3	13·8	6·5	10·1
18 vi	15,920	9,320	1,100	1,340	720	1,200	1,380	1,320	480	16,860	55·4	18·7	15·3	10·7	11·7
26. vi	3,720	8,280	1,140	1,040	1,680	1,400	2,180	1,760	340	17,820	46·5	21·7	20·1	11·8	8·8
3. vii	9,650	5,840	440	360	430	260	550	630	140	8,650	67·5	14·2	9·4	8·9	11·8
7. vii	6,240	8,040	390	300	344	408	408	672	128	10,690	75·2	9·7	7·6	7·5	7·4
31. vii	8,540	16,040	1,400	1,020	740	525	510	865	82	21,182	76·2	14·9	4·9	4·4	8·4
14. viii	7,460	6,050	355	370	305	395	525	895	155	9,050	66·8	11·4	10·2	11·6	6·7
28. viii	2,900	3,850	295	295	225	155	164	218	40	5,242	73·4	15·5	6·1	4·9	7·4
12. ix	6,230	10,170	450	605	470	540	545	735	35	13,550	75·0	11·2	8·0	5·7	6·8
25. ix	1,060	2,454	285	198	124	102	142	206	14	3,529	69·5	17·2	6·9	6·3	7·1
9. x	680	1,400	170	155	145	165	162	138	13	2,348	59·6	20·0	13·9	6·4	8·0
23. x	128	396	54	48	32	24	35	24	1	614	64·4	31·8	9·6	4·1	6·4
17. xi	398	460	36	18	22	28	20	56	10	650	70·7	11·7	7·4	10·2	8·0
11. xii	485	480	115	95	145	55	30	55	..	975	49·2	36·4	8·7	5·6	6 9
22. xii	..	50	30	20	30	5	10	10	..	155	..	..	..	..	..

TABLE VIII. *OITHONA NANA*. ABUNDANCE

Date	Number per cubic metre: Eggs	Nauplii	I	II	III	IV	V	VI ♀	VI ♂	Total excl. eggs	Percentages: N.	I–III	IV–V	VI	Eggs per per egg-sac
31. vii	..	..	40	..	..	..	..	..	..	40	..	..	..	..	..
14. viii	..	40	20	10	..	..	..	10	..	80	..	..	..	..	..
28. viii	..	415	..	..	..	..	..	..	..	415	..	..	..	..	..
12. ix	2120	910	65	25	10	10	85	80	35	1220	74·6	8·2	7·8	9·4	15·1
25. ix	410	1910	60	35	20	30	22	60	14	2137	89·5	5·4	2·4	2·8	13·7
9. x	1900	5870	915	410	435	345	210	120	35	8310	70·6	21·2	6·7	1·5	15·2
23. x	..	1480	174	118	66	24	11	4	..	1887	78·8	19·1	1·9	0·2	..
17. xi	1144	2318	48	20	14	50	12	32	2	2506	92·5	3·3	2·9	1·4	16·8
11. xii	375	1555	370	295	70	40	30	30	30	2420	64·2	30·4	2·9	2·5	10·7
22. xii	..	415	140	90	105	30	15	25	15	835	49·6	40·1	5·4	4·8	..

TABLE IX. *ONCAEA VENUSTA*, *CORYCAEUS ANGLICUS*, *EUTERPINA ACUTIFRONS* AND UNIDENTIFIED NAUPLII. ABUNDANCE

Date	*Oncaea venusta* No. per cu.m.: Juv.	♀	♂	Total	*Oncaea venusta* Percentage: Juv.	Adult	*Corycaeus anglicus* No. per cu.m.: Juv.	♀	♂	Total	*Euterpina acutifrons* Percentage: Juv.	Adult	No. per cu.m.	Unidentified nauplii No. per cu.m.
31. vii	..	..	..	..	..	..	..	..	..	..	..	..	20	..
14. viii	15	..	..	15	..	..	25	3	3	31	..	..	119	340
28. viii	105	..	10	115	91·2	8·8	55	6	20	81	..	..	278	1115
12. ix	150	20	20	190	79·0	21·0	180	25	44	249	72·3	27·7	905	1640
25. ix	28	3	5	36	77·8	22·2	325	13	15	353	92·3	7·9	292	2140
9. x	315	30	10	355	88·8	11·2	1235	63	73	1371	90·1	9·9	490	1220
23. x	114	10	18	142	80·2	19·8	176	98	133	407	43·2	56·7	232	1080
17. xi	172	16	6	194	88·5	11·4	284	69	115	326	43·5	56·5	234	2200
11. xii	175	7	15	197	88·5	11·4	365	12	26	403	90·6	9·4	18	1040
22. xii	200	5	15	220	90·8	9·2	110	..	..	110	100·0	..	..	..

TABLE X. *PSEUDOCALANUS ELONGATUS*. SIZE IN MM.

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	Median size
VI ♂	6. i	16	..	..	..	4	9	1	2	..	..	..	..	..	..	..	0·673
	5. ii	3	..	..	..	2	1	..	..	..	..	..	..	..	..	..	..
	27. ii	10	..	..	..	..	3	5	2	..	..	..	..	..	..	..	0·717
	17. iii	48	..	..	..	1	11	30	6	..	..	..	..	..	..	..	0·728
	3. iv	78	..	..	..	..	3	18	52	5	..	..	..	..	..	..	0·786
	28. iv	26	..	..	..	..	..	..	5	18	3	..	..	..	..	..	0·837
	14. v	64	..	..	..	..	3	22	32	6	1	..	..	..	..	..	0·773
	2. vi	17	..	..	..	1	11	4	..	..	1	..	..	..	..	..	0·692
	18. vi	27	..	..	..	..	20	4	3	..	..	..	..	..	..	..	0·699
	3. vii	47	..	..	..	11	25	11	..	..	..	..	..	..	..	..	0·678
	17. vii	95	..	..	..	11	73	10	1	..	..	..	..	..	..	..	0·679
	31. vii	14	..	..	..	..	10	4	..	..	..	..	..	..	..	..	0·697
	14. viii	8	..	..	..	3	4	1	..	..	..	..	..	..	..	..	..
	28. viii	89	..	..	..	13	71	5	..	..	..	..	..	..	..	..	0·674
	12. ix	11	..	..	2	5	4	..	..	..	..	..	..	..	..	..	0·646
	25. ix	2	..	..	..	1	1	..	..	..	..	..	..	..	..		..
	9. x	8	..	..	..	2	6	..	..	..	..	..	..	..	..		..
	23. x	2	..	..	..		2	..	..	..	..	..	..	..	..		..
	11. xii	2	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
	28. i	4	..	..	..	1	1	2	..	..	..	..	..	..	..	..	..
VI ♀	6. i	112	..	..	..	..	1	27	66	17	1	..	..	..	..	..	0·745
	5. ii	92	..	..	..	..	..	20	57	13	2	..	..	..	..	..	0·785
	27. ii	85	..	..	..	..	2	19	23	14	17	10	..	..	..	..	0·812
	17. iii	120	..	..	..	..	..	16	37	15	20	24	6	2	..	..	0·832
	15. iv	137	..	..	..	..	..	1	5	3	9	23	36	43	15	2	1·017
	28. iv	115	..	..	..	..	..	..	..	..	..	8	20	40	37	10	1·062
	14. v	131	..	..	..	..	..	..	1	8	34	41	25	16	5	1	0·953
	2. vi	119	..	..	..	..	..	3	20	35	23	25	9	3	1	..	0·870
	18. vi	100	..	..	..	..	..	1	24	50	17	6	1	..	1	..	0·836
	3. vii	97	..	..	..	..	..	2	35	48	12	..	..	..	..	..	0·827
	17. vii	64	..	..	..	..	..	5	26	27	5	1	..	..	..	..	0·817
	31. vii	70	..	..	..	..	..	2	25	32	10	1	..	..	..	..	0·827
	14. viii	32	..	..	..	..	..	2	15	12	3	..	..	..	..	..	0·810
	28. viii	154	..	..	..	..	..	22	95	37	..	..	..	..	..	..	0·794
	12. ix	76	..	..	..	..	1	24	39	11	1	..	..	..	..	..	0·776
	25. ix	85	..	..	..	..	4	23	39	19	..	..	..	..	..	..	0·781
	9. x	94	..	..	..	..	..	27	54	11	2	..	..	..	..	..	0·784
	23. x	82	..	..	..	..	..	24	52	6	..	..	..	..	..	..	0·774
	17. xi	55	..	..	..	..	..	24	29	2	..	..	..	..	..	..	0·764
	26. xi	124	..	..	..	..	5	49	66	4	..	..	..	..	..	..	0·769
	11. xii	101	..	..	..	..	2	34	55	9	1	..	..	..	..	..	0·772
	28. i	92	..	..	..	..	..	17	40	20	13	1	1	..	..	..	0·794
V ♂	6. i	25	..	..	..	..	22	3	..	..	..	..	..	..	..	..	0·685
	5. ii	9	..	..	..	..	3	6	..	..	..	..	..	..	..	..	0·736
	27. ii	20	..	..	..	..	..	4	14	2	..	..	..	..	..	..	0·776
	17. iii	74	..	..	..	1	3	28	41	1	..	..	..	..	..	..	0·766
	3. iv	49	..	..	..	..	..	..	23	23	2	1	..	..	..	..	0·816
	28. iv	37	..	..	..	..	..	..	6	24	6	1	..	..	..	..	0·847

	14. v	31	..	..	..	1	3	12	10	2	3	..	..	..	..	..	0·758
	2. vi	29	..	..	..	..	12	14	2	1	..	..	..	..	..	..	0·714
	18. vi	19	..	..	..	1	9	6	2	1	..	..	..	..	..	..	0·706
	3. vii	36	..	..	..	1	24	8	3	..	..	..	..	..	..	..	0·695
	17. vii	32	..	..	..	1	12	19	..	..	..	..	..	..	..	..	0·714
	31. vii	64	..	..	..	..	28	35	1	..	..	..	..	..	..	..	0·711
	14. viii	23	..	..	..	..	22	1	..	..	..	..	..	..	..	..	0·684
	28. viii	102	..	..	..	12	77	12	1	..	..	..	..	..	..	..	0·686
	12. ix	63	..	..	..	9	46	8	..	..	..	..	..	..	..	..	0·676
	25. ix	36	..	..	..	2	25	9	..	..	..	..	..	..	..	..	0·688
	9. x	159	..	..	..	18	128	13	..	..	..	..	..	..	..	..	0·679
	23. x	20	..	..	..	2	15	3	..	..	..	..	..	..	..	..	0·687
	17. xi	3	..	..	..	..	3	..	..	..	..	..	..	..	..	..	..
	11. xii	4	..	..	..	..	3	1	..	..	..	..	..	..	..	..	..
V ♀	6. i	48	..	..	..	6	22	19	1	..	..	..	..	..	..	..	0·700
	5. ii	23	..	..	..	..	5	8	10	..	..	..	..	..	..	..	0·758
	27. ii	26	..	..	..	..	..	4	14	7	1	..	..	..	..	..	0·772
	17. iii	47	..	..	..	..	..	1	18	20	7	1	..	..	..	..	0·819
	3. iv	56	..	..	..	..	..	..	6	12	28	10	..	..	..	..	0·882
	28. iv	34	..	..	..	..	..	..	..	3	17	10	4	..	..	..	0·908
	14. v	36	..	..	..	..	2	6	18	4	5	1	..	..	..	..	0·767
	2. vi	33	..	..	..	..	15	18	..	..	..	..	..	..	..	..	0·712
	18. vi	42	..	..	..	..	6	20	10	6	..	..	..	..	..	..	0·750
	3. vii	38	..	..	..	..	4	28	6	..	..	..	..	..	..	..	0·735
	17. vii	54	..	..	..	..	14	29	11	..	..	..	..	..	..	..	0·729
	31. vii	31	..	..	..	..	1	25	4	1	..	..	..	..	..	..	0·731
	14. viii	18	..	..	..	..	7	10	1	..	..	..	..	..	..	..	0·714
	28. viii	93	..	..	..	7	49	36	1	..	..	..	..	..	..	..	0·699
	12. ix	52	..	..	..	11	31	10	..	..	..	..	..	..	..	..	0·677
	25. ix	38	..	..	..	2	23	12	1	..	..	..	..	..	..	..	0·699
	9. x	128	..	..	..	6	104	17	1	..	..	..	..	..	..	..	0·690
	23. x	11	..	..	..	1	8	2	..	..	..	..	..	..	..	..	0·693
	20. xi	2	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
	11. xii	5	..	..	..	4	..	1	..	..	..	..	..	..	..	..	..
IV ♂	6. i	5	..	1	2	2	..	..	..	..	..	..	..	..	..	..	..
	5. ii	15	..	3	1	8	3	..	..	..	..	..	..	..	..	..	0·614
	27. ii	8	..	..	..	5	1	2	..	..	..	..	..	..	..	..	..
	17. iii	33	..	..	..	13	20	..	..	..	..	..	..	..	..	..	0·660
	3. iv	76	..	..	..	..	38	34	4	..	..	..	..	..	..	..	0·708
	28. iv	61	..	..	..	..	14	39	8	..	..	..	..	..	..	..	0·730
	14. v	16	..	..	3	5	8	..	..	..	..	..	..	..	..	..	0·655
	2. vi	30	..	..	5	25	..	..	..	..	..	..	..	..	..	..	0·622
	18. vi	10	..	..	1	5	4	..	..	..	..	..	..	..	..	..	0·638
	3. vii	11	..	..	..	9	2	..	..	..	..	..	..	..	..	..	0·615
	17. vii	17	..	..	4	13	..	..	..	..	..	..	..	..	..	..	0·625
	31. vii	67	..	..	4	55	8	..	..	..	..	..	..	..	..	..	0·639
	14. viii	34	..	..	15	19	..	..	..	..	..	..	..	..	..	..	0·606
	28. viii	81	..	..	30	50	1	..	..	..	..	..	..	..	..	..	0·608
	12. ix	135	..	1	61	71	2	..	..	..	..	..	..	..	..	..	0·604
	25. ix	66	..	..	15	48	3	..	..	..	..	..	..	..	..	..	0·610
	9. x	122	..	1	56	64	1	..	..	..	..	..	..	..	..	..	0·604
	23. x	2	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..
	11. xii	1	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..

TABLE X (*continued*)

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	Median size
IV♀	6. i	4	..	..	..	4	..	..	..	..	..
	5. ii	21	..	..	1	13	7	..	..	..	..
	27. ii	18	..	..	..	2	14	2	..	..	0·630
	17. iii	47	..	..	..	6	25	16	..	..	0·668
	3. iv	69	..	..	..	3	8	49	9	..	0·693
	28. iv	73	..	..	..	..	6	41	24	2	0·735
	14. v	24	..	..	2	5	13	4	..	..	0·750
	2. vi	55	..	..	8	45	1	1	..	..	0·680
	18. vi	23	..	..	1	14	5	3	..	..	0·615
	3. vii	25	..	..	..	18	7	..	..	..	0·640
	17. vii	19	..	..	5	10	3	1	..	..	0·646
	31. vii	78	..	..	6	58	14	..	..	..	0·625
	14. viii	48	..	..	14	34	..	..	..	..	0·637
	28. viii	82	..	..	27	53	2	..	..	..	0·610
	12. ix	107	..	..	45	61	1	..	..	..	0·614
	25. ix	87	..	..	23	64	..	..	..	..	0·614
	9. x	132	..	..	51	81	..	..	..	..	0·614
	23. x	8	..	..	2	5	1	..	..	..	0·608
III	6. i	13	..	9	4	..	..	..	..	..	0·540
	5. ii	23	..	7	16	..	..	..	..	..	0·555
	27. ii	38	..	5	32	1	..	..	..	..	0·566
	17. iii	70	..	3	46	21	..	..	..	..	0·589
	3. iv	81	..	..	4	62	15	..	..	..	0·634
	28. iv	67	..	..	2	55	9	1	..	..	0·638
	14. v	26	..	4	16	6	..	..	..	..	0·587
	2. vi	51	..	38	13	..	..	..	..	..	0·534
	18. vi	15	1	6	8	..	..	..	..	..	0·550
	3. vii	23	2	17	4	..	..	..	..	..	0·522
	17. vii	4	..	1	3	..	..	..	..	..	..
	31. vii	82	..	24	58	..	..	..	..	..	0·558
	14. viii	28	..	26	2	..	..	..	..	..	0·528
	28. viii	61	5	53	3	..	..	..	..	..	0·523
	12. ix	54	2	51	1	..	..	..	..	..	0·518
	25. ix	42	..	36	6	..	..	..	..	..	0·532
	9. x	17	2	14	1	..	..	..	..	..	0·516

Stage	Date	No.	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	Median size
II	6. i	11	..	..	6	5	..	..	0·441
	5. ii	20	..	..	5	15	..	..	0·458
	27. ii	14	..	..	..	28	..	..	0·467
	17. iii	50	..	..	..	33	17	..	0·487
	3. iv	49	..	..	..	6	38	5	0·519
	28. iv	26	..	..	..	..	21	5	0·537
	14. v	21	..	..	..	12	9	..	0·493
	2. vi	26	..	..	16	10	..	..	0·438
	18. vi	24	..	..	1	20	3	..	0·467
	3. vii	30	..	..	16	14	..	..	0·439
	17. vii	10	..	..	3	7	..	..	0·452
	31. vii	41	..	..	2	39	..	..	0·463
	14. viii	35	..	..	27	8	..	..	0·432
	28. viii	17	..	..	15	2	..	..	0·431
	12. ix	41	..	..	34	7	..	..	0·435
	25. ix	16	..	..	6	10	..	..	0·448
	9. x	4	..	..	3	1	..	..	..
	23. x	2	..	..	1	1	..	..	..
I	6. i	19	..	18	1	..	..	..	0·366
	5. ii	46	..	36	10	..	..	..	0·376
	27. ii	46	..	38	8	..	..	..	0·380
	17. iii	90	..	34	56	..	..	..	0·394
	3. iv	78	..	16	58	4	..	..	0·406
	28. iv	21	..	..	19	2	..	..	0·426
	14. v	68	..	25	42	1	..	..	0·395
	2. vi	10	..	10	..	..	..	..	0·364
	18. vi	25	..	14	11	..	..	..	0·388
	3. vii	46	6	30	10	..	..	..	0·353
	17. vii	14	..	12	2	..	..	..	0·358
	31. vii	32	..	25	7	..	..	..	0·380
	14. viii	32	3	28	1	..	..	..	0·360
	28. viii	26	6	19	1	..	..	..	0·346
	12. ix	44	1	43	1	..	..	..	0·363
	25. ix	26	..	23	3	..	..	..	0·374
	9. x	5	..	5	..	..	..	..	..

TABLE XI. *PARACALANUS PARVUS*. SIZE IN MM.

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–9·020	Median size
VI ♂	6. i	3	..	..	1	2	..	..	..	..	..	..
	27. ii	1	..	..	..	..	..	1	..	..	..	..
	17. iii	6	..	..	..	..	1	4	1	..	..	..
	3. iv	3	..	..	..	..	..	2	1	..	..	..
	14. v	5	..	..	..	..	..	2	..	3	..	..
	17. vi	13	..	..	..	..	..	7	6	..	..	0·757
	3. vii	11	..	..	..	..	..	1	9	1	..	0·790
	17. vii	14	..	..	..	..	..	3	10	1	..	0·784
	14. viii	53	..	..	..	4	44	5	..	..	..	0·683
	28. viii	42	..	..	..	5	24	12	..	..	..	0·695
	12. ix	19	..	..	..	4	10	5	..	..	..	0·692
	25. ix	10	..	..	..	2	5	3	..	..	..	0·699
	9. x	16	..	..	..	4	6	6	..	..	..	0·705
	23. x	9	..	..	..	..	5	4	..	..	..	..
	17. xi	2	..	..	..	..	1	1	..	..	..	..
	20. xi	38	..	..	..	..	24	14	..	..	..	0·701
VI ♀	6. i	64	..	1	19	35	9	..	..	..	..	0·622
	5. ii	46	..	..	1	11	29	5	..	..	..	0·675
	27. ii	45	..	..	..	10	25	10	2	..	..	0·686
	17. iii	56	..	..	..	10	25	17	3	1	..	0·694
	3. iv	22	..	..	..	..	..	9	11	2	..	0·770
	15. iv	21	..	..	..	..	2	7	10	2	..	0·774
	28. iv	15	..	..	..	..	..	..	3	7	5	0·852
	14. v	25	..	..	..	..	..	7	10	8	..	0·777
	2. vi	7	..	..	..	2	4	1	..	..	..	..
	18. vi	60	..	..	..	4	33	20	2	1	..	0·699
	3. vii	70	..	..	..	7	17	41	5	..	..	0·719
	17. vii	67	..	..	..	..	13	45	..	9	..	0·739
	31. vii	36	..	..	..	2	12	19	3	..	..	0·720
	14. viii	234	..	..	44	143	40	7	..	..	..	0·628
	28. viii	227	..	..	12	152	56	7	..	..	..	0·643
	12. ix	220	..	..	14	134	57	15	..	..	..	0·640
	25. ix	153	..	..	10	72	51	18	2	..	..	0·651
	9. x	80	..	..	4	9	36	28	3	..	..	0·700
	23. x	81	..	..	..	7	49	25	..	..	..	0·695
	17. xi	60	..	..	..	2	44	14	..	..	..	0·692
	11. xii	80	..	..	3	15	49	13	..	..	..	0·680
V ♂	6. i	8	..	..	1	2	5	..	..	..	..	..
	5. ii	9	..	..	..	3	6	..	..	..	..	..
	27. ii	18	..	..	..	1	7	10	..	..	..	0·711
	17. iii	21	..	..	..	..	5	13	3	..	..	0·715
	3. iv	7	..	..	..	1	1	1	4	..	..	..
	14. v	2	..	..	..	..	..	..	2	..	..	..
	2. vi	8	..	..	1	1	5	1	..	..	..	..
	18. vi	13	..	..	..	..	6	6	1	..	..	0·710
	3. vii	18	..	..	..	..	3	15	..	..	..	0·729
	17. vii	8	..	..	..	1	..	6	1	..	..	..
	31. vii	16	..	..	..	2	7	7	..	..	..	0·704
	14. viii	5	..	..	12	93	51	..	..	..	..	0·647
	28. viii	..	..	..	1	26	39	..	..	..	..	0·660
	12. ix	114	..	..	2	63	46	3	..	..	..	0·650
	25. ix	37	..	..	..	15	20	2	..	..	..	0·663
	9. x	42	..	..	..	15	22	5	..	..	..	0·667
	23. x	13	..	..	..	2	10	1	..	..	..	0·678
	17. xi	16	..	..	..	5	10	1	..	..	..	0·664
	20. xi	18	..	..	1	9	8	..	..	..	..	0·651
V ♀	6. i	10	..	2	8	..	..	..	..	..	..	0·559
	5. ii	18	..	2	11	4	1	..	..	..	..	0·596
	27. ii	26	..	1	4	15	6	..	..	..	..	0·628
	17. iii	33	..	..	5	17	11	..	..	..	..	0·633
	3. iv	8	..	..	..	1	6	1	..	..	..	..
	28. iv	5	..	..	..	2	3	..	..	..	..	..
	14. v	7	..	..	..	3	3	1	..	..	..	..
	2. vi	28	..	4	22	2	..	..	..	..	..	0·576
	18. vi	16	..	..	8	7	1	..	..	..	..	0·602
	3. vii	12	..	..	1	10	1	..	..	..	..	0·629
	17. vii	4	..	..	..	2	2	..	..	..	..	..
	31. vii	9	..	..	1	8	..	..	..	..	..	..
	14. viii	216	3	109	96	8	..	..	..	..	..	0·548
	28. viii	135	..	30	94	10	1	..	..	..	..	0·568
	12. ix	186	..	43	128	14	1	..	..	..	..	0·565
	25. ix	56	..	13	32	11	..	..	..	..	..	0·569
	9. x	149	1	35	72	41	..	..	..	..	..	0·577
	23. x	33	..	7	17	14	..	..	..	..	..	0·591
	17. xi	13	..	3	10	..	..	..	..	..	..	0·561
	20. xi	20	1	7	2	..	..	..	..	..	..	0·553
IV ♂	6. i	6	..	6	..	..	..	..	..	..	..	..
	5. ii	8	..	2	6	..	..	..	..	..	..	..
	27. ii	18	..	2	16	..	..	..	..	..	..	0·575
	17. iii	12	..	3	7	2	..	..	..	..	..	0·588
	3. iv	6	..	..	..	5	1	..	..	..	..	..
	28. iv	3	..	..	..	3	..	..	..	..	..	..
	14. v	3	..	..	3	..	..	..	..	..	..	..
	2. vi	41	2	31	8	..	..	..	..	..	..	0·535
	18. vi	8	..	..	7	1	..	..	..	..	..	..
	3. vii	16	..	1	13	2	..	..	..	..	..	0·584

TABLE XI (*continued*)

Stage	Date	No.	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	Median size
IV ♂ (cont.)	17. vii	..	..	..	..	..	..	..	..
	31. vii	12	..	..	..	3	9	..	0·562
	14. viii	164	..	..	18	136	10	..	0·520
	28. viii	65	..	..	6	40	18	1	0·535
	12. ix	61	..	..	5	52	4	..	0·522
	25. ix	29	..	..	..	15	12	2	0·547
	9. x	25	..	..	1	17	7	..	0·533
	23. x	7	..	..	1	4	2	..	..
	17. xi	10	..	..	..	10	..	..	0·515
	20. xi	7	..	..	2	5	..	..	..
IV ♀	6. i	12	..	..	8	4	..	..	0·484
	5. ii	22	..	..	11	11	..	..	0·496
	27. ii	18	..	..	..	16	2	..	0·522
	17. iii	17	..	..	2	12	2	1	0·530
	3. iv	12	..	..	..	4	6	2	0·561
	28. iv	7	..	..	..	4	3	..	..
	14. v	11	..	..	..	10	1	..	0·529
	2. vi	71	..	..	57	14	..	..	0·475
	18. vi	22	..	..	1	20	1	..	0·517
	3. vii	15	..	..	..	15	..	..	0·519
	31. vii	15	..	..	5	10	..	..	0·505
	14. viii	203	..	19	177	7	..	..	0·460
	28. viii	97	..	4	84	9	..	..	0·477
	12. ix	83	..	8	65	10	..	..	0·469
	25. ix	34	..	1	16	16	1	..	0·495
	9. x	41	..	1	24	16	..	..	0·490
	23. x	24	..	2	10	10	2	..	0·459
	17. xi	17	..	..	16	1	..	..	0·473
	20. xi	13	..	4	9	..	..	..	0·457
III	6. i	27	..	23	4	..	..	..	0·417
	5. ii	25	7	16	2	..	..	..	0·413
	27. ii	33	..	16	17	..	..	..	0·444
	17. iii	12	..	3	9	..	..	..	0·451
	3. iv	12	..	2	5	5	..	..	0·487
	28. iv	9	..	..	8	1	..	..	..
	14. iv	17	..	7	8	2	..	..	0·455
	2. vi	91	2	73	16	..	..	..	0·421
	18. vi	18	..	9	9	..	..	..	0·443
	3. vii	21	..	15	6	..	..	..	0·431
	31. vii	13	..	11	2	..	..	..	0·423
	14. viii	82	16	66	..	..	..	..	0·403
	28. viii	35	2	31	2	..	..	..	0·412
	12. ix	76	15	58	3	..	..	..	0·402
	25. ix	32	1	25	6	..	..	..	0·423
	9. x	67	11	54	2	..	..	..	0·408
	23. x	50	2	45	3	..	..	..	0·418
	17. xi	21	5	16	..	..	..	..	0·398
	20. xi	22	14	8	..	..	..	..	0·385

Stage	Date	No.	0·177–0·230	0·230–0·283	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	Median size
II	6. i	24	..	..	13	11	..	..	0·334
	5. ii	33	..	..	6	27	..	..	0·353
	27. ii	9	..	..	1	8	..	..	..
	17. iii	18	..	..	4	13	1	..	0·380
	3. iv	18	..	..	1	13	4	..	0·377
	28. iv	8	..	..	..	6	2	..	..
	14. v	11	..	..	1	8	2	..	0·356
	2. vi	18	..	..	9	9	..	..	0·336
	18. vi	20	..	..	2	18	..	..	0·356
	3. vii	10	..	..	4	6	..	..	0·340
	17. vii	1	..	..	1	..	..	..	..
	31. vii	24	..	..	5	19	..	..	0·342
	14. viii	78	..	..	64	14	..	..	0·327
	28. viii	47	..	..	37	10	..	..	0·327
	12. ix	66	..	..	51	15	..	..	0·323
	25. ix	39	..	..	16	23	..	..	0·340
	9. x	48	..	..	31	17	..	..	0·331
	23. x	51	..	..	23	28	..	..	0·338
	17. xi	41	..	..	39	2	..	..	0·318
	20. x	35	..	..	1	34	..	..	0·304
I	6. i	1	..	1	..	..	..	..	..
	5. ii	27	..	17	10	..	..	..	0·275
	27. ii	30	..	22	7	1	..	..	0·276
	17. iii	43	..	27	16	..	..	..	0·279
	3. iv	20	..	8	12	..	..	..	0·287
	28. iv	15	..	2	13	..	..	..	0·297
	14. v	37	..	31	6	..	..	..	0·268
	2. vi	6	..	5	1	..	..	..	..
	18. vi	35	..	28	7	..	..	..	0·274
	3. vii	5	..	5	..	..	..	..	..
	17. vii	6	..	6	..	..	..	..	..
	31. vii	22	..	20	2	..	..	..	0·270
	14. viii	82	1	80	..	..	..	..	0·256
	28. viii	67	..	67	..	..	..	..	0·251
	12. ix	46	..	46	..	..	..	..	0·252
	25. ix	55	..	46	9	..	..	..	0·271
	9. x	54	..	54	..	..	..	..	0·255
	23. x	90	..	88	2	..	..	..	0·263
	17. xi	93	4	8	9	..	..	..	0·246
	20. xi	12	2	10	..	..	..	..	0·240

TABLE XII. *CENTROPAGES TYPICUS*. SIZES IN MM.

Stage	Date	No.	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	1·18–1·24	1·24–1·29	1·29–1·35	1·35–1·40	1·40–1·45	1·45–1·51	1·51–1·56	1·56–1·61	1·61–1·67	1·67–1·72
VI ♀	6. i	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	5. ii	3	1	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	1	..	1	..	..	..	..	..	..	..	..	..	..	..
	14. v	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	2	1
	2. vi	2	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	..	..
	18. vi	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	3. vii	11	..	..	..	..	..	..	..	..	..	1	..	5	3	2	..	..	..	..
	17. vii	1	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
	31. vii	3	..	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..	..
	14. viii	5	..	..	..	..	..	..	..	..	1	1	2	1	..	..	..	..	..	..
	28. viii	5	..	..	..	..	..	..	..	..	..	2	2	1	..	..	..	..	..	..
	4. ix	8	..	..	..	..	..	..	..	..	..	4	3	1	..	..	..	..	..	..
	25. ix	33	..	..	..	..	..	..	1	6	14	5	6	1	..	..	..	..	..	..
	23. x	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	17. xi	4	..	..	..	..	..	..	..	..	..	..	4	..	..	..	..	..	..	..
	20. xi	3	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..	..	..
	11. xii	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	28. i	3		..	..	..	..	..	1	1	1	..	..	..	..	..	..	..	..	..

TABLE XIII. *TEMORA LONGICORNIS*. SIZE IN MM.

Stage	Date	No.	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	1·18–1·24	1·24–1·29	1·29–1·35	1·35–1·40	1·40–1·45	Median size
VI ♂	6. i	3	..	..	..	..	..	..	..	2	1	..	..	..	..	..	..	..	..	..
	14. ii	3	..	..	..	..	..	1	..	1	1	..	..	..	..	..	..	..	..	..
	3. iv	4	..	..	..	..	..	..	1	2	..	1	..	..	..	..	..	..	..	..
	15. iv	8	..	..	..	..	..	..	1	3	3	1	..	..	..	..	..	..	..	..
	28. iv	2	..	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
	14. v	6	..	..	..	..	..	..	2	2	1	1	..	..	..	..	..	..	..	..
	2. vi	102	..	..	..	1	..	4	7	10	17	18	29	10	4	2	..	..	..	1·07
	18. vi	19	..	..	..	1	6	5	2	2	..	1	1	..	1	..	..	..	..	0·852
	3. vii	46	..	3	6	5	7	9	11	4	..	1	..	..	..	..	..	..	..	0·820
	17. vii	79	..	5	10	4	22	17	15	5	1	..	..	..	..	..	..	..	..	0·811
	31. vii	12	..	..	1	2	3	3	1	2	..	..	..	..	..	..	..	..	..	0·815
	14. viii	10	..	..	2	2	3	3	..	..	..	..	..	..	..	..	..	..	..	0·779
	28. viii	38	..	1	3	7	8	13	6	..	..	..	..	..	..	..	..	..	..	0·815
	12. ix	34	..	..	1	18	11	4	..	..	..	..	..	..	..	..	..	..	..	0·756
	25. ix	106	..	..	1	42	61	2	..	..	..	..	..	..	..	..	..	..	..	0·772
	9. x	2	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
	23. x	2	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
	17. xi	7	..	..	..	..	1	4	1	1	..	..	..	..	..	..	..	..	..	..
	26. xi	6	..	..	..	..	2	1	2	1	..	..	..	..	..	..	..	..	..	..
	11. xii	2	..	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..
VI ♀	5. ii	9	..	..	..	..	1	2	1	1	2	2	..	..	..	..	..	..	..	..
	14. ii	2	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..
	27. ii	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	17. iii	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..
	15. iv	12	..	..	..	..	..	..	..	..	2	4	5	1	..	..	..	..	..	1·08
	28. iv	30	..	..	..	..	..	..	..	1	2	4	4	7	11	1	..	..	..	1·17
	14. v	17	..	..	..	..	..	..	..	..	4	3	2	3	1	2	1	1	..	1·11
	2. vi	75	..	..	..	..	2	3	5	4	5	7	11	8	14	8	4	3	1	1·14
	18. vi	14	..	..	..	..	..	1	1	4	5	2	..	..	1	..	..	..	..	0·983
	3. vii	48	..	..	5	6	10	7	8	7	3	2	..	..	..	..	..	..	..	0·851
	17. vii	68	..	..	10	8	8	16	11	9	4	2	..	..	..	..	..	..	..	0·839
	31. vii	9	..	..	..	1	1	1	2	2	2	..	..	..	..	..	..	..	..	..
	14. viii	7	..	..	..	..	..	4	1	1	1	..	..	..	..	..	..	..	..	..
	28. viii	47	..	..	..	5	13	12	12	4	..	1	..	..	..	..	..	..	..	0·840
	12. ix	18	..	..	1	5	6	3	3	..	..	..	..	..	..	..	..	..	..	0·797
	25. ix	120	..	..	5	14	36	48	15	2	..	..	..	..	..	..	..	..	..	0·819
	9. x	3	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..
	23. x	4	..	..	..	..	1	1	..	..	..	2	..	..	..	..	..	..	..	..
	17. xi	11	..	..	..	..	..	4	3	2	..	1	1	..	..	..	..	..	..	0·894
	26. xi	16	..	..	..	..	1	2	3	5	3	2	..	..	..	..	..	..	..	0·956
	11. xii	5	..	..	..	..	..	1	4	..	..	..	..	..	..	..	..	..	..	..
V ♂	5. ii	3	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..
	17. iii	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
	15. iv	2	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..
	28. iv	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
	14. v	3	..	..	..	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..
	2. vi	31	2	1	4	14	9	1	..	..	..	..	..	..	..	..	..	..	..	..
	18. vi	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..	0·735

Stage	Date	No.	0·177–0·230	0·230–0·283	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·449	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·816	0·816–0·920	0·920–0·973	Median size
V ♂	3. vii	20	..	..	..	..	..	..	..	1	1	6	10	2	..	..	..	0·729
	17. vii	8	..	..	..	..	..	..	..	..	..	5	2	1	..	..	..	..
	31. vii	3	..	..	..	..	..	..	..	..	1	1	1	..	..	..	..	..
	14. viii	17	..	..	..	..	..	..	..	..	6	6	5	..	..	..	..	0·680
	28. viii	80	..	..	..	..	..	..	..	..	12	52	16	..	..	..	..	0·686
	12. ix	9	..	..	..	..	..	..	..	1	6	1	1	..	..	..	..	..
	25. ix	30	..	..	..	..	..	..	..	1	6	17	5	1	..	..	..	0·673
	9. x	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
V ♀	5. ii	5	..	..	..	..	..	..	..	..	..	..	3	1	..	1	..	..
	3. iv	6	..	..	..	..	..	..	..	..	..	..	..	1	3	2	..	..
	15. iv	3	..	..	..	..	..	..	..	..	..	..	..	..	2	1	..	..
	28. iv	7	..	..	..	..	..	..	..	..	..	..	1	..	1	2	3	..
	14. v	8	..	..	..	..	..	..	..	..	..	1	1	3	2	..	1	..
	2. vi	21	..	..	..	..	..	..	..	1	..	2	5	12	1	..	..	0·770
	18. vi	3	..	..	..	..	..	..	..	..	..	..	1	2	..	..	..	..
	3. vii	35	..	..	..	..	..	..	..	..	2	3	17	13	..	..	..	0·750
	17. vii	14	..	..	..	..	..	..	..	..	..	3	8	2	1	..	..	0·725
	31. vii	1	..	..	..	....	..	..	..	..	..	..	1	..	..	..	..	..
	14. viii	40	..	..	..	..	..	..	..	..	1	23	14	2	..	..	..	0·699
	28. viii	64	..	..	..	..	..	..	..	..	9	27	28	..	..	..	..	0·700
	12. ix	12	..	..	..	..	..	..	..	..	8	2	2	..	..	..	..	0·650
	25. ix	16	..	..	..	..	..	..	..	..	4	16	6	..	..	..	..	0·688
	9. x	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
	23. x	1	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..
	26. x	1	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	..
IV ♂	5. ii	1	..	..	..	..	..	..	..	..	..	..	..	1	..	..	..	..
	17. iii	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
	3. iv	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
	15. iv	1	..	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..
	14. v	2	..	..	..	..	..	..	..	..	1	..	..	1	..	..	..	..
	2. vi	9	..	..	..	..	..	..	1	7	1	..	..	..	..	..	..	..
	3. vii	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
	31. vii	2	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
	14. viii	19	..	..	..	..	..	1	10	8	..	..	..	..	..	..	..	0·545
	28. viii	19	..	..	..	..	..	..	5	14	..	..	..	..	..	..	..	0·557
	12. ix	3	..	..	..	..	..	..	..	3	..	..	..	..	..	..	..	..
	25. ix	11	..	..	..	..	..	..	3	7	1	..	..	..	..	..	..	0·568
IV ♀	14. ii	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..
	17. iii	2	..	..	..	..	..	..	..	..	1	1	..	..	..	..	..	..
	3. iv	7	..	..	..	..	..	..	..	..	1	4	2	..	..	..	..	..
	15. iv	2	..	..	..	..	..	..	..	..	2	..	..	..	..	..	..	..
	28. iv	4	..	..	..	..	..	..	..	..	..	2	2	..	..	..	..	..
	14. v	9	..	..	..	..	..	..	..	3	3	3	..	..	..	..	..	..
	2. vi	34	..	..	..	..	..	2	5	14	10	3	..	..	..	..	..	0·590
	18. vi	15	..	..	..	..	..	..	..	3	8	4	..	..	..	..	..	0·622
	3. vi	36	..	..	..	..	..	..	..	17	17	2	..	..	..	..	..	0·604
	17. vii	1	..	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..
	14. viii	79	..	..	..	..	..	..	27	50	2	..	..	..	..	..	..	0·562
	28. viii	198	..	..	..	..	..	..	63	122	13	..	..	..	..	..	..	0·560
	12. ix	24	..	..	..	..	..	..	16	6	2	..	..	..	..	..	..	0·542
	25. ix	27	..	..	..	..	..	..	7	15	5	..	..	..	..	..	..	0·525
	9. x	1	..	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..

TABLE XIII (*continued*)

Stage	Date	No.	0·177–0·230	0·230–0·283	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	0·813–0·867	0·867–0·920	0·920–0·973	Median size
III	5. ii	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	27. ii	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	3. iv	..	..	..	..	..	..	..	1	2	..	..	..	..	..	..	..	..
	28. iv	10	..	..	..	..	..	..	5	4	1	..	..	..	..	..	..	0·557
	14. v	6	..	..	..	..	..	1	3	2	..	..	..	..	..	..	..	..
	2. vi	40	..	..	..	..	4	33	3	..	..	..	..	..	..	..	..	0·466
	18. vi	15	..	..	..	..	..	7	8	..	..	..	..	..	..	..	..	0·497
	3. vii	21	..	..	..	..	1	13	6	1	..	..	..	..	..	..	..	0·485
	17. vii	1	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..	..
	31. vii	2	..	..	..	..	..	1	1	..	..	..	..	..	..	..	..	..
	14. viii	97	..	..	..	..	21	74	2	..	..	..	..	..	..	..	..	0·455
	28. viii	78	..	..	..	..	22	55	1	..	..	..	..	..	..	..	..	0·452
	12. ix	17	..	..	..	..	4	12	1	..	..	..	..	..	..	..	..	0·459
	25. ix	8	..	..	..	..	..	4	4	..	..	..	..	..	..	..	..	..
	9. x	2	..	..	..	..	..	..	2	..	..	..	..	..	..	..	..	..
	23. x	1	..	..	..	..	..	..	1	..	..	..	..	..	..	..	..	..
II	27. ii	2	..	..	..	2	..	..	..	..	..	..	..	..	..	..	..	..
	17. iii	10	..	..	..	..	10	..	..	..	..	..	..	..	..	..	..	0·412
	3. iv	6	..	..	..	..	5	1	..	..	..	..	..	..	..	..	..	..
	28. iv	9	..	..	..	..	3	6	..	..	..	..	..	..	..	..	..	..
	14. v	21	..	..	..	..	20	1	..	..	..	..	..	..	..	..	..	0·417
	2. vi	25	..	..	..	18	7	..	..	..	..	..	..	..	..	..	..	0·382
	18. vi	25	..	..	..	2	23	..	..	..	..	..	..	..	..	..	..	0·418
	3. vii	15	..	..	..	6	9	..	..	..	..	..	..	..	..	..	..	0·395
	31. vii	8	..	..	..	3	5	..	..	..	..	..	..	..	..	..	..	..
	14. viii	38	..	..	1	37	..	..	..	..	..	..	..	..	..	..	..	0·366
	28. viii	47	..	..	..	33	14	..	..	..	..	..	..	..	..	..	..	0·374
	12. ix	7	..	..	..	5	2	..	..	..	..	..	..	..	..	..	..	..
	25. ix	11	..	..	..	5	6	..	..	..	..	..	..	..	..	..	..	0·396
	9. x	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
I	5. ii	2	..	..	1	1	..	..	..	..	..	..	..	..	..	..	..	..
	27. ii	3	..	1	2	..	..	..	..	..	..	..	..	..	..	..	..	0·325
	17. iii	42	..	..	36	6	..	..	..	..	..	..	..	..	..	..	..	..
	3. iv	6	..	..	4	2	..	..	..	..	..	..	..	..	..	..	..	0·344
	28. iv	1	..	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..
	14. v	37	..	..	9	28	..	..	..	..	..	..	..	..	..	..	..	0·302
	2. vi	21	..	..	21	..	..	..	..	..	..	..	..	..	..	..	..	0·338
	18. vi	23	..	..	10	13	..	..	..	..	..	..	..	..	..	..	..	..
	3. vii	5	..	..	4	1	..	..	..	..	..	..	..	..	..	..	..	..
	17. vii	1	..	..	1	..	..	..	..	..	..	..	..	..	..	..	..	..
	31. vii	14	..	..	14	..	..	..	..	..	..	..	..	..	..	..	..	0·309
	14. viii	52	..	10	42	..	..	..	..	..	..	..	..	..	..	..	..	0·294
	28. viii	23	..	3	20	..	..	..	..	..	..	..	..	..	..	..	..	0·294
	12. ix	8	..	8	..	..	..	..	..	..	..	..	..	..	..	..	..	..
	25. ix	14	..	..	13	1	..	..	..	..	..	..	..	..	..	..	..	0·295

TABLE XIV. *ACARTIA CLAUSI*. SIZE IN MM.

Stage	Date	No.	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·814	0·814–0·867	0·867–0·920	0·920–0·973	0·973–1·03	1·03–1·08	1·08–1·13	1·13–1·18	Median size
VI ♂	14. ii	2	..	..	..	1	1	..	..	..	..	..	..	..
	3. iv	2	..	..	..	..	2	..	..	..	..	..	..	..
	15. iv	37	..	..	..	..	..	..	23	14	..	..	..	0·966
	28. iv	16	..	..	..	..	..	..	13	3	..	..	..	0·965
	14. v	36	..	..	..	..	..	6	28	2	..	..	..	0·943
	2. vi	88	..	..	..	..	7	74	7	..	..	..	..	0·894
	18. vi	35	..	..	..	..	18	16	1	..	..	..	..	0·866
	3. vii	96	..	..	..	1	56	37	2	..	..	..	..	0·860
	17. vii	122	..	..	1	6	81	31	3	..	..	..	..	0·852
	31. vii	87	..	..	..	1	67	19	..	..	..	..	..	0·847
	14. viii	65	..	..	4	44	16	1	..	..	..	..	..	0·798
	28. viii	46	..	..	1	30	15	..	..	..	..	..	..	0·807
	12. ix	30	..	..	1	17	12	..	..	..	..	..	..	0·810
	25. ix	29	..	..	..	25	4	..	..	..	..	..	..	0·802
	9. x	5	..	..	..	2	3	..	..	..	..	..	..	..
	17. xi	3	..	..	..	..	3	..	..	..	..	..	..	..
	26. xi	17	..	..	..	2	15	..	..	..	..	..	..	0·836
	11. xii	2	..	..	..	..	2	..	..	..	..	..	..	..
	7. i	6	..	..	..	1	3	2	..	..	..	..	..	..
	28. i	1	..	..	..	..	1	..	..	..	..	..	..	..
VI ♀	6. i	9	..	..	..	1	2	5	1	..	..	..	..	..
	5. ii	3	..	..	..	2	..	1	..	..	..	..	..	..
	14. ii	12	..	..	..	2	7	2	1	..	..	..	..	0·838
	27. ii	3	..	..	..	..	2	1	..	..	..	..	..	..
	17. iii	41	..	..	..	7	21	18	..	..	..	..	..	0·851
	3. iv	6	..	..	..	2	1	1	..	..	..	1	1	..
	15. iv	17	..	..	..	..	..	..	..	..	4	11	2	1·10
	28. iv	63	..	..	..	..	..	..	..	..	2	40	21	1·12
	14. v	80	..	..	..	..	..	3	3	3	29	32	10	1·08
	2. vi	92	..	..	..	..	..	2	22	45	19	3	1	0·992
	18. vi	31	..	..	..	..	..	5	16	9	1	..	..	0·960
	3. vii	76	..	..	..	..	..	14	49	13	..	..	..	0·944
	17. vii	138	..	..	..	..	1	34	84	17	1	1	..	0·936
	31. vii	54	..	..	..	..	..	13	35	6	..	..	..	0·936
	14. viii	69	..	..	..	17	32	16	4	..	..	..	..	0·836
	28. viii	62	..	..	..	13	29	17	3	..	..	..	..	0·845
	12. ix	59	..	..	..	9	35	15	..	..	..	..	..	0·845
	25. ix	105	..	..	1	30	61	13	..	..	..	..	..	0·834
	9. x	46	..	..	2	11	23	10	..	..	..	..	..	0·834
	23. x	8	..	..	1	2	3	2	..	..	..	..	..	..
	17. xi	9	..	..	1	2	4	2	..	..	..	..	..	..
	26. xi	21	..	1	4	4	9	3	..	..	..	..	..	0·824
	11. xii	6	..	..	..	3	3	..	..	..	..	..	..	..
	7. i	12	..	..	..	1	3	6	2	..	..	..	..	0·876
	28. i	15	..	..	1	1	6	4	3	..	..	..	..	0·865
V ♂	17. ii	1	..	..	1	..	..	..	..	..	..	..	..	..
	3. iv	4	..	..	4	..	..	..	..	..	..	..	..	..
	15. iv	15	..	..	..	..	12	3	..	..	..	..	..	0·851
	28. iv	2	..	..	..	..	1	1	..	..	..	..	..	..
	14. v	50	..	..	1	23	26	..	..	..	..	..	..	0·815
	2. vi	51	..	..	11	40	..	..	..	..	..	..	..	0·773
	18. vi	24	..	..	3	19	2	..	..	..	..	..	..	0·787
	3. vii	20	..	1	14	5	..	..	..	..	..	..	..	0·750
	17. vii	1	..	..	1	..	..	..	..	..	..	..	..	..
	31. vii	12	..	..	8	4	..	..	..	..	..	..	..	0·755
	14. viii	25	2	17	6	..	..	..	..	..	..	..	..	0·700
	28. viii	12	..	3	9	..	..	..	..	..	..	..	..	0·714
	12. ix	9	..	6	3	..	..	..	..	..	..	..	..	..
	25. ix	10	1	4	5	..	..	..	..	..	..	..	..	..
	9. x	1	..	..	1	..	..	..	..	..	..	..	..	0·707
V ♀	17. xi	3	..	..	3	..	..	..	..	..	..	..	..	..
	5. ii	2	..	..	..	..	..	2	..	..	..	..	..	..
	14. ii	2	..	..	..	..	..	1	1	..	..	..	..	..
	17. iii	1	..	..	..	..	..	1	..	..	..	..	..	..
	3. iv	1	..	..	..	..	..	..	1	..	..	..	..	..
	15. iv	8	..	..	..	..	..	3	4	1	..	..	..	..
	28. iv	6	..	..	..	..	..	4	2	..	..	..	..	..
	14. v	35	..	..	..	2	18	15	..	..	..	..	..	0·859
	2. vi	44	..	..	3	31	10	..	..	..	..	..	..	0·792
	18. vi	25	..	..	..	5	13	7	..	..	..	..	..	0·845
	3. vii	15	..	..	5	8	2	..	..	..	..	..	..	0·776
	17. vii	7	..	..	2	5	..	..	..	..	..	..	..	..
	31. vii	16	..	..	3	13	..	..	..	..	..	..	..	0·784
	14. viii	42	..	27	15	..	..	..	..	..	..	..	..	0·700
	28. viii	20	..	6	14	..	..	..	..	..	..	..	..	0·715
	12. ix	29	..	20	9	..	..	..	..	..	..	..	..	0·693
	25. ix	26	..	11	14	1	..	..	..	..	..	..	..	0·714
	9. x	10	1	9	..	..	..	..	..	..	..	..	..	0·672

TABLE XIV (*continued*)

Stage	Date	No.	0·283–0·336	0·336–0·389	0·389–0·442	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	0·761–0·813	Median size
IV ♂	17. iii	1	..	..	..	..	..	..	1	..	..	..	..
	3. iv	4	..	..	..	..	..	..	..	..	4	..	..
	15. iv	15	..	..	..	..	..	..	..	2	13	..	0·729
	28. iv	3	..	..	..	..	..	..	..	..	3	..	..
	14. v	53	..	..	..	..	..	..	9	33	11	..	0·689
	2. vi	26	..	..	..	..	..	..	22	4	..	..	0·640
	18. vi	16	..	..	..	..	..	..	14	2	..	..	0·664
	3. vii	25	..	..	..	..	..	1	21	3	..	..	0·638
	17. vii	2	..	..	..	..	..	1	1	..	..	..	..
	31. vii	17	..	..	..	..	..	..	15	2	..	..	0·645
	14. viii	26	..	..	..	..	..	13	13	..	..	..	0·602
	28. viii	10	..	..	..	..	..	4	6	..	..	..	0·605
	12. ix	22	..	..	..	..	..	13	9	..	..	..	0·596
	25. ix	4	..	..	..	..	..	2	2	..	..	..	..
	9. x	4	..	..	..	..	..	1	3	..	..	..	..
	17. xi	2	..	..	..	..	..	..	2	..	..	..	..
IV ♀	5. ii	2	..	..	..	..	..	1	1	..	..	..	..
	17. iii	1	..	..	..	..	..	..	1	..	..	..	..
	3. iv	1	..	..	..	..	..	..	..	..	..	1	..
	15. iv	14	..	..	..	..	..	..	..	..	8	6	0·758
	28. iv	7	..	..	..	..	..	..	..	..	4	3	..
	14. v	65	..	..	..	..	..	1	2	29	33	..	0·710
	2. vi	34	..	..	..	..	..	1	19	14	..	..	0·650
	18. vi	15	..	..	..	..	..	..	..	13	2	..	0·685
	3. vii	17	..	..	..	..	..	1	10	6	..	..	0·648
	17. vii	2	..	..	..	..	..	..	1	1	..	..	0·650
	31. vii	22	..	..	..	..	..	..	13	9	..	..	0·595
	14. viii	23	..	..	..	..	..	16	6	1	..	..	0·595
	28. viii	45	..	..	..	..	..	30	15	..	..	..	0·590
	12. ix	37	..	..	..	..	2	21	14	..	..	..	..
	25. ix	9	..	..	..	..	..	6	3	..	..	..	..
	9. x	3	..	..	..	..	..	2	1	..	..	..	..
	17. xi	6	..	..	..	..	..	2	4	..	..	..	..
III	5. ii	1	..	..	..	..	..	1	..	..	..	..	..
	17. iii	1	..	..	..	..	..	1	..	..	..	..	..
	3. iv	4	..	..	..	..	2	2	..	..	..	..	..
	15. iv	5	..	..	..	..	..	..	4	1	..	..	..
	28. iv	8	..	..	..	..	..	..	7	1	..	..	..
	14. v	31	..	..	..	..	..	17	14	..	..	..	0·600
	2. vi	56	..	..	..	1	43	12	..	..	..	..	0·536
	18. vi	34	..	..	..	..	7	26	1	..	..	..	0·569
III	3. vii	28	..	..	..	1	22	5	..	..	..	..	..
	17. vii	6	..	..	..	..	5	1	..	..	..	..	..
	31. vii	36	..	..	..	..	25	11	..	..	..	..	0·529
	14. viii	44	..	..	..	15	28	1	..	..	..	..	0·542
	28. viii	18	..	..	..	4	13	1	..	..	..	..	0·502
	12. ix	9	..	..	..	6	3	..	..	..	..	..	0·505
	25. ix	3	..	..	..	1	2	..	..	..	..	..	..
	9. x	2	..	..	..	..	2	..	..	..	..	..	..
	17. xi	3	..	..	..	..	3	..	..	..	..	..	..
	11. xii	1	..	..	..	..	1	..	..	..	..	..	..
II	17. iii	1	..	..	1	..	..	..	..	..	..	..	..
	3. iv	6	..	..	..	2	2	2	..	..	..	..	..
	28. iv	13	..	..	..	3	10	..	..	..	..	..	0·516
	14. v	38	..	..	..	16	22	..	..	..	..	..	0·498
	2. vi	48	..	..	34	14	..	..	..	..	..	..	0·434
	18. vi	36	..	..	..	35	1	..	..	..	..	..	0·455
	3. vii	20	..	..	4	16	..	..	..	..	..	..	0·453
	17. vii	7	..	..	6	1	..	..	..	..	..	..	0·443
	31. vii	49	..	..	24	25	..	..	..	..	..	..	..
	14. viii	8	..	1	7	..	..	..	..	..	..	..	..
	28. viii	3	..	..	3	..	..	..	..	..	..	..	..
	12. ix	2	..	..	2	..	..	..	..	..	..	..	..
	25. ix	1	..	..	1	..	..	..	..	..	..	..	..
	9. x	2	..	1	1	..	..	..	..	..	..	..	..
	23. x	3	..	..	3	..	..	..	..	..	..	..	..
	17. xi	8	..	..	7	1	..	..	..	..	..	..	..
	11. xii	4	..	..	3	1	..	..	..	..	..	..	..
I	17. iii	1	..	1	..	..	..	..	..	..	..	..	..
	3. iv	10	..	..	10	..	..	..	..	..	..	..	0·415
	28. iv	17	..	1	15	1	..	..	..	..	..	..	0·427
	14. v	35	..	15	20	..	..	..	..	..	..	..	0·392
	2. vi	23	2	21	..	..	..	..	..	..	..	..	0·356
	18. vi	34	..	29	5	..	..	..	..	..	..	..	0·369
	3. vii	19	1	17	1	..	..	..	..	..	..	..	0·356
	17. vii	7	1	6	..	..	..	..	..	..	..	..	..
	31. vii	82	5	77	..	..	..	..	..	..	..	..	0·331
	14. viii	6	6	..	..	..	..	..	..	..	..	..	..
	28. viii	10	7	3	..	..	..	..	..	..	..	..	0·338
	12. ix	1	1	..	..	..	..	..	..	..	..	..	..
	25. ix	5	..	5	..	..	..	..	..	..	..	..	..
	9. x	3	2	1	..	..	..	..	..	..	..	..	..
	23. x	4	3	1	..	..	..	..	..	..	..	..	..
	17. xi	7	1	5	1	..	..	..	..	..	..	..	..
	11. xii	2	..	2	..	..	..	..	..	..	..	..	..

TABLE XV. *OITHONA SIMILIS*. SIZE IN MM.

Stage	Date	No.	0·301–0·336	0·336–0·372	0·372–0·407	0·407–0·442	0·442–0·477	0·477–0·513	0·513–0·548	0·548–0·584	Median size
VI ♂	6. i	12	..	..	4	6	2	..	..	..	0·428
	5. ii	9	..	..	..	3	5	1	..	..	..
	27. ii	7	..	..	..	1	6	..	..	..	..
	17. iii	6	..	..	..	2	1	3	..	..	..
	3. iv	14	..	..	..	..	1	12	1	..	0·493
	28. iv	9	..	..	..	..	..	9	..	..	..
	14. v	16	..	..	..	..	9	4	2	1	0·475
	2. vi	12	..	..	..	1	6	5	..	..	0·474
	18. vi	23	..	..	..	3	17	3	..	..	0·461
	3. vii	16	..	..	..	2	14	..	..	..	0·453
	17. vii	33	..	..	2	21	10	..	..	..	0·435
	31. vii	41	..	..	3	20	18	..	..	..	0·440
	14. viii	31	..	..	2	26	3	..	..	..	0·427
	28. viii	19	..	..	1	17	1	..	..	..	0·430
	12. ix	7	..	..	..	6	1	..	..	..	..
	25. ix	11	..	..	1	9	1	..	..	..	0·433
	9. x	6	..	..	1	5	..	..	..	..	..
	23. x	2	..	..	2	..	..	..	..	..	..
	17. xi	9	..	..	3	6	..	..	..	..	..
	11. xii	3	..	..	1	2	..	..	..	..	..
VI ♀	6. i	68	..	..	6	33	29	..	..	..	0·438
	5. ii	31	..	..	4	13	12	2	..	..	0·438
	27. ii	41	..	..	..	6	22	13	..	..	0·467
	17. iii	102	..	..	..	11	47	36	8	..	0·473
	3. iv	64	..	..	..	2	13	15	17	17	0·517
	28. iv	47	..	..	..	..	3	13	25	6	0·533
	14. v	43	..	..	..	..	1	15	25	3	0·523
	2. vi	54	..	..	..	..	17	24	10	3	0·491
	18. vi	66	..	..	..	1	40	25	..	..	0·474
	3. vii	63	..	..	..	1	32	29	1	..	0·477
	17. vii	186	..	..	..	49	121	15	1	..	0·453
	31. vii	173	..	..	..	13	129	25	5	1	0·465
	14. viii	179	..	..	4	100	72	3	..	..	0·439
	28. viii	109	..	..	2	37	51	17	2	..	0·448
	12. ix	148	..	..	4	88	53	3	..	..	0·438
	25. ix	116	..	..	1	69	45	1	..	..	0·438
	9. x	61	..	..	4	45	12	..	..	..	0·430
	23. x	31	..	..	2	23	5	..	..	..	0·430
	17. xi	38	..	..	2	23	13	..	..	..	0·435
	11. xii	28	..	..	1	12	15	..	..	..	0·444
V ♂	6. i	29	..	..	9	12	8	..	..	..	0·417
	5. ii	22	..	1	9	5	7	..	..	..	0·428
	27. ii	20	..	..	..	1	12	7	..	..	0·460
	17. iii	38	..	..	2	11	22	3	..	..	0·457
	3. iv	64	..	..	..	..	7	47	10	..	0·498
	28. iv	20	..	..	..	..	3	14	3	..	0·494
	14. v	46	..	..	..	13	18	15	..	..	0·460
	2. vi	15	..	..	..	33	39	3	..	..	0·447
	18. vi	69	..	..	2	37	29	1	..	..	0·440
	3. vii	55	..	..	1	24	30	..	..	..	0·445
	17. vii	104	..	..	40	57	7	..	..	..	0·414
	31. vii	102	..	..	6	54	42	..	..	..	0·437
	14. viii	104	..	1	46	52	2	..	..	..	0·409
	28. viii	82	..	1	30	42	8	..	..	..	0·419
	12. ix	108	..	..	33	71	4	..	..	..	0·419
	25. ix	70	..	..	16	44	10	..	..	..	0·426
	9. x	58	..	1	29	27	1	..	..	..	0·406
	23. x	47	..	4	25	18	..	..	..	..	0·402
	17. xi	18	..	..	6	12	..	..	..	..	0·418
	11. xii	28	..	..	3	17	8	..	..	..	0·434
IV	6. i	8	..	4	4	..	..	..	..	..	..
	5. ii	28	7	9	10	2	..	..	..	..	0·354
	27. ii	10	..	2	6	1	1	..	..	..	0·389
	17. iii	25	..	7	5	13	..	..	..	..	0·401
	3. iv	56	..	..	5	32	18	1	..	..	0·417
	28. iv	16	..	..	1	9	6	..	..	..	0·438
	14. v	36	..	5	12	19	..	..	..	..	0·423
	2. vi	44	..	3	29	12	..	..	..	..	0·397
	18. vi	60	..	9	46	5	..	..	..	..	0·388
	3. vii	26	..	5	20	1	..	..	..	..	0·388
	17. vii	103	..	80	23	..	..	..	..	..	0·360
	31. vii	103	..	20	82	1	..	..	..	..	0·384
	14. viii	79	3	63	13	..	..	..	..	..	0·358

TABLE XV (*continued*)

Stage	Date	No.	0·301–0·336	0·336–0·372	0·372–0·407	0·407–0·442	0·442–0·477	0·477–0·513	0·513–0·548	0·458–0·584	Median size
IV	28. viii	35	..	20	15	..	..	..	..	..	0·369
	12. ix	108	2	70	36	..	..	..	..	..	0·365
	25. ix	21	..	5	16	..	..	..	..	..	0·380
	9. x	36	2	29	5	..	..	..	..	..	0·353
	23. x	29	1	22	6	..	..	..	..	..	0·358
	17. xi	14	..	8	6	..	..	..	..	..	0·379
	11. xii	28	..	11	14	3	..	..	..	..	0·378

	Date	No.	0·159–0·195	0·195–0·230	0·230–0·265	0·265–0·301	0·301–0·336	0·336–0·372	0·372–0·407	0·407–0·442	Median size
III	6. i	13	..	..	..	..	7	6	..	..	0·334
	5. ii	26	..	..	..	3	19	4	..	..	0·321
	27. ii	19	..	..	..	..	5	13	1	..	0·343
	17. iii	23	..	..	..	..	1	11	11	..	0·371
	3. iv	43	..	..	..	..	..	7	36	..	0·382
	28. iv	24	..	..	..	..	..	1	23	..	0·384
	14. v	25	..	..	..	..	12	10	3	..	0·339
	2. vi	42	..	..	..	1	11	30	..	..	0·346
	18. vi	36	..	..	..	..	11	25	..	..	0·344
	3. vii	42	..	..	..	..	8	34	..	..	0·346
	17. vii	87	..	..	..	6	78	3	..	..	0·314
	31. vii	37	..	..	..	..	15	22	..	..	0·339
	14. viii	61	..	..	..	5	56	..	..	..	0·313
	28. viii	44	..	..	..	..	37	7	..	..	0·328
	12. ix	96	..	..	..	7	80	9	..	..	0·321
	25. ix	33	..	..	..	..	16	17	..	..	0·337
	9. x	29	..	..	..	1	28	..	..	..	0·318
	23. x	27	..	..	..	..	22	5	..	..	0·326
	17. xi	13	..	..	..	..	10	3	..	..	0·328
	11. xii	24	..	..	..	..	5	19	..	..	0·346
II	6. i	7	..	..	..	7	..	..	..	..	..
	5. ii	15	..	..	7	7	1	..	..	..	0·274
	27. ii	12	..	..	1	11	..	..	..	..	0·277
	17. iii	38	..	..	..	18	20	..	..	..	0·302
	3. iv	45	..	..	..	13	31	1	..	..	0·307
	28. iv	20	..	..	..	7	13	..	..	..	0·305
	14. v	35	..	..	9	15	11	..	..	..	0·291
	2. vi	66	..	..	..	65	1	..	..	..	0·282
	18. vi	67	..	..	14	53	..	..	..	..	0·274
	3. vii	36	..	..	1	34	1	..	..	..	0·284
	17. vii	30	..	1	26	3	..	..	..	..	0·255
	31. vii	51	..	..	10	41	..	..	..	..	0·274
	14. viii	42	..	..	35	7	..	..	..	..	0·257
	28. viii	59	..	..	32	27	..	..	..	..	0·264
	12. ix	121	..	..	78	43	..	..	..	..	0·261
	25. ix	37	..	..	6	31	..	..	..	..	0·275
	9. x	30	..	..	27	3	..	..	..	..	0·254
	23. x	27	..	..	2	25	..	..	..	..	0·276
	17. xi	9	..	..	3	6	..	..	..	..	..
	11. xii	19	..	..	4	15	..	..	..	..	0·280
I	6. i	4	..	1	3	..	..	..	..	..	..
	5. ii	9	..	4	4	1	..	..	..	..	..
	27. ii	24	..	16	8	..	..	..	..	..	0·225
	17. iii	39	..	18	21	..	..	..	..	..	0·231
	3. iv	35	..	10	25	..	..	..	..	..	0·236
	28. iv	15	..	5	10	..	..	..	..	..	0·235
	14. v	27	1	11	15	..	..	..	..	..	0·232
	2. vi	78	..	55	23	..	..	..	..	..	0·225
	18. vi	55	..	49	6	..	..	..	..	..	0·219
	3. vii	43	..	35	8	..	..	..	..	..	0·222
	17. vii	39	7	31	1	..	..	..	..	..	0·204
	31. vii	70	..	69	1	..	..	..	..	..	0·215
	14. viii	71	14	57	..	..	..	..	..	..	0·202
	28. viii	59	2	57	..	..	..	..	..	..	0·204
	12. ix	90	..	90	..	..	..	..	..	..	0·208
	25. ix	57	..	46	11	..	..	..	..	..	0·222
	9. x	33	1	32	..	..	..	..	..	..	0·204
	23. x	28	..	28	..	..	..	..	..	..	0·219
	17. xi	19	..	19	..	..	..	..	..	..	0·213
	11. xii	..	..	8	..	..	..	..	..	..	..

TABLE XVI. *OITHONA NANA*. SIZE IN MM.

Stage	Date	No.	0·124–0·159	0·159–0·195	0·195–0·230	0·230–0·265	0·265–0·301	0·301–0·336	0·336–0·372	0·372–0·407	Median size
VI ♂	12. ix	8	..	..	..	..	1	7	..	..	..
	25. ix	6	..	..	..	..	..	6	..	..	..
	9. x	7	..	..	..	..	..	7	..	..	..
	23. x	..	..	..	..	..	..	..	..	..	..
	17. xi	2	..	..	..	..	..	2	..	..	..
	20. xi	6	..	..	..	..	..	6	..	..	..
	11. xii	6	..	..	..	..	3	3	..	..	..
VI ♀	12. ix	17	..	..	..	..	..	15	2	..	0·325
	25. ix	22	..	..	..	..	1	15	6	..	0·330
	9. x	23	..	..	..	..	..	21	2	..	0·328
	23. x	4	..	..	..	..	..	2	2	..	..
	17. xi	25	..	..	..	..	..	13	12	..	0·335
	20. xi	41	..	..	..	..	8	31	2	..	0·310
	11. xii	14	..	..	..	..	..	11	3	..	0·330
V	12. ix	17	..	..	..	..	9	7	1	..	0·300
	25. ix	3	..	..	..	..	..	3	..	..	..
	9. x	42	..	..	..	..	28	14	..	..	0·296
	23. x	13	..	..	..	..	9	4	..	..	0·294
	17. xi	8	..	..	..	..	4	4	..	..	..
	20. xi	27	..	..	..	..	26	1	..	..	0·282
	11. xii	10	..	..	..	..	..	10	..	..	0·310
IV	12. ix	2	..	..	..	2	..	..	..	..	..
	25. ix	6	..	..	..	..	6	..	..	..	..
	9. x	68	..	..	..	52	16	..	..	..	0·259
	23. x	24	..	..	..	12	12	..	..	..	0·265
	17. xi	25	..	..	..	15	10	..	..	..	0·262
	20. xi	28	..	..	..	24	4	..	..	..	0·254
	11. xii	8	..	..	..	..	8	..	..	..	..
III	12. ix	2	..	..	1	1	..	..	..	..	..
	25. ix	..	..	..	..	6	..	..	..	..	..
	9. x	87	..	..	28	59	..	..	..	..	0·234
	23. x	36	..	..	7	29	..	..	..	..	0·238
	17. xi	7	..	..	3	4	..	..	..	..	..
	20. xi	6	..	..	3	3	..	..	..	..	..
	11. xii	14	..	..	..	14	..	..	..	..	0·244
II	12. ix	5	..	5	..	..	..	..	..	..	..
	25. ix	7	..	1	6	..	..	..	..	..	..
	9. x	58	..	37	21	..	..	..	..	..	0·191
	23. x	58	..	27	31	..	..	..	..	..	0·196
	17. xi	10	..	8	2	..	..	..	..	..	0·188
	20. xi	5	..	5	..	..	..	..	..	..	..
	11. xii	30	..	17	13	..	..	..	..	..	0·194
I	12. ix	13	12	1	..	..	..	..	..	..	0·151
	25. ix	12	11	1	..	..	..	..	..	..	0·151
	9. x	183	183	..	..	..	..	..	..	..	0·151
	23. x	89	88	1	..	..	..	..	..	..	0·151
	17. xi	24	24	..	..	..	..	..	..	..	0·151
	20. xi	1	1	..	..	..	..	..	..	..	..
	11. xii	74	74	..	..	..	..	..	..	..	0·151

TABLE XVII. *CORYCAEUS ANGLICUS*. SIZE IN MM.

Stage	Date	No.	0·442–0·495	0·495–0·548	0·548–0·602	0·602–0·655	0·655–0·708	0·708–0·761	Median size
VI ♂	14. viii	3	..	2	1	..	..	..	..
	28. viii	20	..	14	6	..	..	..	0·535
	12. ix	59	..	26	33	..	..	..	0·552
	25. ix	15	..	7	8	..	..	..	0·550
	9. x	72	..	44	28	..	..	..	0·544
	23. x	126	1	84	41	..	..	..	0·539
	17. xi	60	..	33	27	..	..	..	0·546
	20. xi	100	..	78	22	..	..	..	0·537
	11. xii	26	1	21	4	..	..	..	0·536
VI ♀	14. viii	3	..	..	..	..	3	..	..
	28. viii	6	..	..	..	..	6	..	..
	12. ix	25	..	..	..	2	20	3	0·681
	25. ix	13	..	..	..	3	10	..	0·666
	9. x	63	..	..	..	7	50	6	0·686
	23. x	96	..	..	..	47	49	..	0·655
	17. xi	45	..	..	..	21	24	..	0·656
	20. xi	29	..	..	..	18	11	..	0·649
	11. xii	15	..	..	..	11	4	..	0·633

Table XVIII. Cruises of January 1947.

(Numbers of copepods per m.³)

	Cruise A (6–8 January)			Cruise C (17–18 January)	
Station No. ..	1	6	7	2	4
Position ..	50° 02′ N., 4° 22′ W. (= E 1)	48° 34′ N., 5° 13′ W.	48° 49′ N., 5° 23′ W.	49° 46′ N., 6° 00′ W.	49° 46′ N., 6° 34′ W.
Calanus finmarchicus	..	27	15	11	20
Pseudocalanus elongatus	86	52	29	87	42
Paracalanus parvus	121	34	53	66	71
Centropages typicus	2	..	..	..	..
C. hamatus	..	..	..	..	..
Temora longicornis	4	..	..	..	..
Metrida lucens	..	2	11	14	71
Acartia clausi	5	..	..	..	..
Oithona similis	141	263	229	95	144
Median size of *Oithona* VI, ♀ (mm.)	3·438	0·434	..	0·479	0·475
Median size of *Paracalanus* VI, ♀ (mm.)	0·772	0·810	..	0·890	0·875

Table XIX. Cruise of 26–27 June 1947

(Numbers of copepods per m.³)

	L 4	1	2	3	4	5	6
Position ..	50° 15′ N., 4° 13′ W.	50° 03′ N., 4° 30′ W.	49° 56′ N., 4° 45′ W.	49° 30′ N., 5° 03′ W.	49° 14′ N., 5° 20′ W.	49° 14′ N., 5° 53′ W.	49° 14′ N., 6° 12′ W.
Calanus finmarchicus	30	30	53	960	180	70	130
Pseudocalanus elongatus	3040	2060	2454	3780	1225	1250	965
Paracalanus parvus	360	130	134	1380	90	175	360
Centropages typicus	60	70	59	100	30	45	80
C. hamatus	10	..	7	600	110	40	90
Temora longicornis	226	740	440	800	40	20	15
Acartia clausi	1840	850	693	220	25	30	..
Oithona similis	9540	3700	3834	4020	900	1140	2150
O. nana	10	10	13	..	5	..	..
Median size of *Pseudocalanus* VI, ♀ (mm.)	0·847	0·815	0·830	0·826	0·895	0·844	0·850

Table XX. Cruise of 5–7 August 1947

(Numbers of copepods per m.³)

Station no. ..	1	2	3	4	5
Position ..	L 4	Eddystone	49° 30′ N., 4° 17′ W.	49° 3′ N., 4° 58′ W.	48° 40′ N., 5° 32′ W.
Pseudocalanus elongatus	3345	3780	565	3500	1865
Paracalanus parvus	1965	1320	270	1100	830
Centropages typicus	160	220	175	400	605
C. hamatus	95	20	25	..	..
Temora longicornis	590	40	10	..	10
Acartia clausi	2760	1280	80	140	65
Oithona similis	9040	9040	2915	4440	3840
Median size of *Pseudocalanus* VI, ♀ (mm.)	0·805	0·810	0·783	0·853	0·804

Station no. ..	7	8	11	12	13
Position ..	49° 5′ N., 3° 33′ W.	49° 35′ N., 2° 54′ W.	50° 4′ N., 2° 11′ W.	50° 4′ N., 2° 58′ W.	50° 4′ N., 3° 46′ W.
Median size of *Pseudocalanus* VI, ♀ (mm.)	0·802	0·805	0·805	0·810	0·812

A BIOLOGICAL STUDY OF *FUCUS VESICULOSUS* L. AND *F. SERRATUS* L.

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(Text-figs. 1–33)

CONTENTS

INTRODUCTION

Though the two common species of *Fucus*—*F. vesiculosus* and *F. serratus*—are perhaps the best known of British seaweeds, an investigation into growth-rate and longevity for utilitarian purposes has revealed information of a scientific nature which is worthy of record.

Marine algae have provided material for research with varied objectives. The record of it reflects the changing viewpoints common to other branches of botany. The foundation of knowledge of British marine algae was laid by the naturalists of a hundred and fifty years ago, but its value has been overlaid,

and in some respects obscured, by deflexion into phylogenetics, amplified by detailed inquiry into life cycles, with an emphasis on the light which such study might shed on problems of evolution. Ecological study of marine algae is of comparatively recent growth. Some careful investigation of restricted areas has been made, and modern text-books now tend to assess ecological data as an essential complement to description. Nevertheless, information on behaviour of a plant, and the rhythm of successive growth-phases through which it passes in the course of its life, apart from cytological life cycles, is rarely given.

An investigation has been conducted over a period of five years, with the object of eliciting information on the behaviour of the two fucoid species over a period of time. The methods adopted were those used, with modification in detail, by other algologists (Hariot, 1909; Lemoine, 1913; Nienburg, 1930; Hatton, 1932).

One of the methods employed was to clear certain areas on the shore, varying in extent from single-metre squares to broad strips 16 m. wide, running through the entire fucoid zone from top to bottom of the shore, and penetrating into the upper fringe of the sublittoral zone. The second method entailed the marking of selected plants *in situ*. The method of marking which proved most satisfactory was the attachment to the plant of numbered chicken- or hen-rings. Very small plants were marked by small celluloid tablets with a split into which the frond could be inserted.

A very short period of experiment revealed the high mortality-rate among seaweeds. From a batch of marked plants quite often 75 % had disappeared after an interval of only a few weeks. The use of large marked plants was of limited value because of the extensive frond-breakage which occurred, even if the plants were not carried bodily away. Very large numbers of plants had to be marked in order to secure data of statistical significance.

Use was also made of prepared concrete blocks placed on the shore (see Lund, 1936). The blocks needed a preliminary soaking in sea water for some time before they could be used with success.

Preliminary inquiry also showed that growth-rate varied with locality, and, to obtain complete data, three stations were selected: south Devon (Wembury, near Plymouth); the south-west corner of the Isle of Man; and a station on the west coast of Argyll. Localities varying in aspect and exposure were chosen on each station to give opportunity of comparing growth-rates under different conditions.

One of the authors (M.K.) is responsible for the data from the Isle of Man, the illustrations, and the compilation of the report. The other (M.P.) has carried out all the observations on the Devon and Scottish stations.

Acknowledgements are due from the authors to the Development Commission, and to the Ministry of Supply, who sponsored the larger investigation from which the facts recorded have emerged.

Collection of data from the Isle of Man was facilitated by the willing assistance of a large number of students in the University of Liverpool, to whom acknowledgement is due, in particular to Miss Marion Anderton who gave valuable help with the treatment of data. Miss Emily Clay, M.Sc., acted as full-time assistant to Dr Parke.

Distribution of the Fucoid Vegetation

The first point worthy of note which emerged from a comparison of the three areas is that the bathymetric levels of the fucoid zones on the three stations did not coincide.

The restricted area on which observations were made on the Devon coast carried a fucoid vegetation which lay wholly below mid-tide level, whereas a corresponding belt on the Manx and Scottish coasts was much broader and occupied the zone between H.W.N.T. and L.W.S.T.

The findings of the authors for the restricted area at Wembury are not wholly in agreement with the records of Colman (1933) and Evans (1947) for slightly different areas on the same beach.

Colman made four transects on Church Reef at Wembury, three of them radiating from a convenient central point and the fourth set at an angle with one of the other transects. Two of Colman's transects gave a distribution of the fucoid belt quite in keeping with the authors' findings, i.e., except in pools, the fucoid vegetation is confined below or just reaches up to the line of M.S.L. On these two transects, no *Pelvetia* or *Fucus spiralis* was present in any quantity.

On the other two transects, the upper limits of the fucoid zone came well above the line of M.S.L. Colman (1933, p. 462, fig. 13) assesses the limits of distribution of the components of the fucoid belt as follows: *Pelvetia*, from half-way between M.H.W.S.T. and M.H.W.N.T. to the extreme lowest level of H.W.N.T; *Fucus spiralis*, from M.H.W.N.T. down to 1 ft. below the extreme lowest H.W.N.T; *Ascophyllum*, from just below extreme lowest H.W.N.T. to a level half-way between M.L.W.N.T. and M.L.W.S.T; *Fucus serratus*, from M.S.L. down to L.W.S.T.

Evans (1947, p. 182, fig. 2) included the same area, Church Reef, Wembury, in a general survey of a larger area on the Devon coast with Plymouth as the centre. He claims a higher upper limit for *Pelvetia* and raises it to a level above E.H.W.S.T. The upper limit for *Fucus spiralis* is also raised to a level midway between M.H.W.N.T. and M.H.W.S.T. These levels are considerably higher than those found by Colman on his transects, and agree with the authors' findings on the Manx and Scottish coasts. Evans also raises the upper zone of the *Ascophyllum* belt to M.H.W.N.T. He states that the top of the *Laminaria* zone is exposed only at the deepest of neap tides on the Devon coast. Evans's survey shows clearly the alteration in level of various algal zones in relation to the

degree of shelter from wave action, though the alteration is not necessarily in the same direction for all species.

In comparing the zonation of the fucoid belt on areas so widely separated as Devon, the Isle of Man and the coast of Argyll, it is obvious that caution must be exercised in making comparisons when the degree of wave action on each area has not been ascertained. Unfortunately, there is no means of assessing the force of wave action. Nevertheless, the areas selected by the authors in the three stations covered a very wide range of variation in the exposure factor from full surf on a headland facing west to an almost land-locked inlet. On the Manx and Scottish stations, the upper levels of *Ascophyllum* and *Fucus vesiculosus* lie higher on the shore than is shown by any of the records for Wembury, or, indeed, for any of the Devon areas surveyed so far. The difference in level amounts to not less than two vertical feet.

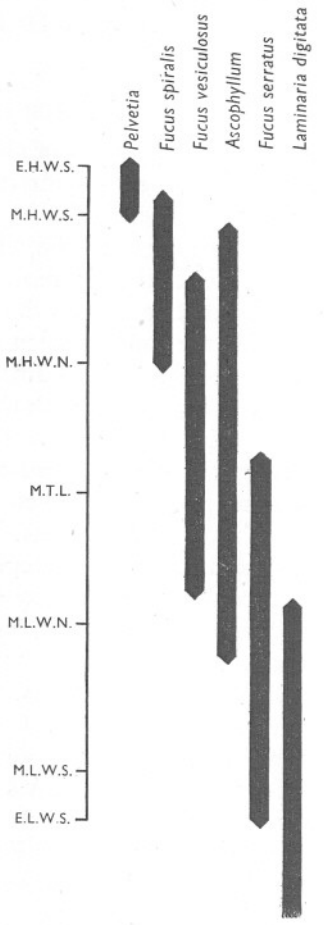

Fig. 1. The distribution of fucoids in relation to tidal level at Port Erin, Isle of Man.

The distribution of the fucoid zones on the Manx coast is shown in Fig. 1. It can be seen from the figure that *Pelvetia* lies at or, in sheltered places, above the level of E.H.W.S.T. and that *Fucus spiralis* reaches the M.H.W.S.T. level. *Ascophyllum*, accompanied by *Fucus vesiculosus*, reaches up to midway between M.H.W.N.T. and M.H.W.S.T. The distribution of *F. serratus* on the Manx coast appears to coincide with that on the Devon coast. Its upper level lies on M.S.L., but its lower limit lies in the fringe of the sublittoral zone. *Laminaria digitata* also appears to lie higher on the shore on the Manx coast when compared with the Devon coast. From Evans's records it would appear that the upper fringe of the *Laminaria* zone is exposed only by the deeper low waters of neap tides. On the Manx coast the highest *L. digitata* plants emerge at every low water level.

The relative alteration in level of the fucoid zones on shores of latitudes so far apart as Devon and the Isle of Man is to be expected. Tables for insolation and air humidity and the prevalence of mist or fog show that intertidal exposure on the south coast of Britain is likely to have more severe effects than in the north. The reduction in level of the plants on the south coast by

shortening the periods of exposure may compensate for the greater danger of desiccation.

Germination

The periods during which eggs are released from the plants are protracted for both species. Receptacles releasing gametes may be found in varying numbers somewhere or other on the shore for periods of 6 months for *Fucus vesiculosus* and 8 months for *F. serratus*. Receptacles in various stages of depletion may be found at other times when the egg supply falls to a minimum. The supply of eggs is enormous. Large plants may bear over 1000 fruiting apices, each carrying a large number of conceptacles in which egg development is maintained over a period. The largest number of receptacles recorded on single plants is 4678 for *F. serratus* and 3269 for *F. vesiculosus*. The number of eggs released by such large plants in the course of one fruiting season must be more than a million.

The large number of eggs produced is reflected in the large number of minute plants crowding the substratum below the larger plants. Table I records the number of young plants under 3 cm. in length growing on 1-metre-square experimental areas at Wembury. Both the original and final populations after clearance are recorded. The average proportion of young plants under 3 cm. in length, which may be regarded as indicative of the conditions for germination for each square, was 87·1 % for the original and 85·6 % for the final populations on *F. serratus* areas at Wembury. The proportion of such plants on the *F. vesiculosus* areas was somewhat less—74·1 % was recorded for the original and 57·4 % for the final populations.

From these results it would appear that the eggs of *F. serratus* have better opportunity for settlement and germination than those of *F. vesiculosus*. The range of variation in the data for the two species is from 28·2 to 98·9 % for *F. serratus* and from 15·2 to 95·2 % for *F. vesiculosus*. The discrepancy between the squares obviously reflects the physical conditions, because the total number of the plants in populations on the squares varies in parallel with the proportion of young plants.

The number of large plants in any area is affected by the degree of exposure of the area to wave action. *F. serratus* is more sensitive and the proportion of large plants in exposed places falls, thus making the proportion of young plants rise steeply. Conditions for germination may be good, but the rate of depopulation so high that the great majority of the plants may be less than 20 cm. in length. Port Erin Bay, on the Manx coast, faces west, and despite the partial shelter of a ruined breakwater, must be called an exposed coast. Data for the proportion of young plants in the population are given in Table II.

The records from Port Erin show some differences when compared with those from Wembury. The three strips were on a steeply shelving coast and subject to considerable battering by the waves. Metre-squares 8, 9, 19 and 20

on strip 1 sloped backwards towards the land and thus gained some shelter from the force of the waves. On these squares alone did the numbers of the

TABLE I. THE PROPORTION OF YOUNG PLANTS IN POPULATIONS ON 1-METRE-SQUARE EXPERIMENTAL AREAS AT WEMBURY

	Original population			Final population		
Metre sq. no.	Time of clearance	Total no. of plants	% under 3 cm. in length	No. of months of growth	Total no. of plants	% under 3 cm. in length
			F. serratus			
H 1	7. x. 41	8,163	87·9	35	5,471	95·4
2	6. xii. 41	634	28·2	33	1,761	47·3
3	15. vi. 42	3,978	90·5	27	1,837	81·0
L 1	6. x. 41	4,775	94·0	35	4,157	95·5
2	4. xii. 41	2,205	90·7	33	2,508	91·7
3	4. ii. 42	1,129	87·5	31	4,855	93·1
4	4. iv. 42	1,068	74·9	29	4,349	91·9
5	23. v. 42	7,056	93·5	28	2,271	79·2
6	14. vi. 42	4,934	97·3	27	9,373	97·3
7	13. vii. 42	2,970	97·5	26	8,022	96·7
8	15. viii. 42	2,594	93·8	25	400	60·0
9	11. ix. 42	7,651	95·5	24	1,635	80·8
10	9. x. 42	1,056	72·9	23	1,034	85·7
11	7. xi. 42	5,634	97·9	22	3,065	90·0
12	6. xii. 42	1,319	81·8	21	1,790	83·1
13	23. i. 43	1,019	95·7	20	6,863	92·6
14	17. ii. 43	1,004	87·6	19	9,668	89·0
15	26. iii. 43	1,361	88·1	18	12,858	91·3
16	21. iv. 43	5,664	98·8	17	5,263	84·3
	Total	64,214	Mean 87·1		Total 87,180	Mean 85·6
			F. vesiculosus			
1	5. ii. 42	317	66·6	30	11,589	95·2
2	7. iii. 42	—	—	29	(6,669)	(90·2)
3	13. iv. 42	1,159	69·0	29	1,991	76·3
4	13. v. 42	4,786	91·9	28	5,720	85·1
5	16. vi. 42	1,583	83·1	27	1,574	74·3
6	14. vii. 42	1,153	76·3	34	3,997	80·0
7	13. viii. 42	1,827	90·8	33	2,316	92·4
8	10. ix. 42	3,837	91·2	32	646	49·5
9	8. x. 42	1,259	73·0	31	345	46·4
10	6. xi. 42	1,698	87·1	30	405	19·8
11	5. xii. 42	1,289	71·3	29	629	19·0
12	20. i. 43	1,608	72·7	28	1,415	48·0
13	18. ii. 43	902	88·7	27	699	51·5
14	24. iii. 43	721	44·3	26	1,365	49·3
15	20. iv. 43	1,617	64·3	25	1,044	15·2
16	22. v. 43	1,776	40·5	24	1,161	58·5
	Total	25,532	Mean 74·1		Total 34,896 (less sq. 2)	Mean 57·4

F. serratus: 1-metre-square areas all re-cleared in September 1944. H = top of *Fucus serratus* zone; L = lower part of the *F. serratus* zone.

F. vesiculosus: Nos. 1–5 areas re-cleared August–September 1944. Nos. 6–16 areas re-cleared April–May 1945.

population approach those for the Wembury area. On the other squares the difficulty in settlement of the eggs is shown by the small numbers of plants in

TABLE II. THE PROPORTION OF YOUNG PLANTS IN POPULATIONS ON 1-METRE-SQUARE EXPERIMENTAL AREAS AT PORT ERIN

Strip 1. *Fucus serratus* and *F. vesiculosus*

Metre sq. no.	Total no. of plants	% under 10 cm. in length
1	124	41·1
2	847	94·6
3	962	93·7
4	332	70·2
5	788	92·5
6	660	48·9
7	310	98·3
8	1166	98·9
9	2168	99·2
10	421	93·5
11	393	82·9
12	243	83·1
13	597	93·8
14	907	92·1
15	957	88·1
16	876	81·3
17	904	84·2
18	1286	63·6
19	755	88·1
20	1150	87·6
21	433	79·4
22	636	92·6
23	720	87·1
24	381	82·4
25	14	21·4
26	27	88·5
27	47	29·7

Strip 2

	Original population		Final population			
			F. vesiculosus		*F. serratus*	
Metre sq. no.	Total no. of plants	% under 10 cm. in length	Total no. of plants	% under 10 cm. in length	Total no. of plants	% under 10 cm. in length
11	68	39·7	214	85·5	125	46·4
12	12	0	188	21·2	161	90·1
13	3132	98·8	614	84·3	481	58·2
14	981	96·1	214	85·5	700	65·8
15	—	—	2	0	626	75·1
16	1637	97·6	—	—	1194	62·8
17	4615	98·3	218	82·1	1114	60·1

Strip 3

	Final population	
Metre sq. no.	Total no. of plants	% under 10 cm. in length
13	1248	31·2
14	866	22·1
15	1110	10·2
16	1212	44·2

Note: Strip 1. Original clearance August 1941.
Strip 2. Original clearance April 1942; re-cleared September 1944.
Strip 3. Original clearance August 1942; re-cleared September 1944.

the populations. The depletion factor is also very high and varies from square to square, so that the range of proportions of plants under 10 cm. in length on the various squares is from 21·4 to 99·2 %.

Strips 2 and 3 were taken across a sharp ridge. Metre-squares 13 and 17 on strip 2 and all four metre-squares on strip 3 lay at a lower angle than the other squares, and the better conditions for settlement are reflected in the larger populations on these squares.

Eggs are sown broadcast over the shore and begin development wherever they fall, even in places where further growth will be impossible. The egg becomes attached to the rock within a few hours of settlement and may adhere firmly enough to the substratum to resist removal by the next returning tide.

An enormous number of eggs are, doubtless, washed away. Many more fall a prey to browsing molluscs, especially limpets and species of *Littorina*; but, even discounting these risks, there is a sufficient supply of attached eggs to replace plants removed from the population by accident or old age.

Estimation of the time required for the development of a fertilized egg into a visible germling was made by clearing small areas on the shore by a method which ensured the destruction of all eggs and microscopic germlings. This was done by one of three methods: exposing the rock surface, roughly cleared by scraping, to the action of a blow-lamp; by chipping off the surface rock to expose a new surface; by laying down blocks of prepared concrete. After each of these treatments experiment shows that colonization is rapid. From Table III it is seen that the time required for re-establishment of minute plants after all eggs and germlings had been removed does not differ greatly from that required when the surface was merely scraped.

The experimental area on the Manx coast was cleared in August 1941, but there was no opportunity of examining it until December, 100 days later. Consideration of the data provided by the first inspection of the area shows that the time required for germination of the eggs was not dissimilar to that given for the Wembury plants (Tables III, IV, V).

From the foregoing, it may be assumed that growth of the germling is continuous from the time it settles on the substratum, and that it may be visible to the naked eye within 2 weeks of settling.

The experimental areas covered every level at which the two species appear on the shores. There does not appear to be any level which is particularly favourable to settlement of eggs. The differences in settlement in various metre-squares on the areas are not due to difference in level, but they may be due to difference in the texture of the surface of the rock or to the slope of the substratum. Local increase in angle of slope enhances the difficulty in settlement of eggs; a smooth rock surface and absence of cracks is also a deterrent. This is clearly shown by the fact that the earliest and most rapid development of young plants takes place in cracks and fissures in the rock surface.

Germination of eggs of *Fucus serratus* is likely to be more uniform at all levels than that of *F. vesiculosus*. The higher level at which the latter species grows exposes the eggs to a greater range of inimical physical factors. Light

TABLE III. RECOLONIZATION OF *FUCUS SERRATUS* AFTER CLEARANCE ON THE ARGYLL AND DEVON COASTS

Experimental area	Method of clearance	No. of days after clearance	Maximum size of germlings in cm.
Argyll:			
Serratus Rock	Scraping	41	1·0
Ascophyllum Rock, E. strip	Scraping	41	3·0
Devon:			
Strip sq. 14	Rock surface removed	58	5·2
Strip sq. 15	Cleared by blow-lamp	47	1·1
Strip sq. 19	Rock surface removed	38	1·0
Strip sq. 19A, 2	Rock surface removed	175	2·0
F.S.L. 1	Scraping	59	2·0
6	Scraping	71	4·0
7	Scraping	42	3·0
8	Scraping	28	1·5
9	Scraping	58	3·0
10	Scraping	64	3·5
11	Scraping	64	3·5
12	Scraping	49	2·0
13	Scraping	27	1·0
14	Scraping	31	1·0
15	Scraping	26	1·5
16	Scraping	30	3·0

TABLE IV. RECOLONIZATION OF *FUCUS SERRATUS* AFTER CLEARANCE AT PORT ERIN ON THE MANX COAST

Experimental area	Method of clearance	No. of days after clearance	Maximum size of germlings in cm.	
			Range	Mean
Strip 1, metre sq. nos. 10–23	Scraping	100 ± 4	3·0–14·0	9·4
Strip 2, metre sq. nos. 12–15	Scraping	101	6·0–16·0	8·8
Strip 3, metre sq. nos. 1–2	Cleared by blow-lamp	54	0·5– 1·0	0·8

TABLE V. RECOLONIZATION OF *FUCUS VESICULOSUS* AFTER CLEARANCE ON THE DEVON AND MANX COASTS

Experimental area	Method of clearance	No. of days after clearance	Maximum size of germlings in cm.	
			Range	Mean
Wembury, metre sq. nos. 5–16	Scraping	28 ± 14	1·0– 3·0	1·5
Port Erin, strip 1, metre sq. nos. 1–7	Scraping	101 ± 1	3·0–10·5	6·0

favours germination; hence a greater population of small plants in the upper levels of the *F. vesiculosus* zone might be expected. It is a fact that on coasts where the *F. vesiculosus* zone lies high on the shore, as on the Manx coast, the upper edge of the zone carries a dense carpet of young plants, without any larger plants. The factor of desiccation appears to work in contrary direction to

that of increased illumination, with the result that, though germination may be easy in the upper levels of the belt, further growth is difficult where the periods of exposure are great relative to those of submergence. The result of these two opposing factors on the Manx coast is the maintenance of a dwarf population at the top level of the zone, where the plants remain in a condition of protracted juvenility. An area of plants in this position was kept under observation for 2 years. The plants were 2–3 cm. long and remained at that length for the whole period. That they were still alive was demonstrated by the fact that when the boulder on which the plants were growing was removed to a lower level on the shore in the *F. vesiculosus* zone, the plants began to elongate at once, and within 3 months had reached a length of 9 cm. Their further progress in the new position was quite normal.

On shores sloping towards the south in the Isle of Man, and frequently on the Devon coast near Plymouth, no germlings appear on a cleared area until after a carpet of *Enteromorpha* or *Ulva* has developed as a cover to the rock surface. The most vulnerable early stages of germination thus take place under the *Enteromorpha* carpet, and, by the time the tips of the germlings project above it, they are strong enough to resist desiccation and the depredations of molluscs. Hatton (1932), working at St Vaast-la-Hougue, found the same interaction between *Enteromorpha* and *Fucus* germlings. In this more southerly station, Hatton found that a carpet of *Enteromorpha* was almost an essential condition for good germination of *Fucus* eggs, and that the latter were noticeably fewer where the *Enteromorpha* did not develop. Normally, of course, on an uncleared area, the eggs develop under cover of the adult population, which provides adequate protection from desiccation and reduces the risk of destruction by molluscs.

The influence of increased light after clearance of the original population from an area might have been expected to facilitate germination of eggs and lead to a denser population on the experimental areas. This hypothesis has been borne out by experiment. Reference to Table I will show that the final population on the Devon coast was larger than the original population for both species of *Fucus*. The total original population figures for a series of 16 squares, each 1 metre square, are: *F. serratus* 64,214, *F. vesiculosus* 25,532; the numbers in the final populations were: *F. serratus* 87,180, an increase of 36 %, and *F. vesiculosus* 34,896, an increase of 37 %. The data for the Isle of Man showed an increase of 9·8 % for the final population of *F. serratus*. The figure for *F. vesiculosus* would have been much higher. There was an obvious increase in density of population on the experimental squares, but final analysis was prevented by a storm which covered the experimental area with a pile of boulders.

It is probable that *F. vesiculosus* and *F. serratus* would extend their natural boundaries in the absence of mutual competition. Experiments have shown that areas cleared artificially or accidentally in one zone may be

colonized by plants proper to another zone. The intruders may persist for a year or longer but will eventually be driven out by competition.

In latitudes more northerly than those investigated by the authors, *F. serratus* may rise higher on the shore and has been found on the upper levels in the Orkney Islands. There are also references to *F. serratus* at fairly high levels on the south coast of England, but in these circumstances the plants come early into the fruiting stage and die out within a year.

Larger plants are found distributed over the zone at all levels except the extreme upper limits. The best population is found in the middle region where a mixed population of all sizes develops. It is possible that the light factor controls the lower limit of *F. vesiculosus* on the Devon coast, compared with that in higher latitudes. The claim that light is the determining factor was made by Gail (1918). The lower position of *F. serratus* relative to that of *F. vesiculosus* may indicate a greater tolerance of reduced light and/or a greater intolerance of exposure to the drying action of the atmosphere.

Growth-rate

Measurement of Growth

Two methods were employed to determine growth-rate. The first was to clear an area of its population and then record the sizes of plants in the new population at intervals. Two difficulties immediately became apparent. Eggs from plants in the vicinity of the experimental areas are shed continuously over a long period; later, when the short sterile period approaches, the egg output falls but may not fail completely. The result is that the experimental areas are almost continuously resown with eggs after the experiment has started. The new population on the areas is thus of different ages. Records were made at intervals of the length of the longest plants, on the assumption that the longest would be the oldest in a population of young plants of all sizes, down to just visible germlings. The assumption that the longest plants were the oldest is not necessarily justified because the germlings possess, as is common to seedlings of higher plants, great variation in individual vigour. It is difficult to explain the precocious advance in length of some germlings relative to others on any other grounds. It may be stated, however, that competition may play a part in the early stages of growth, because isolated germlings usually showed higher growth-rate than those which were crowded together; germlings which developed in cracks in the rock also seemed to gain an advantage from their position.

The second difficulty was the very rapid depopulation-rate. Serial records of maximum size sometimes showed a decrease, because the largest germlings had been removed by some agency or another in the interval between the observations.

The other method used was to mark individual plants and to measure

them at intervals. Here, again, the ease with which plants are broken and the longest fronds removed by rough water or the depredations of molluscs proved a hindrance. This difficulty naturally increased as the plants grew longer.

Increase in length appears to be a uniform process for young plants of both *F. vesiculosus* and *F. serratus* during their first year, irrespective of the time of year at which they start life. This fact was established by clearing metre squares at intervals of 1 month to cover a whole year. Inspection of older plants suggested that there might be an alternation of periods of vegetative growth and reproductive periods in which extension of the frond was reduced. Serial records of growth through the reproductive period does not, however, bear out this hypothesis. The impression is given by the fact that as the reproductive fronds wear away they leave the new vegetative frondage in full view and very conspicuous by the lighter colour of the frond tips.

Elongation alone is, of course, no full measure of growth. Dichotomy of the fronds and development of lateral frondage goes on simultaneously with linear extension. An attempt was made in some of the experiments to record the degree of 'bushiness' by counting the number of frond apices at the times when their length was recorded. In this feature plants showed individual variation, some developing dichotomies in lateral frondage more vigorously than others. An example of the degree of branching is given in Table IX in the Appendix (p. 501). Plant A4 showed an increase in the number of frond apices from 16 to 1777 in a period of 377 days, during which it increased in length from 21·0 to 61·0 cm. This plant was evidently a very vigorous specimen because the increase in length in one year was 39·0 cm. compared with the normal yearly extension of 22·4 cm. It was impossible to count the frond apices on all the experimental plants, and as normal extension of frond branching was concomitant with extension, the elongation factor was used as a criterion for growth.

Growth-rate in Fucus vesiculosus

Observations on frond extension were made in all three areas using the methods of cleared areas and marked plants (Tables IX–XVII, pp. 501–4).

The experiments in the Isle of Man (Table XV) were brought to a premature conclusion by the incidence of a heavy gale in April 1943, during which the experimental strip was buried under piles of large stones to a depth of several feet and many of the boulders under observation were removed bodily. Data from the Isle of Man, therefore, refer only to a period of 1 year and 9 months. From the data it has been determined that an average growth-rate of 0·45 cm. per week is maintained by *F. vesiculosus*.

Growth-rate data from Wembury are obtained from a large number of plots selected from all levels and under varying conditions of exposure in the *F. vesiculosus* zone (Tables IX–XIV). A summary of the results from Wembury

is contained in Table VI. The variation in growth-rate from the individual plots is from 0·25 to 0·71 cm. per week. The average rate from twenty-eight separate plots is 0·48 cm. per week. This figure agrees reasonably well with the average growth-rate of 0·45 cm. per week for the Manx plants, bearing in mind that the Devon plants had a longer period in which to grow. It has been established that the growth-rate in the second year and succeeding years may be slightly higher than that for the first year.

TABLE VI. RATE OF GROWTH IN LENGTH IN *FUCUS VESICULOSUS* ON THE EXPERIMENTAL AREAS ON THE DEVON COAST

Experimental area	No. of sites	Growth-rate per week (cm.) Min.	Max.	Mean
F. vesiculosus area	6	0·25	0·63	0·42
Strip, sqs. 14 and 16*a*	6	0·43	0·71	0·55
F. vesiculosus metre sqs.	16	0·32	0·57	0·47

Average growth-rate on 28 sites, 0·48 cm. per week.

The rate of elongation of the Scottish plants showed considerable variation (Tables XVI, XVII). The range of exposure on the individual plots in the Scottish station was very wide and the records show the effect on the growth-rate. On the very exposed plot on Sgeir Bhuidhe the rate of elongation for *F. vesiculosus* was, on the average, 0·31 cm. per week, a value which is less than that for growth-rate of *F. vesiculosus* on the Manx and Devon coasts. On the other hand, growth-rates for the other plots on the Scottish station showed much higher values. The Ascophyllum Rock plot which was in a sheltered locality gave a growth-rate of 0·68 cm. per week, a value which is much higher than the average for *F. vesiculosus* on any other station.

Breakage on exposed coasts is higher than in sheltered localities, and the recorded interim lengths may well be less than the real lengths, but a sufficient number of plants escaped breakage to establish the principle that the rate of growth in exposed places is actually slower than in sheltered localities.

Growth-rate in Fucus serratus

Comparison of the data from the three stations showed considerable variation in growth-rate. On the Devon coast a large number of marked plants were studied, as well as cleared areas. The data from these experiments are given in Tables XVIII–XXVII in the Appendix (pp. 505–10). Summarizing the data from the Devon coast, it may be stated that the average elongation rate for *F. serratus* from all sources was 0·49 cm. per week with a range of variation of 0·31–0·71 cm. per week. The value 0·49 cm. per week is very close to that found in the same area for *F. vesiculosus*, but the range is slightly more restricted than for the latter species, viz. 0·48, range 0·25–0·71 cm.

Three areas were examined on the Manx coast. Three strips were cleared in Port Erin Bay. Strip 1 ran down on a fairly steep coast from H.W.N.T. to

E.L.W.S.T., passing through the entire fucoid zone. Squares 10–27 ran through the *F. serratus* zone. Table XXVIII in the Appendix gives the details of observations on this strip. The elongation-rate is slightly reduced in the extreme upper and lower levels, but is fairly uniform throughout the greater part of the strip. The average growth-rate is 0·57 cm. per week, with a range of 0·43–0·65 cm. per week. The period of the experiment was 2 years and 9 months. Two other shorter strips alongside strip 1 gave average rates of 0·58 and 0·68 cm. per week, with ranges of 0·53–0·63 and 0·65–0·70 cm. per week respectively.

The other two Manx areas lay on the south-east coast at Port St Mary and Castletown (Table XXIX). The growth-rates from these two areas gave rather higher values than those from the Port Erin area. Average values of 0·73 (Port St Mary) and 0·84 (Castletown) cm. per week were obtained.

This variation in growth-rate appears to be correlated with the degree of shelter from direct wave action on the three areas. Port Erin Bay with a steeper coast, facing west, experiences considerable battering by the waves, driven by prevailing westerly winds. Port St Mary and Castletown lie on that part of the coast where the tide runs parallel with the land. The coast is also formed of very gently inclined terraces of limestone, and the waves tend to roll over the shore rather than impinge with battering force against it. The breakage factor on the Port Erin shore is likely to be greater than on either of the other two Manx stations, and it is probable that the observed average elongation-rate here falls rather further below the real elongation-rate than on the sheltered areas. There is, however, other evidence that the growth-rate on the protected areas is really greater than that on the exposed shore at Port Erin. Not only is the maximum length of plants normally greater in the sheltered areas, but the internodes between forkings are also longer. It must be admitted that the records from the two stations on the sheltered coast were drawn from observations over a period of 1 year only, but comparison of normal populations from the three areas supports the view that growth-rate rises with increasing shelter.

It must be pointed out that the lowest growth-rate recorded for the Isle of Man, even on the exposed coast, exceeds that for the Devon plants and suggests that a higher latitude with reduced inimical factors operating during periods of exposure may also have a beneficial effect on growth-rate.

This hypothesis is borne out by the fact that the highest growth-rates for *F. serratus* come from the Argyll coast (Tables XXX, XXXI). The various plots on the Scottish coast give a range of elongation-rates from 0·56 to 0·91 cm. per week for three stations, but the range of variation for plots and marked plants within each area is from 0·15 to 1·82 cm. per week. The Serratus Rock station was specially chosen because of the luxuriant growth of *F. serratus* in the original population. The average growth-rate on this station was 0·90 cm. per week for cleared areas and 0·91 cm. per week for marked plants. This

gives a rate for the Scottish plants which is nearly double that of the Devon plants. The greater growth-rate is also accompanied by greater internode length.

A summary of recorded growth-rates for *F. serratus* from all sources is given in Table VII.

TABLE VII. RATE OF GROWTH IN LENGTH IN *FUCUS SERRATUS* ON THE EXPERIMENTAL AREAS ON THE DEVON, MANX AND ARGYLL COASTS

Experimental area	No. of sites	Growth-rate per week (cm.) Min.	Max.	Mean
Devon:				
Strip, sqs. 15–22	19	0·31	0·71	0·48
F. serratus metre sqs.	19	0·41	0·63	0·53
Average growth-rate for 38 sites, 0·49 cm. per week.				
Isle of Man:				
Port Erin, strips 1–3	26	0·43	0·70	0·59
Port St Mary	5	0·58	0·90	0·73
Castletown	5	0·74	1·04	0·84
Average growth-rate for 36 sites, 0·68 cm. per week.				
Argyll:				
Serratus Rock	11	0·72	1·10	0·93
Ascophyllum Rock	3	0·47	0·66	0·57
Average growth-rate for 14 sites, 0·85 cm. per week.				

COMPARISON OF OBSERVED GROWTH-RATES WITH RECORDS FROM OTHER AREAS

A very wide range of growth-rate is given for *F. vesiculosus* and *F. serratus* from other areas. On the French coast, Lemoine (1913) records from Roscoff a growth-rate for *F. vesiculosus* of 2·5–3·3 cm. per month. The period of experiment was short, but if the rate had been maintained over a longer period it would have given a slightly higher rate than that found for *F. vesiculosus* on British coasts. The same is true for *F. serratus*. Lemoine records an increase in length of 12 cm. in 2 months, which is a much higher growth-rate than is shown on British coasts. Records from other French stations show slower rates. Hatton (1932) records elongation-rates from St Servan of 9·8–13·3 cm. in 7 months. This would give a weekly elongation of 0·31–0·47 cm., a rate comparable with those of British plants. Hariot (1909) records growth-rates of 4·5 cm. in 8 months for *F. vesiculosus* and *F. spiralis* from St Vaast-la-Hougue. This rate is low and may possibly be attributable to peculiar factors of the environment.

Results from other areas show slower growth-rates. Nienburg (1930) reports an average length of 20–25 cm. per year for both species. Furthermore, Lund (1936) quotes growth-rates of 4–6 cm. per year for the Danish coast and illustrates a plant which measured only 14 cm. at the end of 3 years. Records from the Norwegian coast at Trøndelagen (Printz, 1926) give growth-rates of

4–7 cm. per year, but Gislén (1930) records for the Gullmar Fjord on the Swedish coast a growth-rate of 6–14 cm. in 7 months. In extreme northern waters the effect of reduced light has to be considered, as little growth takes place in the dark winters.

The effect of changing salinity may also have an effect on growth-rate. It certainly affects the form of the plant, usually by causing dilatation of the receptacles, and may also affect growth-rate. Colman quotes the work of Segerstråle from Finland in water with a salinity of 4 °/₀₀ and a very small tidal range, in which the author records plants of *F. vesiculosus* which reached a length of 2–3 m. Such a great length has not been equalled by any of the plants which came under observation in the course of the present survey,

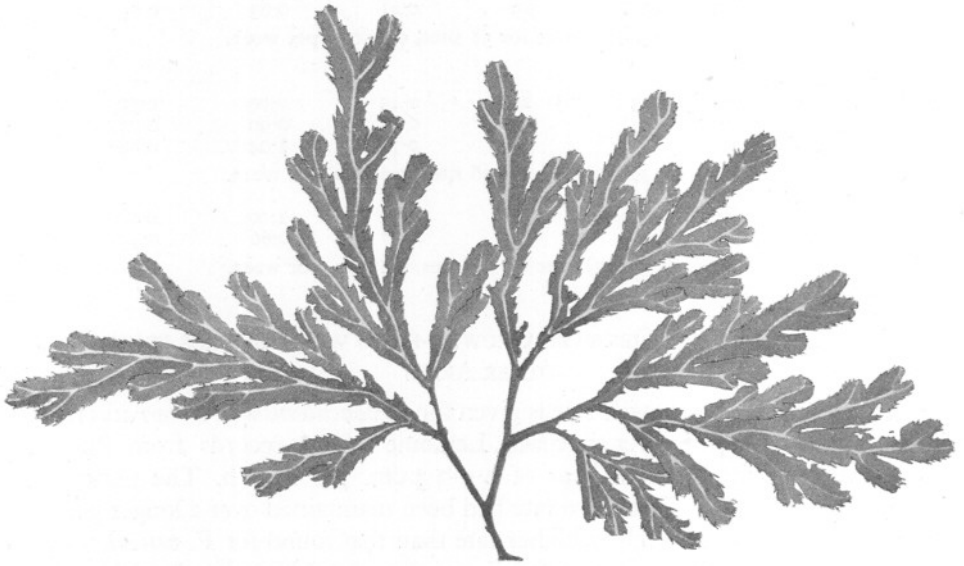

Fig. 2. Sterile plant of *Fucus serratus* from the Devon coast just over 1 year old. ×0·22.

though old plants of *F. vesiculosus*, consisting of twisted defoliated strands of more than 1 m. in length, are frequently met with in sheltered places.

Rees (1932) is of the opinion that aeration of the water plays a determining part in the development of both *F. vesiculosus* and *F. serratus*. He reports that at Lough Ine, on the south-west coast of Ireland, *F. serratus* occurs only in the almost land-locked lough at stations where the tidal current moves with its greatest rapidity.

The greatest contrast in growth-rate found by the authors is between plants of *F. serratus* at Wembury and on the Argyll coast. Fig. 2 shows a plant of *F. serratus* from the Devon station in its second year. This should be compared with Fig. 3, which represents a plant from the Argyll station in its first year.

Morphological Rhythm in Frond Development

Dichotomy of the frond takes place repeatedly, thus dividing it into sections which may be called, for convenience, 'internodes'. In a young plant the first internode is commonly longer than those which follow. On a growing frond the youngest internodes are naturally shorter than in the older ones, but even

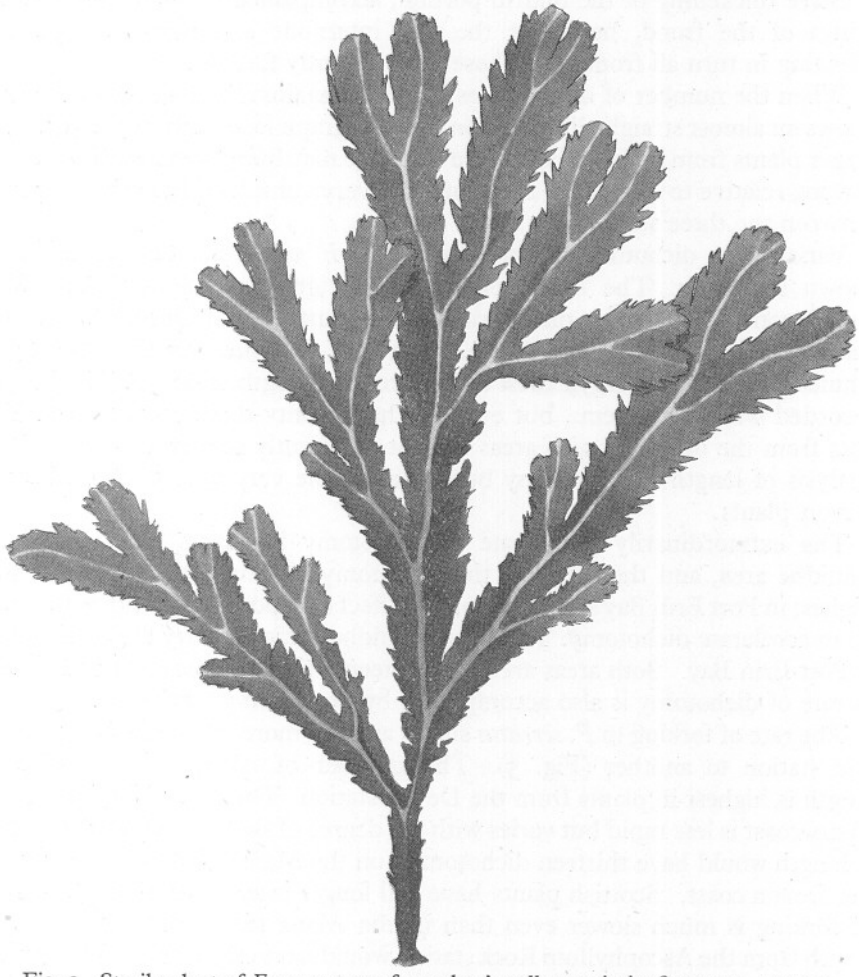

Fig. 3. Sterile plant of *Fucus serratus* from the Argyll coast in its first year. ×0·25.

mature lengths of internodes vary considerably. The variation in internode length is not so marked in the first year, but as the plant approaches reproduction, those fans that are destined to bear receptacles are forked at short intervals.

When an internode is delimited by apical dichotomy, it may have reached only 40–50 % of its final length. Subsequent elongation is brought about by

secondary tissue-formation and by swelling of internal cell-walls. The secondary extension diminishes in rate with the passage of time and finally ceases. As a plant grows larger, the basal internodes thicken to form a stipe. The thickening is accompanied by a secondary shortening of internodal length, which may amount to 18 % of the original (maximum) length. Progressive thickening of the midrib portion, accompanied by denudation of the wings of the frond, begins at the first internode and moves acropetally, affecting in turn all fronds but those most recently formed.

When the number of dichotomies is plotted against frond-length the result shows an almost straight-line relation, but the graph loses form somewhat with larger plants from which much of the frondage may have been lost. The rate of forking relative to length has been found to vary considerably for both species between the three stations.

Variation in dichotomy/length relation for *F. vesiculosus* on all stations is shown in Fig. 4. The Manx plants show a greater rate of forking than the Devon plants. Manx plants would have fourteen and Devon plants nine dichotomies for a length of 60 cm. Plants of *F. vesiculosus* from the Sgeir Bhuidhe area on the Argyll coast did not reach a length of 60 cm. The longest recorded was only 40 cm., but even so, had twenty-three dichotomies. The data from the other Scottish areas are not sufficiently numerous to permit of analysis of length to dichotomy but appear to lie very near to those for the Devon plants.

The extraordinarily rapid rate of dichotomy in plants from the Sgeir Bhuidhe area, and the fact that the dichotomy rate on the Manx coast was highest in Port Erin Bay suggests that one effect of exposure to rough water may be to accelerate dichotomy. The Sgeir Bhuidhe station is very exposed and so is Port Erin Bay. Both areas are also on steeply shelving coasts. The increase in rate of dichotomy is also accompanied by decreased growth-rate.

The rate of forking in *F. serratus* shows an even more marked variation from one station to another (Fig. 5). The number of dichotomies relative to length is highest in plants from the Devon station. The rate of forking on the Manx coast is less rapid but varies with the degree of shelter. A plant of 60 cm. in length would have thirteen dichotomies on the Manx coast and nineteen on the Devon coast. Scottish plants have still longer internodes, that is, the rate of forking is much slower even than in the Manx plants. Plants 60 cm. in length from the Ascophyllum Rock station would have only eleven dichotomies, and those from the Serratus Rock plot would have only nine dichotomies.

It is clear that rate of forking and elongation-rate are correlated inversely with one another. The more slowly a plant grows, the more rapidly it forks. It appears probable that in both species a reaction to inimical conditions is shown by retarded growth-rate and increased forking. Despite this variation in response to local conditions, especially degree of shelter, there is no doubt that there is an over-all increase in growth-rate and a marked diminution in the

rate of forking as one moves from the south coast, via the Isle of Man, to the Argyll coast.

After a dichotomy has been established, the two arms develop into frondage, but at very different rates. One arm has the advantage and grows more quickly than the other arm (Figs. 6, 7 A). Examination of an old frond may show that more than two-thirds of the total frondage has been developed from one

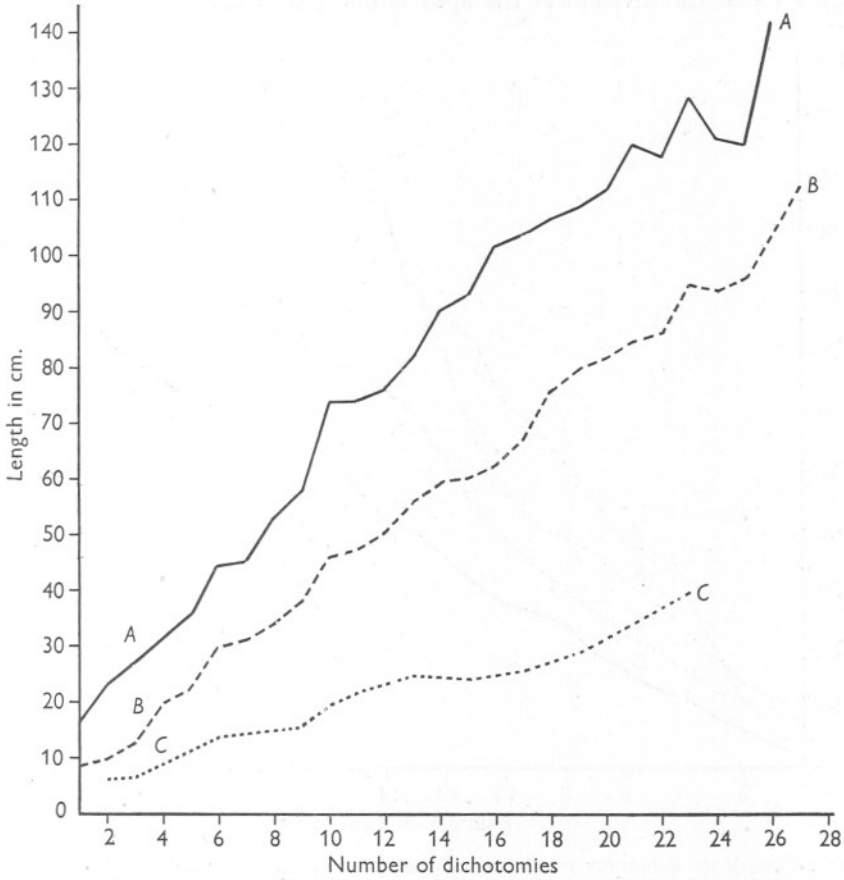

Fig. 4. Length to dichotomy relations in *Fucus vesiculosus* on the Devon, Manx and Argyll coasts. *A*, Church Reef, Wembury, Devon; *B*, Port Erin, Isle of Man; *C*, Sgeir Bhuidhe, off the west coast of the island of Luing, Argyll.

arm of the first dichotomy. Occasionally, in *F. serratus* and more rarely in *F. vesiculosus*, the rate of development of the two arms of the first dichotomy is approximately equal and a 'twin-thallus' is formed. This is seen in *F. serratus* in Fig. 7 B. Fig. 10 shows an almost similar condition for *F. vesiculosus*.

If the dichotomies are followed in sequence along the length of a frond, it will be seen that the emphasis of development of one arm of a fork compared

with the other shows regular alternation from side to side of the frond. This overgrowth of alternate arms of a fork at successive dichotomies appears to be a fundamental morphological feature of both species, though it is more strictly maintained in *F. serratus* than in *F. vesiculosus* (Figs. 8, 9).

This inequality between the two arms of a fork is obviously due to a difference in growth-potential between the products of division of an apical cell. It suggests that the division of the apex is not a true dichotomy, as it is, for

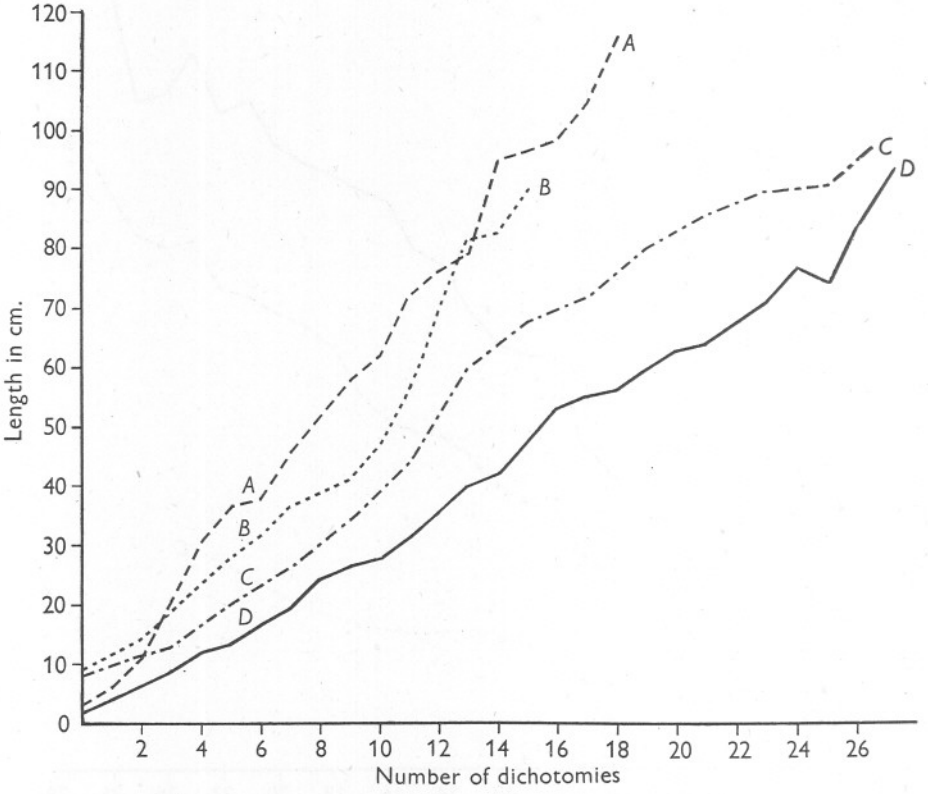

Fig. 5. Length to dichotomy relations in *Fucus serratus*. *A*, 'Serratus Rock', off the west coast of the island of Luing, Argyll; *B*, 'Ascophyllum Rock', west coast of the island of Luing, Argyll; *C*, Port Erin, Isle of Man; *D*, Church Reef, Wembury, Devon.

example, in *Dictyota*, but that one arm of the fork is due to the activity of a segment cut off from the apical cell which itself serves as the growing point for the other arm of the fork. The inequality of growth-potential would be explained by the excess of vigour of the original apical cell over the segment, to the activity of which the lesser arm of the fork is due. The alternation of excess growth-potential is therefore only an effect of regular segmentation from alternate sides of an apical cell.

On this view the two species of *Fucus* under discussion might be regarded as having a monopodial rather than a dichotomous habit of branching, but it is a monopodial system in which the lateral branch initial arises in the immediate vicinity of the apical cell and thus simulates a dichotomy. This method of unequal development of the two arms of a fork is, of course, carried to much greater degree by members of allied families as, for example, the Sargassaceae.

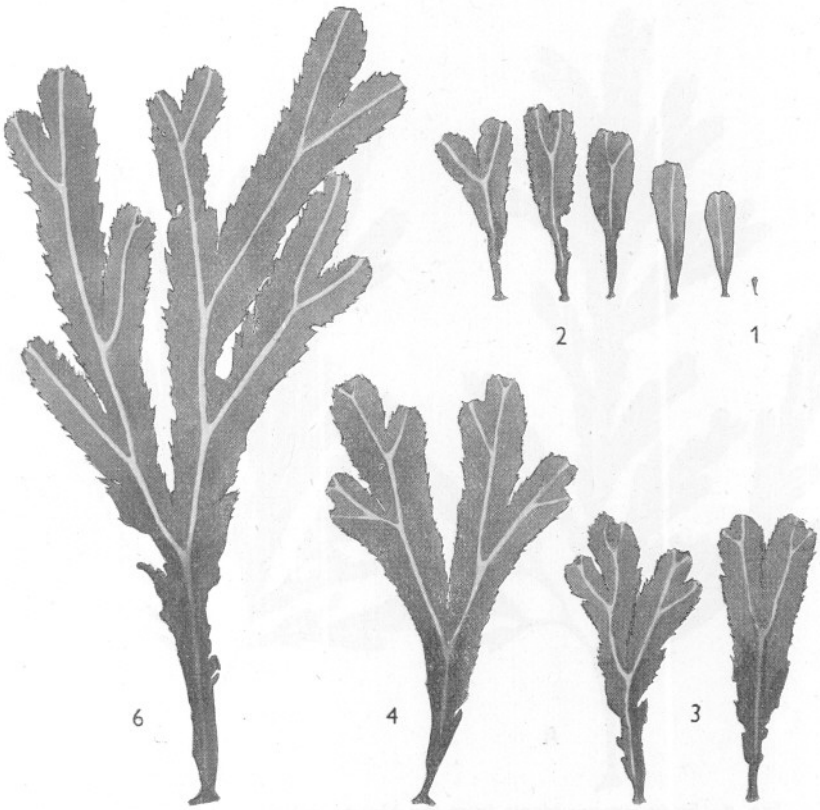

Fig. 6. Germlings of *Fucus serratus* from 1 to 6 months in age. ×0·27.

Not only is there an unequal capacity for frond development between the two arms of a fork, but the fate of the frondage developed from the arms may also differ. For example, in *F. vesiculosus* that arm of a fork which has the lower growth-potential usually forms a reproductive fan, forked at short intervals and forming receptacles at the tips of the fronds (Fig. 10). The other arm grows forward as a 'leader' and may give off *seriatim*, left and right, other reproductive fans. Occasionally one or two apices on the younger reproductive fans may remain sterile and act as secondary 'leaders', repeating the behaviour of the primary 'leaders' and adding to the bushiness of the plant.

At the time of fruiting, both primary and secondary leaders may be observed projecting beyond the general periphery of the frondage (Fig. 10). It may be noticed that receptacle development has been imposed simultaneously on lateral fronds of different ages. The basal older ones have undergone the greater number of dichotomies and bear the larger number of receptacles. The fruiting fronds will be ultimately removed after fruiting, and the leaders will

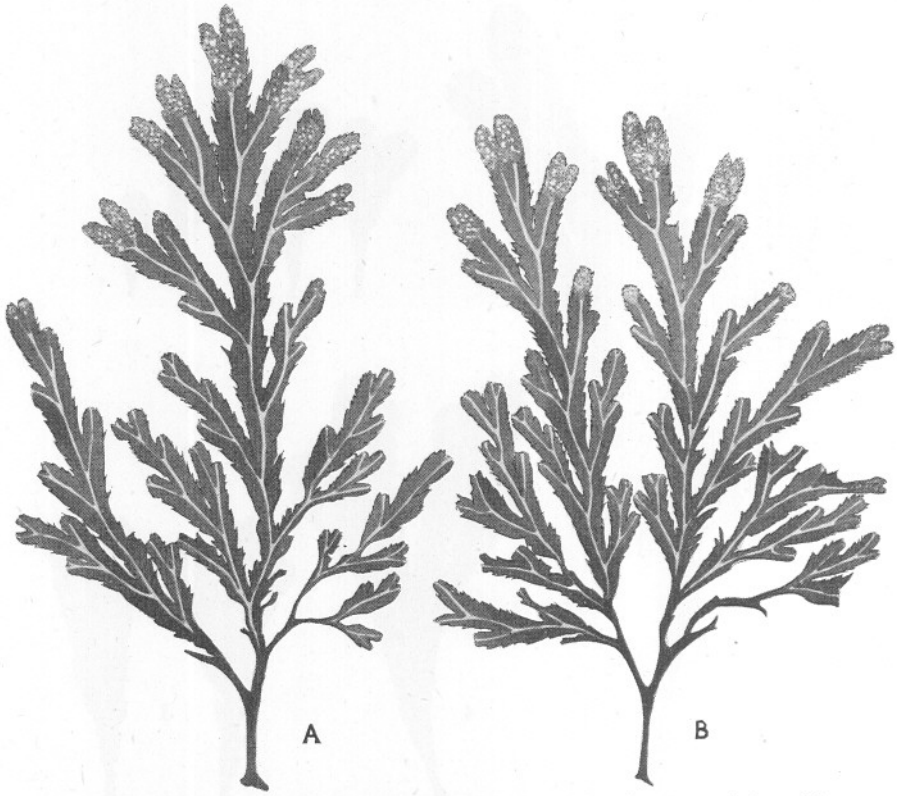

Fig. 7. *Fucus serratus* plants from the Manx coast showing normal form (A) and 'twin thallus' form (B). ×0·23.

grow forward to produce new distal frondage, with the result that no frondage is left on the proximal part of the plant, except where proliferation may give new frondage from old midribs. The basal part of an old plant, therefore, consists of a tangle of midribs from which the wings have been denuded, beset with spines to mark the places of excised fruiting fronds.

In the development of its frondage, *F. serratus* stands in sharp contrast to *F. vesiculosus*. Each dichotomy shows a different growth potential between the two arms, but the amount of difference decreases from the base of the plant upwards. If the lower dichotomies on a plant are examined it will be found that

one arm has produced a good deal of frondage but that the other has done very little. It forks only rarely and its growth-rate is extremely slow. In Fig. 11 only very little frondage has been produced by one arm of the second and third dichotomies. Following the dichotomies upwards it can be seen that there is an acropetal gradient of increasing activity, although the difference in potential between the two arms is maintained. In other words the basal part of the plant has a high degree of latency compared with the distal frondage.

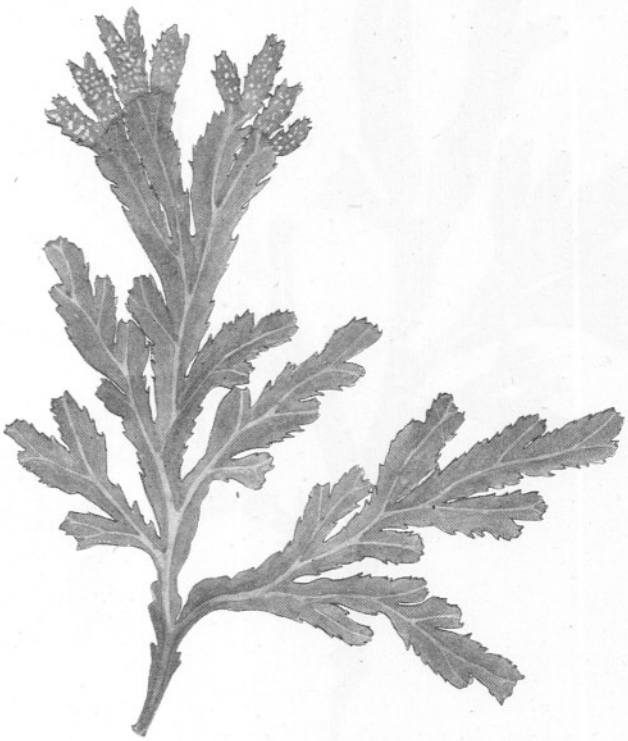

Fig. 8. First year plant of *Fucus serratus* showing unequal dichotomy. ×0·27.

When reproduction sets in, it affects the distal frondage of both arms of the youngest dichotomies and there is no prominent vegetative leader as in *F. vesiculosus*. This is clearly to be seen in Fig. 11 where receptacles occupy distal positions. When the reproductive frondage is excised, further extension of the frond must take place by the activity of vegetative apices lying below the perimeter of the plant. Vegetative apices lie at all levels on the plant and are of various ages. It is the youngest of these tips nearest to the periphery which first begin to accelerate while the peripheral fruiting fronds are degenerating. After successive fruitings, apices lying at successively lower levels take up the role of elongation, and last of all, if the plant survives long enough, the vegetative apices at the base of the plant.

In the first year of growth reproduction may not affect all the peripheral tips. Some may remain vegetative, with the result that elongation is a continuous process, but after the second year, when peripheral tips become reproductive, elongation of the plant takes place by a kind of relay system.

The habit of retaining vegetative frondage on the lower parts of the plant gives *F. serratus* a much more bushy form than *F. vesiculosus*. Bearing in mind

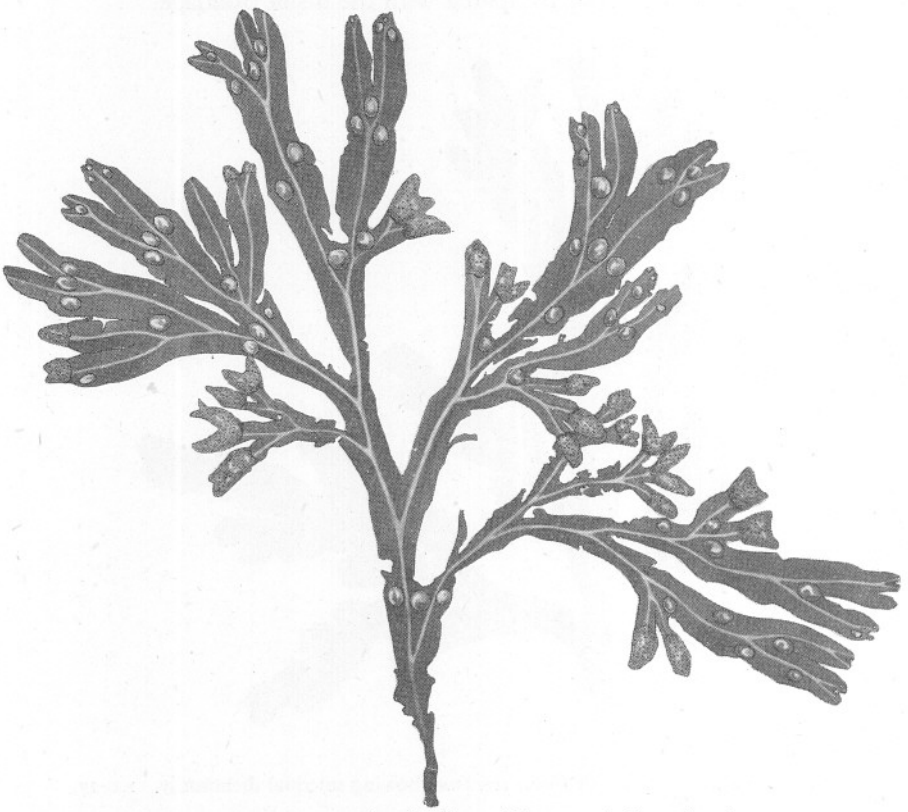

Fig. 9. Eighteen months old plant of *Fucus vesiculosus* showing unequal dichotomy. ×0·21.

that the behaviour of the main fronds is repeated in the secondary branches it will be realized that the body of an old plant of *F. serratus* is built up on a complicated system of branching.

Comparison between the habit of branching in *F. serratus* and the sympodial habit of branching of higher plants is inescapable. The similarities which exist between the mechanisms whereby plant form is achieved by plants on land and plants in the sea is striking.

Plants of both species normally live 3 years (Rees, 1932) and some may survive a fourth and even a fifth year in very sheltered positions. Plants in the

Fig. 10. Plant of *Fucus vesiculosus* with vegetative leaders extending in preparation for next season's frondage-development. ×0·29.

most exposed situations rarely live longer than 2 years. *F. vesiculosus* plants in moderately exposed situations achieve their maximum weight in the fruiting season of their third year, but plants of *F. serratus* may gain in weight in their fourth year and are commonly heavier than *F. vesiculosus* on account of their more bushy habit. In both species the weight of the fronds at the end of the

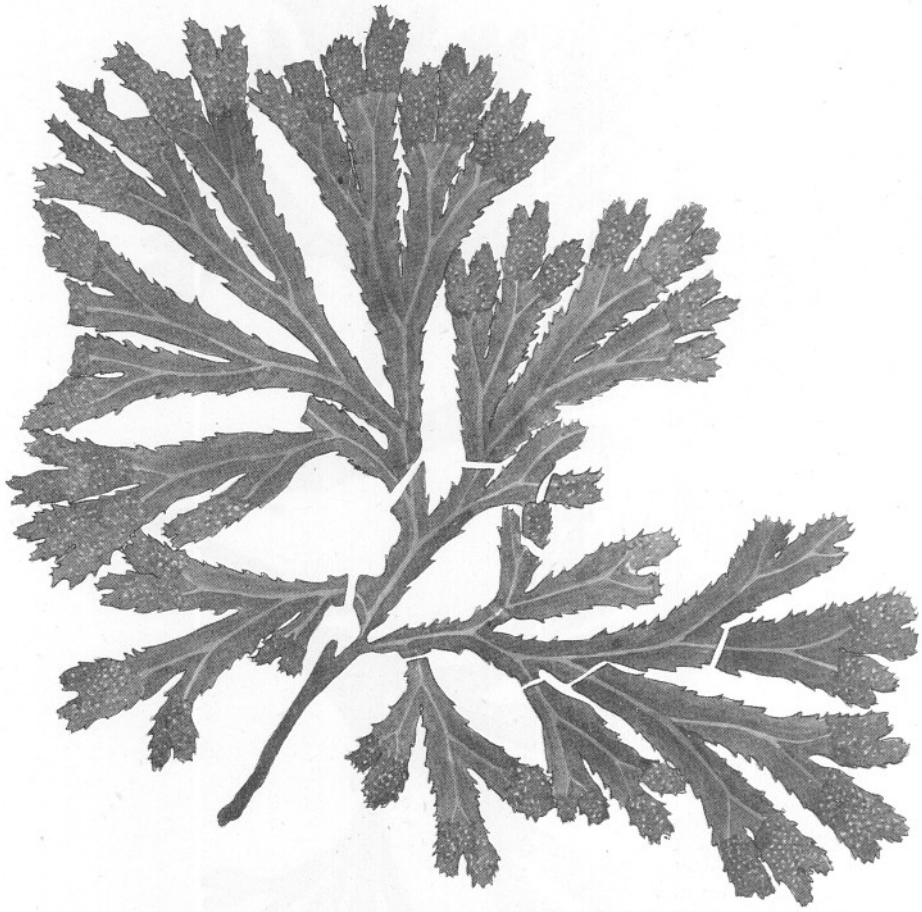

Fig. 11. *Fucus serratus* plant illustrating the amount of defoliation that occurs after fruiting. Fronds distal to the gaps will be shed. ×0·27.

first year is from 1 to 2 oz. (28 to 57 g.); weight increases to about 1 lb. (454 g.) in the second year, and rises steeply in the third year to several pounds. The greatest weight recorded for *F. serratus* was 6½ lb. (2·95 kg.). This is an exceptional weight and was recorded for a plant in its fourth year, growing in a sheltered situation.

Frond-width shows some variation. Cotton (1912) suggests that breadth increases with shelter. To a large extent this suggestion has been confirmed

by observation in the course of the present investigation. It is true that plants of *F. vesiculosus* in extremely exposed places show narrow, dark-coloured and tough fronds. Apart from this generalization, however, there is a great deal of variation in frond-width shown by plants growing even in sheltered situations. Such variation is often accompanied by diversity in number and shape of vesicles and receptacles, and is to be regarded as attributable to factors other than exposure. Broad thalli are commonly found on very young plants, especially where they develop on cleared ground, but frond-width on these young plants may be reduced with each successive addition of frondage. When denudation of the wings of the lower part of the thallus takes place, there may be eventually no sign of the original broad frondage.

Vesicle-formation in *Fucus vesiculosus*

Vesicles are formed in spring. Appearing in March, the vesicles increase in numbers during April, being added serially by activity of apical tissue (Fig. 12). The great majority of them have been laid down by the end of April, but occasional vesicles may be added in June and July and even as late as August.

The vesicles first appear as minute globular swellings in the wings of the frond, immediately behind the apical notch (Figs. 12, 13). They usually arise in pairs, but a single one is often formed also in the angle formed by a dichotomy. They may occur in the lower internodes of large receptacular fronds.

Plants form vesicles when they have reached a length of from 10 to 14 cm. Young plants which have not reached this length by the end of the vesicle-formation period postpone the process until the appropriate time in the following year. It is clear that the seasonal process of vesicle-formation—a process lasting for a few weeks only—must be brought about by seasonal changes in the physical factors of the environment, but there must also be an internal control which permits of vesiculation in plants at a certain stage of maturity and prevents it in plants below the limit of size.

Speaking generally, vesiculation appears to bear some relation to vertical distribution. This is most marked in the upper limits of the zone, for plants found high on the shore where they are mixed with *F. spiralis* frequently show few vesicles or even none at all. These forms have been considered by some authorities (Cotton, 1912) to be a distinct variety, *F. vesiculosus* L. var. *evesiculosus* Cotton. On the coast of Argyll, however, on the Serratus Rock station a high belt of *F. vesiculosus* growing above the *Ascophyllum* zone bore a conspicuous number of vesicles. An almost complete absence of vesicles characterizes the whole *F. vesiculosus* zone, on the Devon, Manx and Argyll coasts, in very exposed places such as the foot of vertical cliffs exposed to full surf-action. There is a possibility that this condition depends on degree of exposure.

From the point of view of vesiculation, the species shows so much variety that it is difficult to describe what might be considered the normal condition.

Vesicles may be in pairs with one axillary vesicle, or the latter may be absent. The numbers of pairs in the internodes may vary from one to ten or more. Usually the vesicles are grouped near the sixth internode on young plants and affect one to four of the internodes of each yearly addition of frondage; but there are plants, attributed to a distinct variety, *F. vesiculosus* L. var. *vadorum* Aresch. (Fig. 14), in which vesiculation appears to be a continuous process. As many as ten pairs of vesicles may occur in the length of one internode, and there appears to be no recognizable gap between the sets laid down in

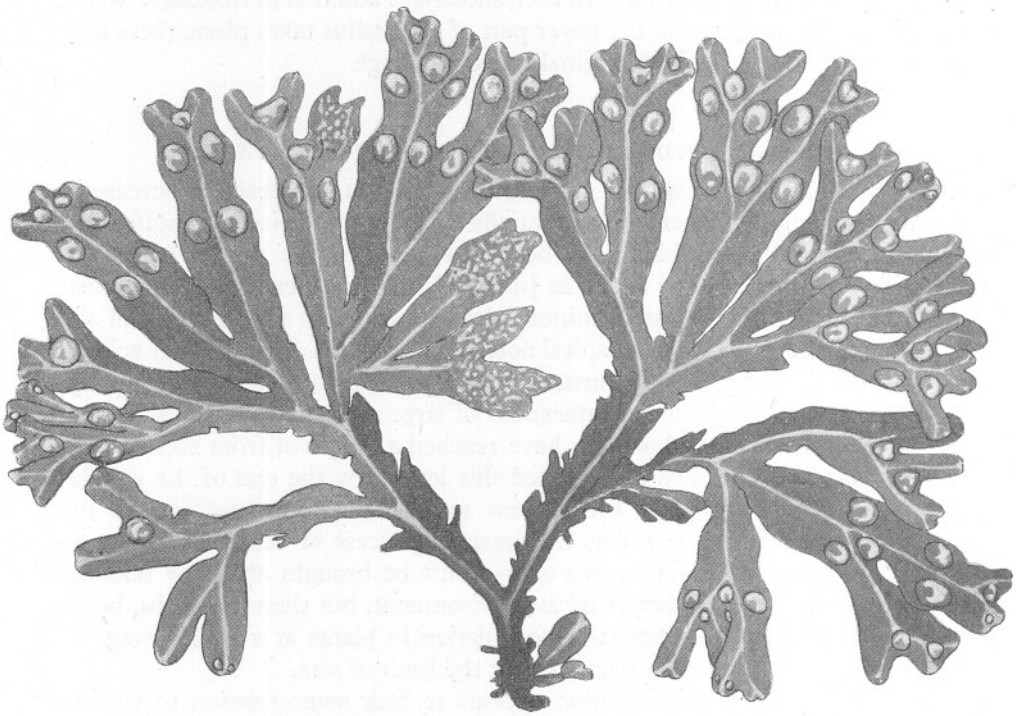

Fig. 12. Vesicle-formation in a plant of *Fucus vesiculosus* L. in the spring. ×0·40.

successive years. This form is frequently associated with a sheltered habitat, but there is evidence that it occurs also in less sheltered places. It has been suggested that vesiculation increases in less well-aerated waters, but this hypothesis has yet to be proved.

Fig. 13 might be considered as illustrative of the most usual arrangement of vesicles, with one to three pairs in the internode and one axillary vesicle, and with a distinct gap between one set of vesicles and the next. The first vegetative period in the plant's life is marked by the production of the first set of vesicles and the frondage between the two sets of vesicles has been developed in the second year.

Fig. 13. Plant of *Fucus vesiculosus* L. with first and second set of vesicles. ×0·23.

The number of sets of vesicles present on a plant may thus be used as a criterion of age. This criterion, however, breaks down in an old plant, if the lowest set of vesicles has been removed by denudation of the wings of the basal part of the frond. Distribution and number of the vesicles is the character which most greatly affects the general appearance of the plant. Many of the varieties claimed by various authors are distinguished from one another largely by their characteristic number and arrangement of the vesicles.

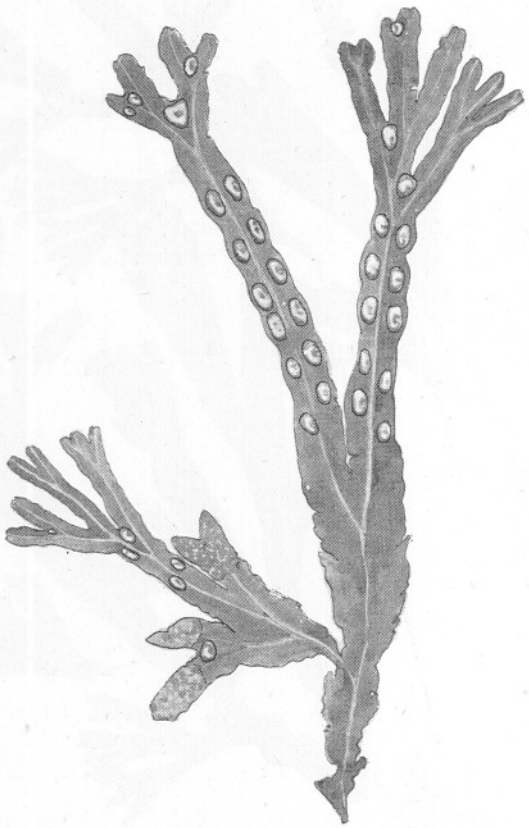

Fig. 14. *Fucus vesiculosus* L. var. *vadorum* Aresch. ×0·32.

Figs. 14–19 will illustrate the range of form-variation met with in the course of the investigation. It is difficult to determine without far-reaching genetic and cytological inquiry whether these forms are fixed varieties or not. They have been accepted as such by many algologists (Gard, 1916). In some of the forms illustrated there is close agreement with the descriptions of accepted varieties, but the authors have not had opportunity to consult type specimens. Fig. 15 with a single vesicle in the axils of forks and a very wide divergence of

the arms agrees with the description of *F. vesiculosus* L. var. *divaricatus* Good. & Woodw. Similarly, Fig. 14 may be a young plant of *F. vesiculosus* L. var. *vadorum* Aresch., in larger plants of which there may be as many as ten pairs of vesicles per internode. It is possible that Fig. 16 represents a hybrid between *F. vesiculosus* and *F. serratus*. Such hybrids between the two species are not uncommon; they usually have the vegetative features of *F. vesiculosus* and a receptacle-form more nearly resembling that of *F. serratus*. Fig. 17 represents an unidentified variety which was quite distinct from the evesiculate type characteristic of high levels or exposed coasts. Fig. 18

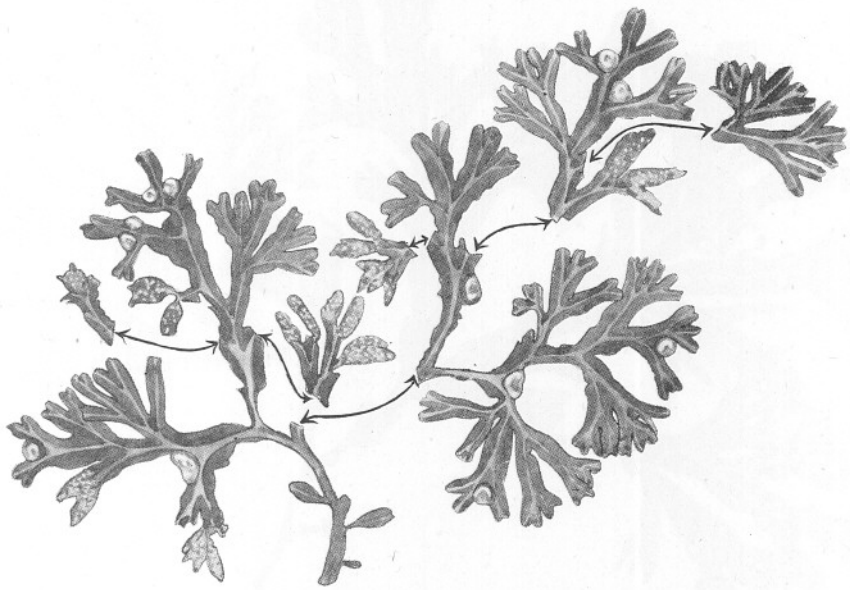

Fig. 15. *Fucus vesiculosus* L. var. *divaricatus* Good. & Woodw. ×0·31.

shows a plant almost without vesiculation but bearing small spherical, air-filled receptacles agreeing in form with the description of *F. vesiculosus* L. var. *sphaerocarpus* J. Ag.

The presence of fresh water draining down the shore affects the form of plants of *F. vesiculosus* lying in its path. On these plants receptacles are usually greatly distended and water-filled (Fig. 19). The same general character is shown by the *F. vesiculosus* population of the banks of the river Mersey, where the salinity of the water is less than that of the open sea.

It is quite certain that the varieties met with are not all to be explained on the score of ecological growth-forms, due to differences in habitat. It is true that modification in vesiculation in relation to bathymetric level is an observed fact; but such modification is defined in terms of growth-rate and internode length as well as in the presence or absence of vesicles; moreover, the range of

variation shown in relation to level is much less than that shown by the different habit-forms described for plants growing side by side at the same level in what appear to be identical circumstances. The extreme forms are linked by a series of intergrades. If they are not to be regarded as fixed, separate varieties, the only explanation of their occurrence would be that *F. vesiculosus* is subject to spontaneous form-variation unrelated to the physical factors of the environment.

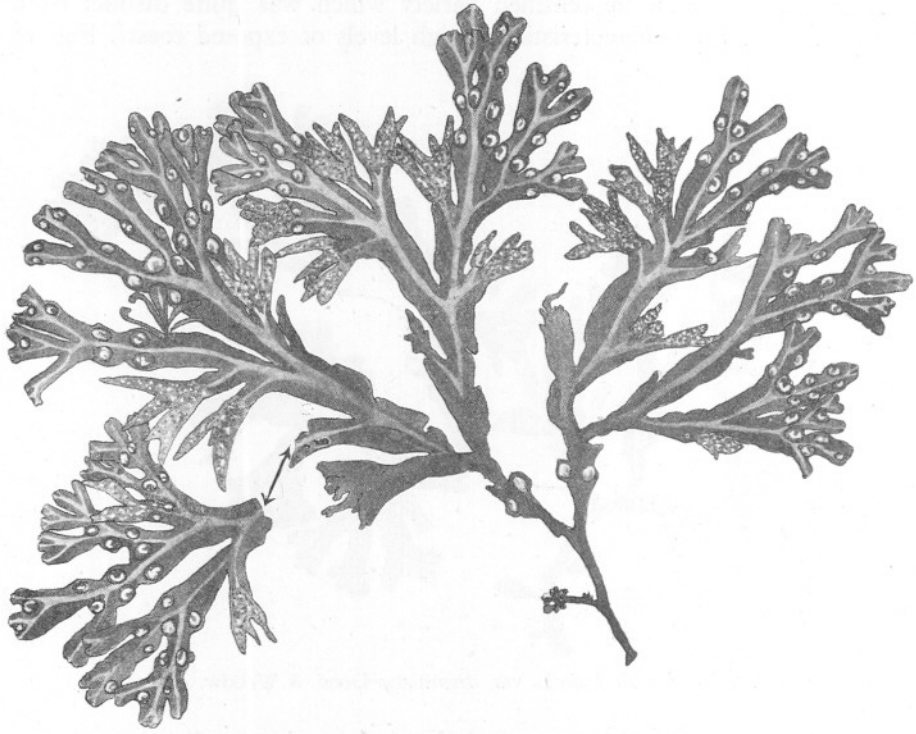

Fig. 16. Suspected hybrid of *Fucus serratus* L. and *Fucus vesiculosus* L. ×0·27.

Reproduction

Reproduction shows a seasonal rhythm. Initiation, maturation of receptacles and retrogressive stages after gamete-release cover a long period. The peak of reproduction is reached in the spring and summer by *F. vesiculosus*, and in the autumn and winter by *F. serratus*, though the latter species shows great variety in the timing of reproduction at various points on the British coasts.

Initiation of receptacles is continued over a period of at least 5 months, and 3 months are required for the development of a receptacle from its initiation up to the stage when gametes are released.

Receptacle-initiation begins in a few plants at first and only gradually affects the bulk of the population. When the peak of gamete-release is passed, some plants continue the process for some weeks. In general, plants in the upper levels begin to fruit first and plants at lower levels come successively into fruit. The timing of receptacle-formation also appears to be affected by the degree of shelter. In sheltered localities reproduction may be initiated earlier than in

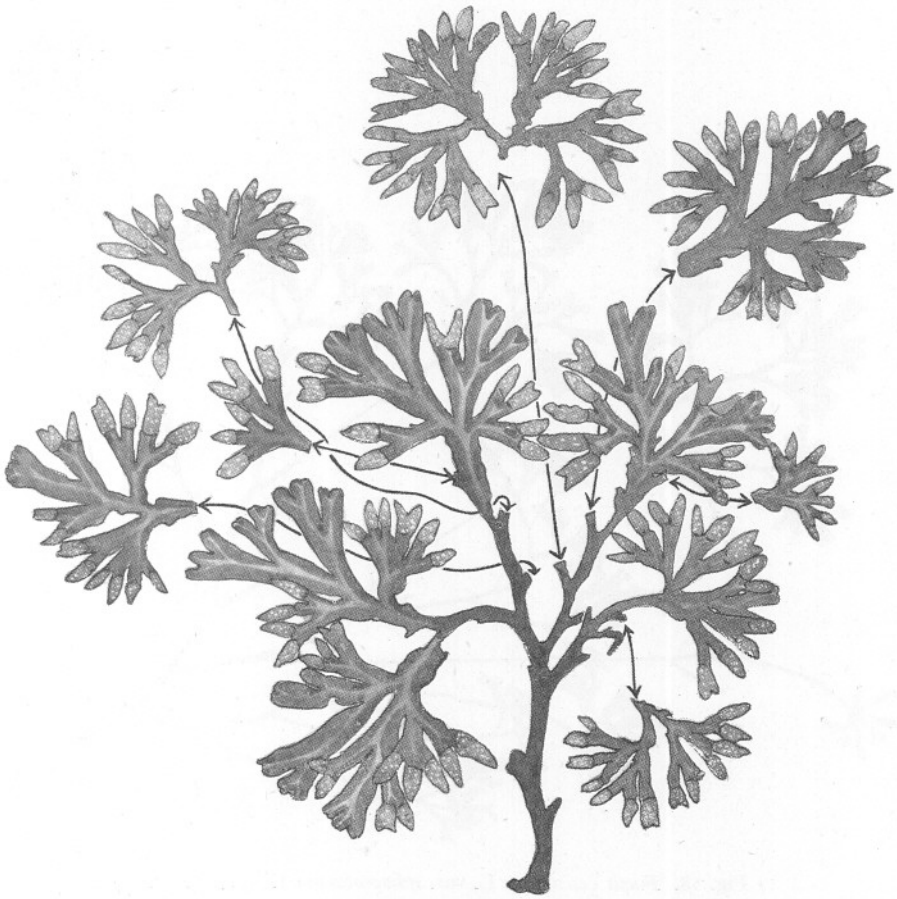

Fig. 17. Unidentified variety of *Fucus vesiculosus* L. ×0·34.

exposed places, and the reproductive stages may be passed through more slowly, thus prolonging the whole reproductive period.

After initiation of new receptacles is over for the season, those still present on the plant pursue the later stages of retrogression, and some of them may be still present on the plant when the next season's receptacles are beginning to be formed.

Young plants of *F. vesiculosus* usually reach a length of 15–20 cm. before they form receptacles. The corresponding length for plants of *F. serratus* is 18–25 cm. Only a small proportion of the plants fruit in their first year. On these plants receptacles are few and are developed on the lowest frond branches. Not infrequently, the frondage produced in the first year becomes reproductive simultaneously with the frondage of the second year. First year plants may

Fig. 18. *Fucus vesiculosus* L. var. *sphaerocarpus* J. Ag. ×0·20.

reproduce either early in the season before the older plants (Port Erin) or later in the reproductive season after the older plants have fruited (Devon).

The receptacles of *F. vesiculosus* and *F. serratus* differ somewhat in development. The apical cell, giving rise to a receptacle in *F. vesiculosus*, continues activity until the receptacle is shaped, but ceases to divide before the oogonia and antheridia are established in the conceptacles. The apical groove then flattens out, and further elongation and swelling of the receptacle is brought

Fig. 19. Plant of *Fucus vesiculosus* L. showing the influence of fresh water. ×0·25.

about by secondary extension of tissues and by increase in swelling of the mucilage of the cell walls. The apex may dichotomize once or twice before it ceases to function. In *F. serratus* the apical cell retains its activity for a much longer period and may be responsible for several dichotomies before it dies out. The receptacles of *F. serratus* may achieve considerable length; they often reach a length of 14 cm.

Occasionally the apices of receptacles in *F. vesiculosus* show variation by retaining their power of cell-division for a much longer period than is normal. The tissue behind the apex forms a very long receptacle with a series of conceptacles interrupted by one or more sterile bands. This peculiarity is usually shown by receptacles developing out of the normal fruiting season.

Though the formation and ripening of the receptacles is a continuous process, it has been arbitrarily divided into serial stages for purposes of making comparative records in the field. The stages are as follows:

(1) Receptacles just indicated by swelling and thickening of the extreme tips of the fronds.

(2) Receptacles swollen and shaped, but with no conceptacles visible to the naked eye.

(3) Conceptacles initiated and their positions just discernible when the receptacle is held up against the light.

(4) Conceptacles shown as faint dots against the light.

(5) Conceptacles showing clearly as *dark* dots against the light; gametes forming but not yet ready for release.

(6) Free release of gametes.

(7) Base of the receptacle emptied.

(8) Receptacles completely depleted and beginning to decay.

(9) Receptacles worn off and their positions indicated by the torn edges of subtending frondage and, later still, by mere spines of midrib from which the wings have been removed.

All three areas showed agreement in the sequence of stages in reproduction, but the periods of the year at which the stages were shown were not coincident.

Reproduction in Fucus serratus

From the many records of fruiting of *F. serratus* on the Devon coast, a typical example may be selected. In February 1942, six groups of young plants, varying in length from 17·5 to 48 cm., were labelled and observed at frequent intervals until August 1944, covering a period of 2 years and 6 months. Two complete reproductive cycles were thus included in the experimental period.

Apart from slight individual variations the groups behaved similarly. The course of reproduction is illustrated by Fig. 20, and details are given in

the following schedule. The timing of reproductive stages in *F. serratus* in the Isle of Man is given for comparison:

Comparison of the timing of stages of reproduction of Fucus serratus *on the Devon and Manx coasts*

Wembury, Devon		Port Erin, Isle of Man	
Apr.	Thickening observable in tips of fronds of largest plants.	Aug.	A few frond tips show thickening.
May	Initiation of receptacles general in population.	Sept.	Initiation of receptacles general in population.
June	Initiation of new receptacles still continues. Those formed earliest have reached the stage of forming oogonia and antheridia.		
July	There is still some initiation of new receptacles. The first gametes are released at the end of the month from the older receptacles.	Oct.	Initiation of new receptacles still continues at reduced rate. The majority of receptacles are approaching maturity and a few have reached the stage of gamete-release.
Aug.	Initiation of new receptacles wanes and release of gametes is general.	Nov.	No further initiation of receptacles takes place and gamete-release is general in the population.
Sept.	No further receptacles are initiated and gamete-release continues. Depleted receptacles show deterioration stages.	Dec. Jan.	Gamete-release begins to wane and all stages in deterioration of depleted receptacles are to be found.
Oct. Nov. Dec.	Receptacles formed late in the season may be still releasing gametes, but deterioration of the majority of the receptacles reaches the last stages.	Feb.	Very few receptacles still release gametes. Most of them are torn off and the plants present a battered appearance.
Jan. Feb. Mar.	Sterile period, though a few old depleted receptacles may be found on the plants.	Mar. to July	Sterile period in which old empty receptacles are rare.

On the more sheltered parts of the Manx coast, at Castletown and Port St Mary, receptacle-formation begins in July, nearly a month earlier than on the more exposed Port Erin beach. The peak of gamete-release is also reached a month earlier, but the whole fruiting period is longer than that for plants on exposed beaches, so that the end of the fruiting periods for plants in both habitats coincides.

The fruiting period for *F. serratus* on the Argyll coast begins 3 weeks later than on the Devon coast, and is therefore intermediate in time between that station and the sheltered coasts of the Isle of Man.

Apart from observations made at the three stations under discussion, there is evidence that the range of times of fruiting of *F. serratus* may be considerably extended elsewhere. Plants of *F. serratus* in full release of gametes have been observed on the Northumbrian coast in July, a date earlier than for any other station.

The degree of fruiting, i.e. the number of receptacles per plant and the proportion of plants in fruit simultaneously in the population, varies from one station to another. From the records, it appears to be heaviest in exposed places. At Port Erin in December, just after the peak of gamete-release, the average percentage of the population bearing receptacles was 60. On a strip running right through the *F. serratus* zone the proportion of fruiting plants varied from 40 to 70 %, being heaviest in the lowest third of the strip. The records from Wembury do not show so high a proportion of plants in fruit. The discrepancy may be due to the fact that a much larger proportion of young plants fruit in their first year on the Manx than on the Devon coast.

Comparison of the proportions of fruiting to sterile tips per plant on the two stations shows a much higher percentage of receptacles on the Manx plants.

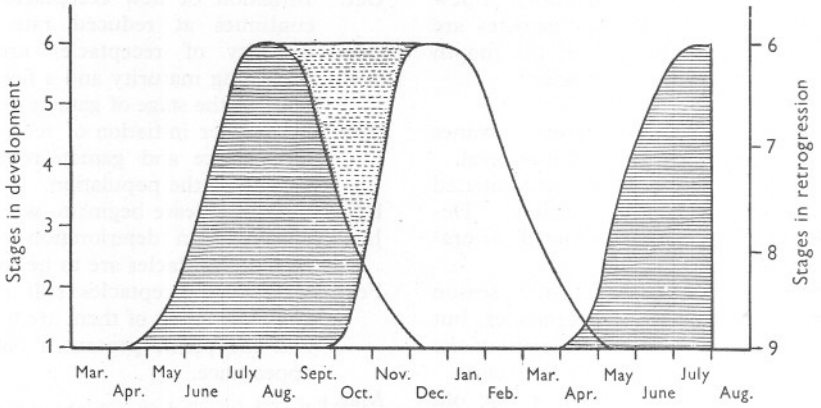

Fig. 20. Seasonal fruiting in *Fucus serratus* on the Devon coast. See p. 474 for definition of stages.

In many 3-year-old plants, only 5 % of the tips remain sterile; individuals have been found also in which every apex has been transformed into a receptacle (Fig. 26, p. 485). Fig. 21 shows a typical young plant from Port Erin, fruiting for the first time when it was only 10 months old. Fig. 2 (p. 454) illustrates a plant from the Devon coast which has not yet fruited though it is 1 year and 2 months old. Fig. 22 shows a plant of *F. serratus* from Wembury fruiting for the first time in its second year; the receptacles on the plant represent 58·7 % of the total frond-tips.

Reproduction in Fucus vesiculosus

The series of stages in the reproduction of *F. vesiculosus* and the length of time required for their development correspond with similar data for *F. serratus*, but the timing of reproduction is different for the two species.

A comparison of the timing of equivalent stages in reproduction of *F. vesiculosus* on the Devon and Manx coasts follows:

Comparison of timing of stages of reproduction in Fucus vesiculosus *on the Devon and Manx coasts*

Wembury, Devon	Port Erin, Isle of Man
Dec. Earliest stages in receptacle formation observable in some of the plant population.	Dec. Earliest stages of initiation shown by plants of less than 1 year old.
Jan. Initiation of receptacles general in the population.	Jan. General initiation of receptacles on plants of all ages.
Feb. Older receptacles swollen and shaped. Initiation of new receptacles is continued.	Feb. New receptacles still being formed. The older ones show the positions of conceptacles.
Mar. A few new receptacles may be formed but the majority have advanced to the stage when conceptacles are just discernible.	Mar. No further initiation of receptacles, but those already formed may have reached the stage of gamete-formation. Release of gametes begins.
Apr. No further initiation of receptacles. Antheridia and oogonia formed in older receptacles.	Apr. Release of gametes increases towards the end of the month.
May Full release of gametes.	May, June: Gamete-release passes its peak and the older receptacles show all stages in deterioration.
June Many receptacles show deterioration stages and the youngest are releasing gametes.	July 10 % of the population may still be releasing gametes and the rest bear depleted receptacles.
July Release of gametes comes to an end and receptacles show all stages of disintegration.	Aug. Plants releasing gametes fall to 3 % of the population. Receptacles in the rest of the population are fast disappearing.
Aug. Only depleted and decayed receptacles present.	Sept., Oct., Nov.: Fruiting finished. Initiation of new receptacular fronds.
Sept., Oct.: Sterile period.	
Nov. A few tips may show the earliest stages of receptacle-initiation.	

There is only about 1 month's difference in the timing of reproduction on the Manx and Devon coasts. The Devon plants begin first (Fig. 23 and Table XXXIII, facing p. 514). Another point of difference lies in the reproduction of young plants. On the Devon coast they usually bear receptacles late in the season, after the main population is in fruit. On the Manx coast, the fruiting of young plants usually precedes that of the older plants. There is also, as was described for *F. serratus*, a precocity of fruiting shown by plants in sheltered situations. On the promontory of Langness on the south-east coast of the Isle of Man, where there is considerable shelter, the factors of the environment combine to make the locality particularly favourable to algal development. Not only do young plants grow more quickly in this area, but they come into fruit at least 3 weeks earlier than on any other area. This precocity is hard to explain unless it be that a river about a mile away may contribute extra organic

nutrient matter to the sea water in the neighbourhood. The set of the tides is such that mud in very small quantities is carried by the tide and deposited above the algal zone. The mud is just sufficient to support a very narrow belt of saltmarsh.

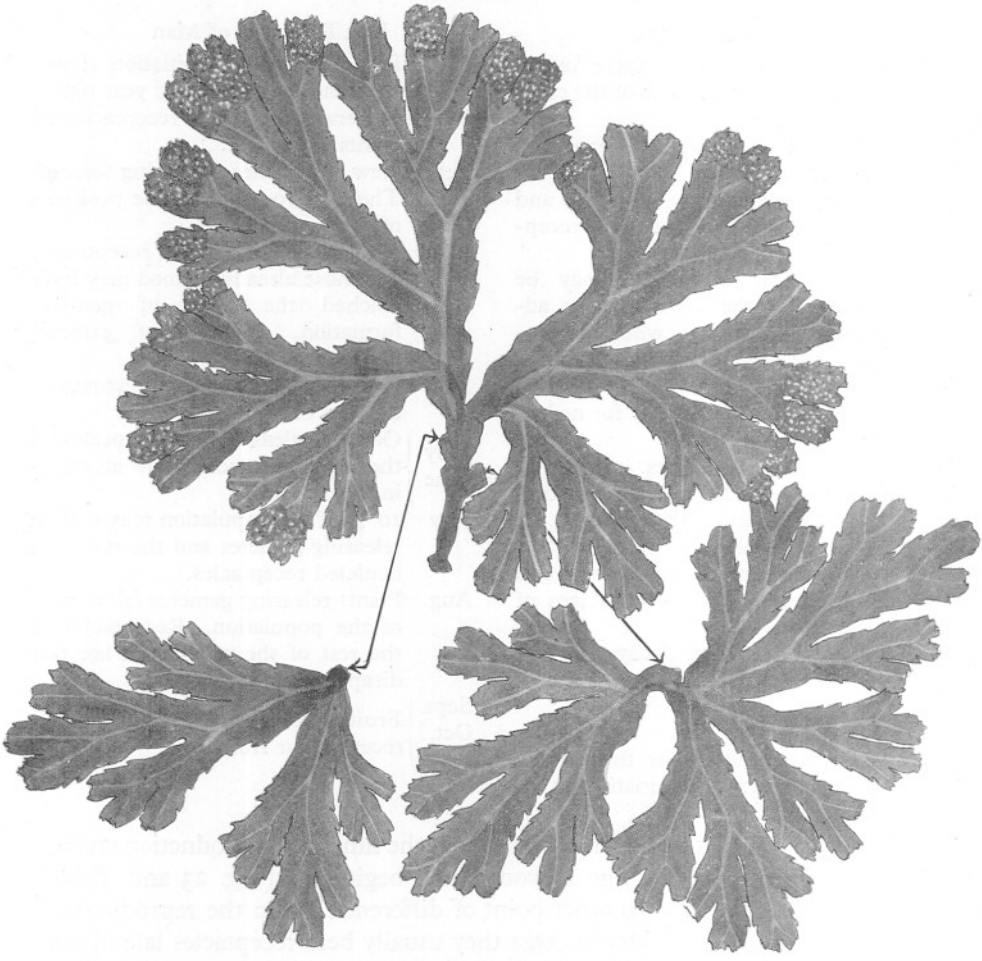

Fig. 21. Plant of *Fucus serratus* from the Manx coast showing distal fruiting in the first year. × 0·29.

With *F. vesiculosus* as with *F. serratus* a higher proportion of young plants fruit within the first year on this coast than on the Devon coast. Clearance was effected, in the first week of August, of a strip running through the *F. vesiculosus* zone. Analysis of the new population 37 weeks later showed that 70 % of young plants over 14 cm. in length bore receptacles. The fruiting branches bore only one or two receptacles. In the second and succeeding years the number of pseudo-lateral fronds destined to bear receptacles increases greatly,

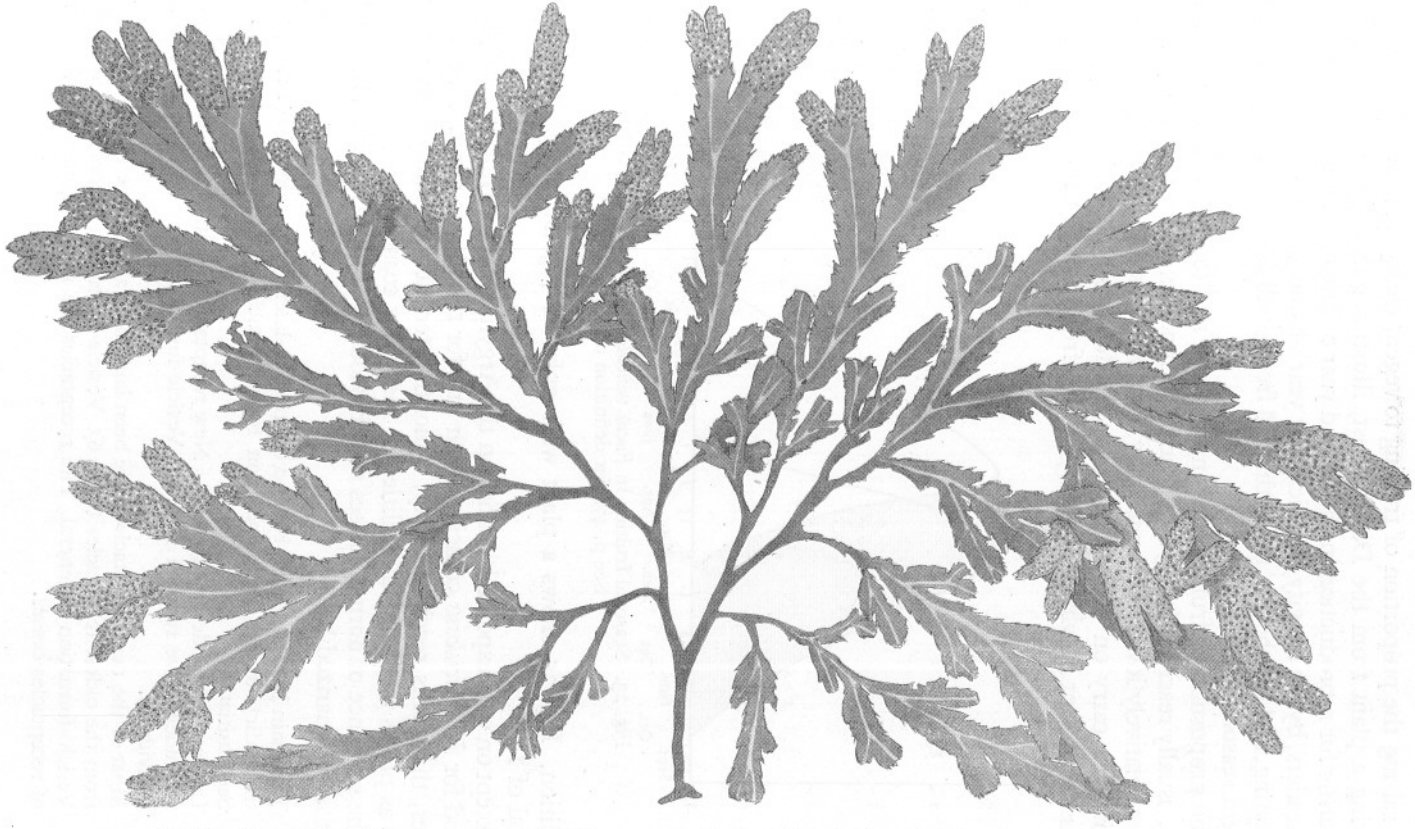

Fig. 22. Plant of *Fucus serratus* from the Devon coast fruiting for the first time in the second year. ×0·29.

thus raising the proportion of fruiting to vegetative tips on the plants. Fig. 24 showing a plant from the Devon coast, illustrates the appearance of plants preparing for reproduction in the second year of growth. Some of the vegetative leaders, by the activity of which next year's frondage will be developed, are projecting, and the shorter, much divided fronds will develop receptacles in the current season.

The proportion of fruiting tips in the third and fourth years may be very high, usually reaching 80–95 % of the total frondage. Some very bushy forms with a relatively low growth-rate may have very few vegetative tips left after fruiting, to carry on development for the following year. Fig. 17 (p. 471) illustrates a plant in which only 18 % of the frond tips remain in a vegetative

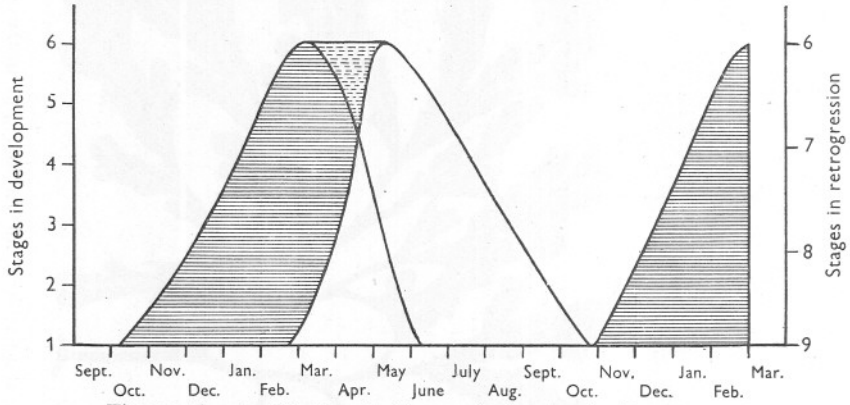

Fig. 23. Seasonal fruiting in *Fucus vesiculosus* on the Devon coast.
See p. 474 for definition of stages.

condition. Fig. 25 shows a plant with only six vegetative tips left out of a total of 158.

Except on very exposed localities on the Argyll coast, the time of the fruiting period for *F. vesiculosus* coincides with that for the Devon coast. In exposed places, the plants reach maturity, a month later, at approximately the same time as plants in sheltered localities on the Manx coast.

The sequence of normal phases of behaviour for *F. vesiculosus* on the Manx coast is summarized below:

Jan. The main leaders project beyond the pseudo-lateral fans, which have completed their dichotomies in preparation for receptacle-initiation. Receptacles have been initiated.

Feb. Leaders still undergo extension. New receptacles are still being laid down, but the oldest have reached stage 3. Vesicle-formation may be initiated in a few individuals.

Mar. Most of the new receptacles have been laid down and release of gametes begins from the oldest receptacles (stage 6). Vesicle-formation becomes more marked.

Apr. Vesicle-formation is general. The receptacles are releasing gametes. Initiation of receptacles ceases.

May The peak period of gamete-release is reached and passed. Leaders have now developed pseudo-lateral fans which are in process of dichotomy at short intervals.
June Gamete-release wanes. Old receptacles have reached stage 7. The form of next season's receptacular fronds is discernible.
July Decay of old receptacular fronds takes place. Many turn yellow and are shed.
Aug. Deterioration of old receptacles is nearly complete. New pseudo-laterals have developed into large fans which form the most conspicuous part of the vegetation, and hide the remains of old fruiting fronds.
Sept. A few old receptacles in stage 8 may still be found. New frondage grows in length.
Oct. Final disappearance of old receptacular fronds and further enlargement of new fans.
Nov. Pseudo-lateral frondage prepares for initiation of new receptacles.
Dec. Tips of lateral fronds begin to thicken for receptacle-formation.

The data for this schedule are drawn from the experiments on the Manx station. The schedule would be applicable to the Devon station if the sequence were shifted back about 1 month.

Defoliation

When fruiting is over for the season, both species rid themselves of all frondage which has fruited. The amount of such frondage dependent on the degree of fruiting may be considerable. When the gametes are all shed from a receptacle, it becomes gelatinous and open to the attack of fungi and animal parasites. It is readily rubbed off by friction against the rock, but actual necrosis of tissues also takes place. Necrosis starts in the receptacle but extends to the subtending internodes. The latter are not under control of an apical cell because the apical cell dies out in the later stages of receptacle-formation. Necrosis works basipetally downwards crossing forks if both arms have borne receptacles and is arrested only when it reaches a fork, one arm of which is still provided with a functional apical cell, however distant. In this way all fruiting fronds are shed; all that remains is the axis bearing vegetative apices from which next season's frondage will be developed. Fig. 11 (p. 464) shows a plant of *F. serratus* fruiting for the first time. The gaps in the illustration indicate the frondage which will be shed. New frondage will be produced from vegetative apices while deterioration of receptacular fronds goes on; in the specimen illustrated all new fronds will originate from the half-dozen apices left on the plant. On the Manx coast fruiting in *F. serratus* is heavy, and it sometimes happens that all the apices may produce receptacles. The plant then pays the penalty of 100 % reproduction, being left without a vegetative leader for the production of new frondage (Fig. 26).

The process of defoliation is more gradual in *F. serratus* than in *F. vesiculosus*. In the former species, after reproduction, the frondage shows broken ends and has a very battered appearance for about a month until the upgrowth of new frondage hides the broken ends. The final stages of deterioration are completely hidden under cover of the new frondage which now becomes the most conspicuous feature of the vegetation.

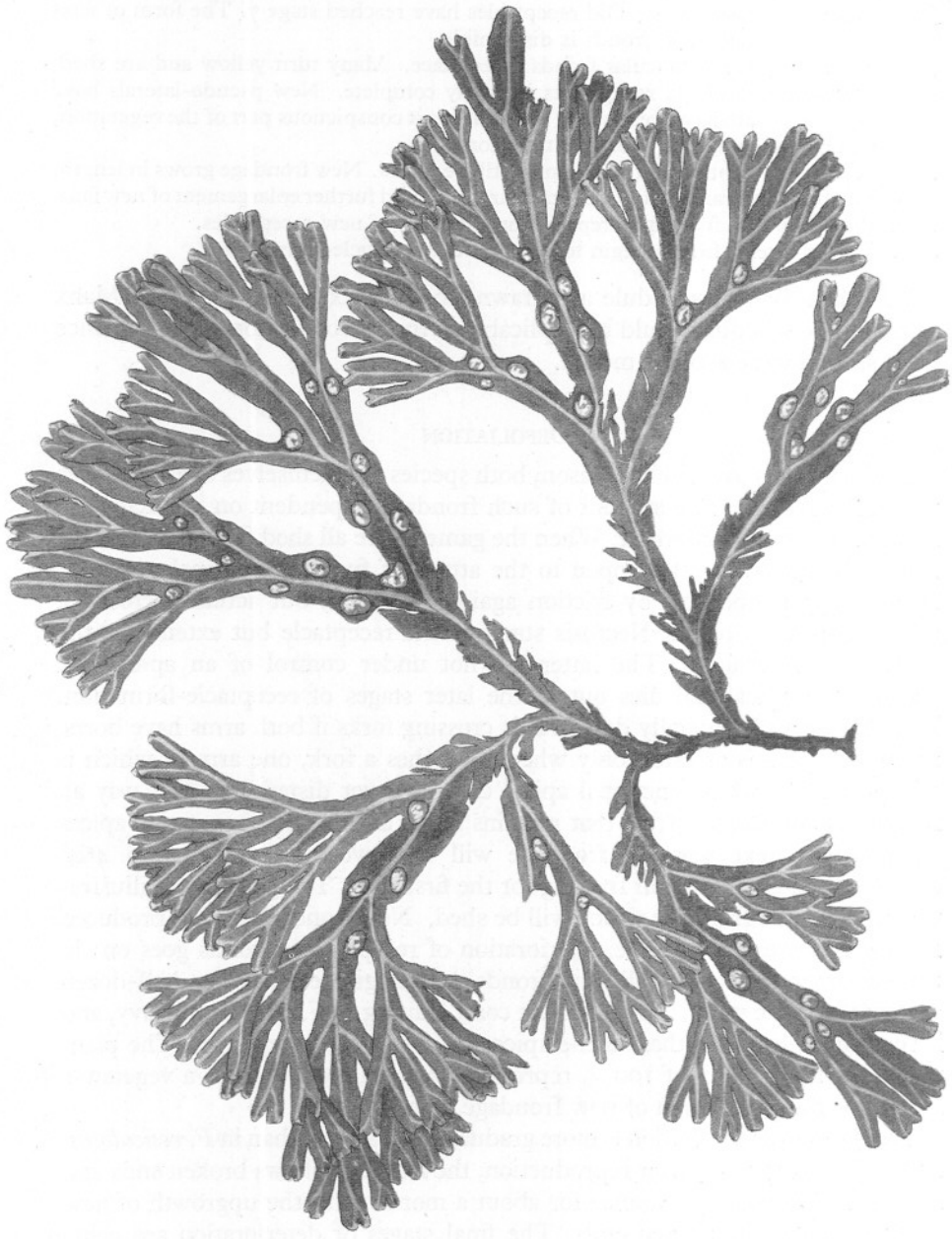

Fig. 24. Plant of *Fucus vesiculosus* from the Devon coast preparing to fruit for the first time in the second year. ×0·275.

In *F. vesiculosus* the pseudo-lateral fronds turn yellow after fruiting. The colour change affects the whole fan simultaneously (Fig. 27); the frond becomes

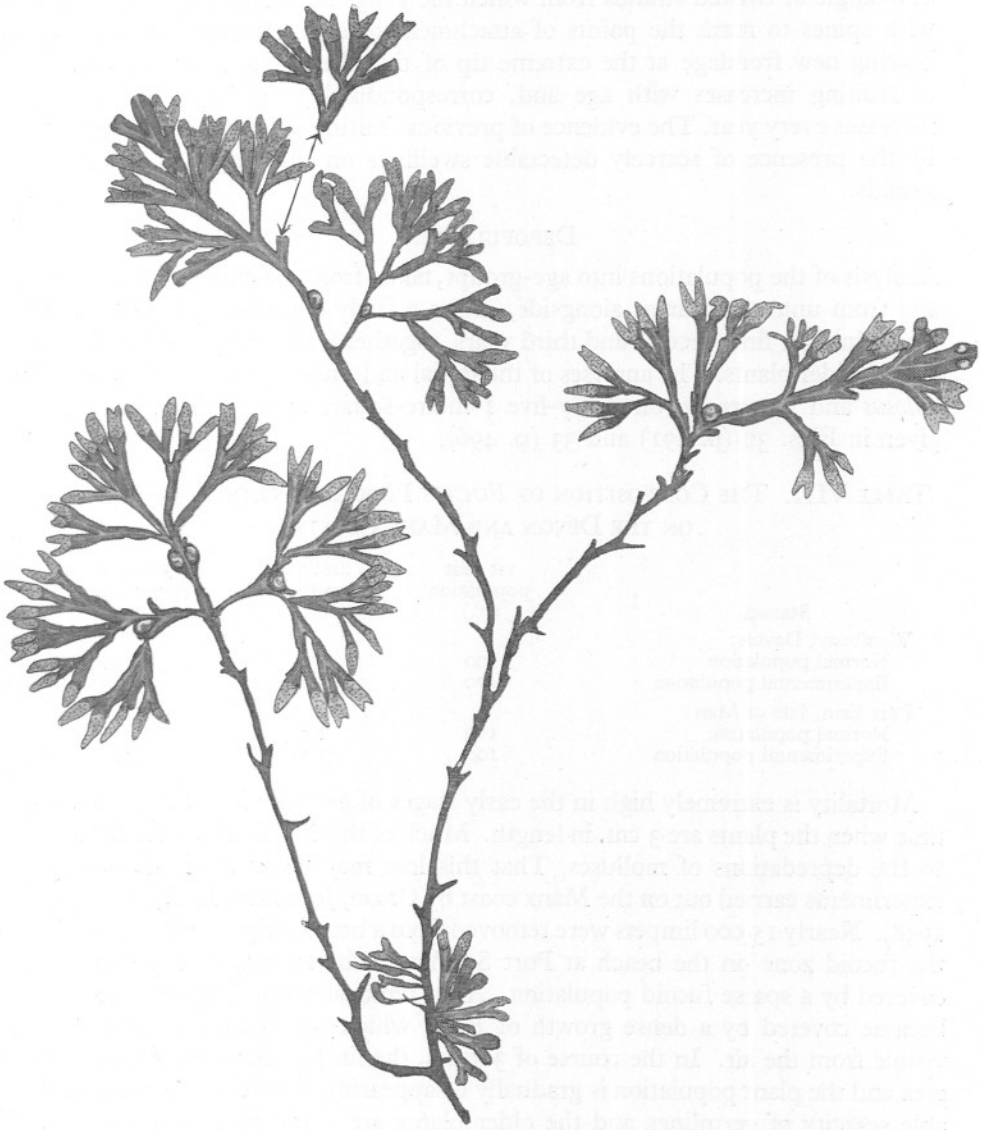

Fig. 25. Plant of *Fucus vesiculosus* with spines' showing the position of excised fronds. Six vegetative leaders only remain. ×0·23.

limp and gelatinous (Fig. 28) and is ultimately shed more rapidly than that of *F. serratus*. During the deterioration stages the new frondage from terminal leaders and from vegetative apices lower on the plant cover the old

fruiting fans, and the effect of defoliation is not so evident as in *F. serratus*. An old plant of *F. vesiculosus* which has fruited several times usually consists of a tangle of twisted strands from which the wings have been denuded, beset with spines to mark the points of attachment of earlier fruiting fronds and bearing new frondage at the extreme tip of the plant (Fig. 25). The degree of fruiting increases with age and, correspondingly, the loss of frondage increases every year. The evidence of previous fruiting on an old plant is given by the presence of scarcely detectable swellings on the length of the main strands.

Depopulation

Analysis of the populations into age-groups, taken from the experimental areas and from untouched areas alongside, shows a fairly consistent proportion of plants in their first, second and third years, together with a very small proportion of older plants. The analyses of the initial and final populations of *F. vesiculosus* and *F. serratus* on thirty-five 1-metre-square areas at Wembury are given in Figs. 30 (p. 491) and 33 (p. 496).

Table VIII. The Composition of *Fucus* Populations in Year-Classes on the Devon and Manx Coasts

Station	1st year population (%)	2nd year population (%)	3rd year population (%)
Wembury, Devon:			
Normal population	100	57	17·3
Experimental population	100	33·8	5·0
Port Erin, Isle of Man:			
Normal population	100	30·8	10·0
Experimental population	100	31·4	9·5

Mortality is extremely high in the early stages of germination and up to the time when the plants are 3 cm. in length. Much of this loss is undoubtedly due to the depredations of molluscs. That this loss may be severe is shown by experiments carried out on the Manx coast by Orton, Jones and Lodge (Lodge, 1948). Nearly 15,000 limpets were removed from a broad strip running through the fucoid zone on the beach at Port St Mary. The zone was only scantily covered by a sparse fucoid population. After removal of the limpets the zone became covered by a dense growth of *Fucus* which was thick enough to be visible from the air. In the course of 3 years, the limpets have reinvaded the area and the plant population is gradually disappearing. There is now a noticeable scarcity of germlings and the older plants are dying out. A large proportion of the plants reaching the end of their first year are lost during the second year, and only a small proportion survive to the third year. The proportions vary with the physical risks of the environment and depopulation rate rises with exposure. The Devon and Manx areas are compared in Table VIII.

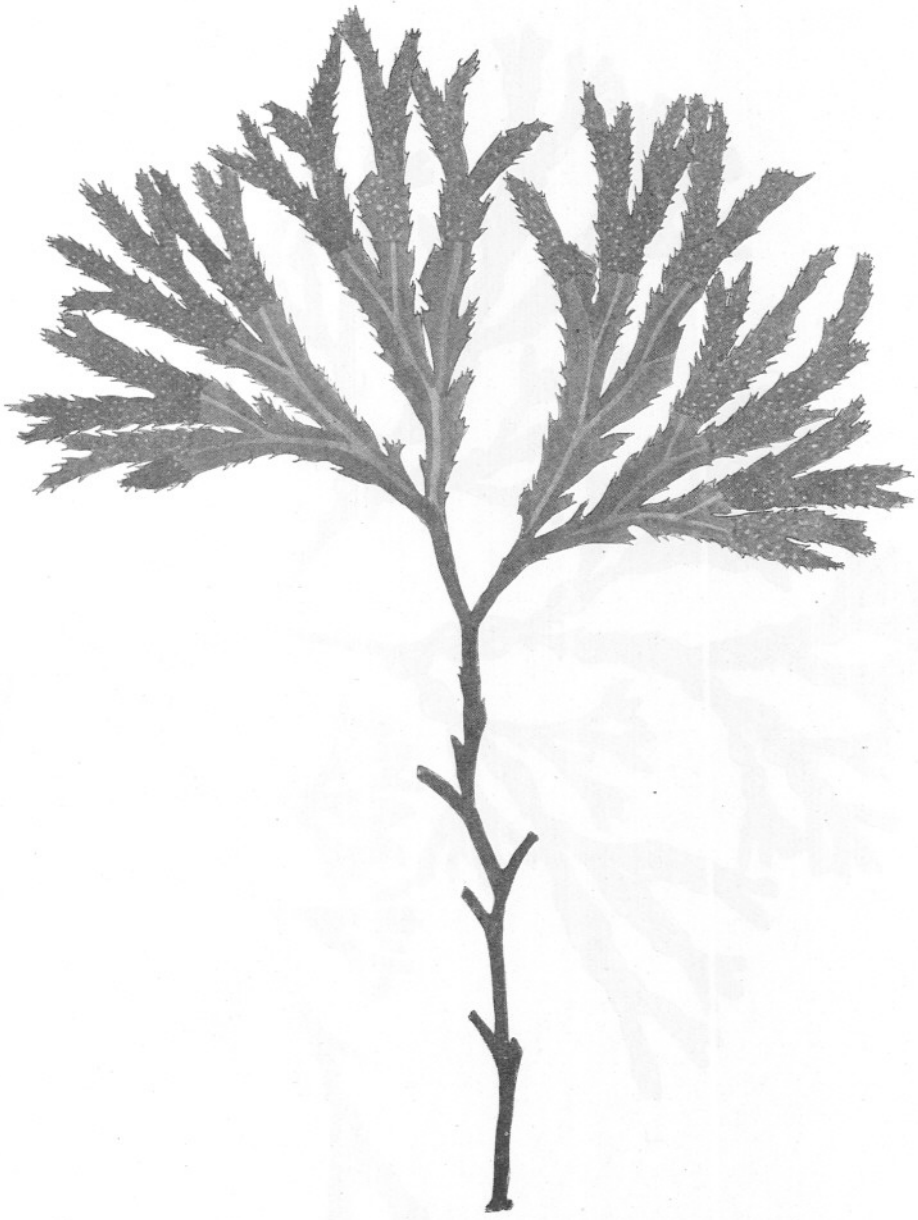

Fig. 26. Plant of *Fucus serratus* in which copious fruiting has left no vegetative apex for further frond-development. ×0·275.

Fig. 27. Defoliation in a plant of *Fucus vesiculosus* from the Manx coast. The fruiting fans turn yellow and will be ultimately shed. ×0·29.

In assessing the age-groups in the population, the number of first year plants is taken as 100 %, whatever it may be, and the numbers of plants in the other age-groups taken as percentages of it.

It appears that the experimental and normal populations on the Manx station agree very well. On the Devon coast there is some difference between

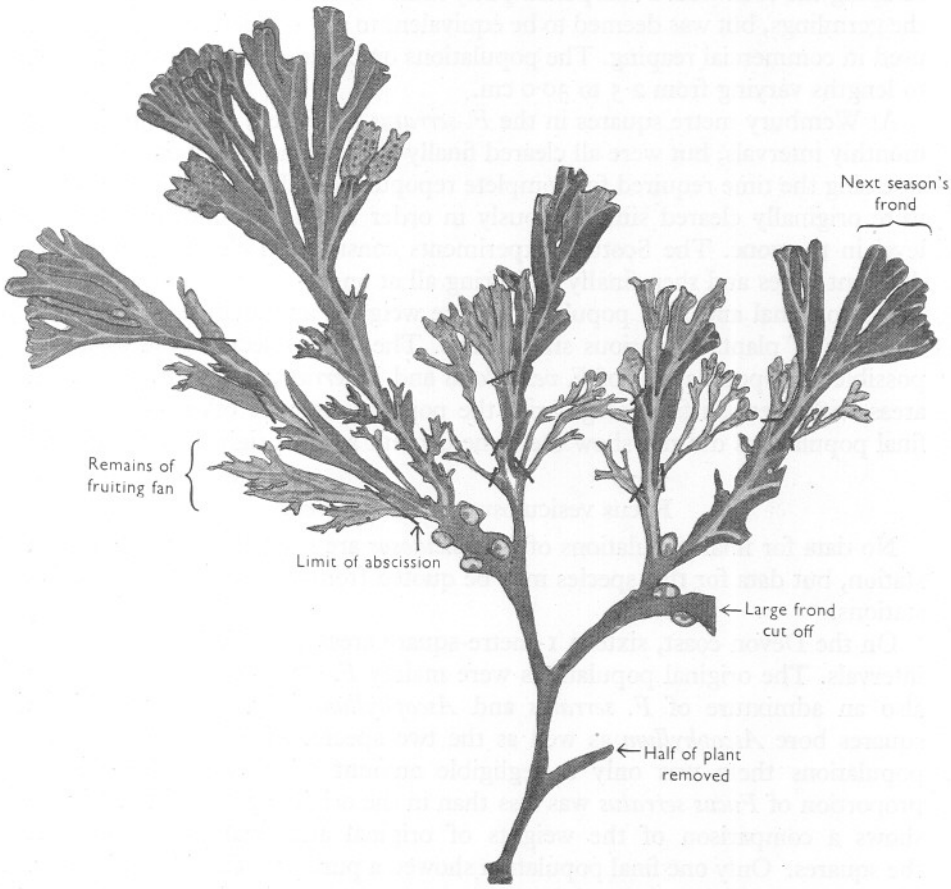

Fig. 28. Plant of *Fucus vesiculosus* showing a late stage in deterioration of the fruiting fans. The limit of abscission is marked by thick lines across the frond. The vegetative leaders are undergoing dichotomies to form next season's fruiting fans. ×0·295.

the two populations. It can be assumed that the fucoid population on the Manx coast, which is exposed, returns to normal after an interval of 3 years from the original clearance, but 4 years would probably be needed before the population returns to normal on the Devon coast.

Repopulation

In order to test the effect of reaping, a series of experiments were undertaken in all three areas. Selected plots either in the form of strips or individual squares at various levels were used for experiment. Some were cleared by scraping the rock with a sharpened putty knife. This did not completely clear the germlings, but was deemed to be equivalent to any method which might be used in commercial reaping. The populations on other squares were cut down to lengths varying from 2·5 to 30·0 cm.

At Wembury metre squares in the *F. serratus* zone were cleared initially at monthly intervals, but were all cleared finally at the same time, with a view to assessing the time required for complete repopulation. The strips at Port Erin were originally cleared simultaneously in order to find the most productive level in the zone. The Scottish experiments consisted in clearing squares at different times and then finally reclearing all at once.

The original and final populations were weighed and analysed to find the numbers of plants in various size groups. The areas selected bore as far as possible pure populations of *F. vesiculosus* and *F. serratus*, but in the strips on areas with great surface irregularity the populations were often mixed. The final populations did not show the same content as the original populations.

Fucus vesiculosus *on cleared areas*

No data for final populations of *F. vesiculosus* are available from the Manx station, but data for this species may be quoted from the Devon and Scottish stations.

On the Devon coast, sixteen 1-metre-square areas were cleared at monthly intervals. The original populations were mainly *F. vesiculosus*, but there was also an admixture of *F. serratus* and *Ascophyllum* (Fig. 29). Five of the squares bore *Ascophyllum* as well as the two species of *Fucus*. In the final populations there was only a negligible amount of *Ascophyllum* and the proportion of *Fucus serratus* was less than in the original populations. Fig. 29 shows a comparison of the weights of original and final populations on the squares. Only one final population showed a pure growth of *F. vesiculosus*. The clearance of the squares in sequence gave opportunity for the settlement of eggs from whichever species was in fruit at the time of clearance, but despite the fact that some of the squares were cleared when *F. serratus* was in fruit and *F. vesiculosus* in the almost sterile condition, the final populations, after a lapse of nearly 3 years, consisted mostly of *F. vesiculosus*.

The total original weight on all the squares was 108·6 kg., and the final weight was 107·1 kg., thus giving a net loss of 1·5 kg. The period of experiment varied for each square, but the interesting fact emerges that, with the exception of square 16, the weights in the final populations exceed those in the original populations on those squares which had the shortest experimental periods.

Square 6 was cleared sixth in the series and was re-cleared later than some of the other squares. It had therefore the longest experimental period of 34 months, yet the final population weighed only 7·4 kg. compared with 9·0 kg. in the

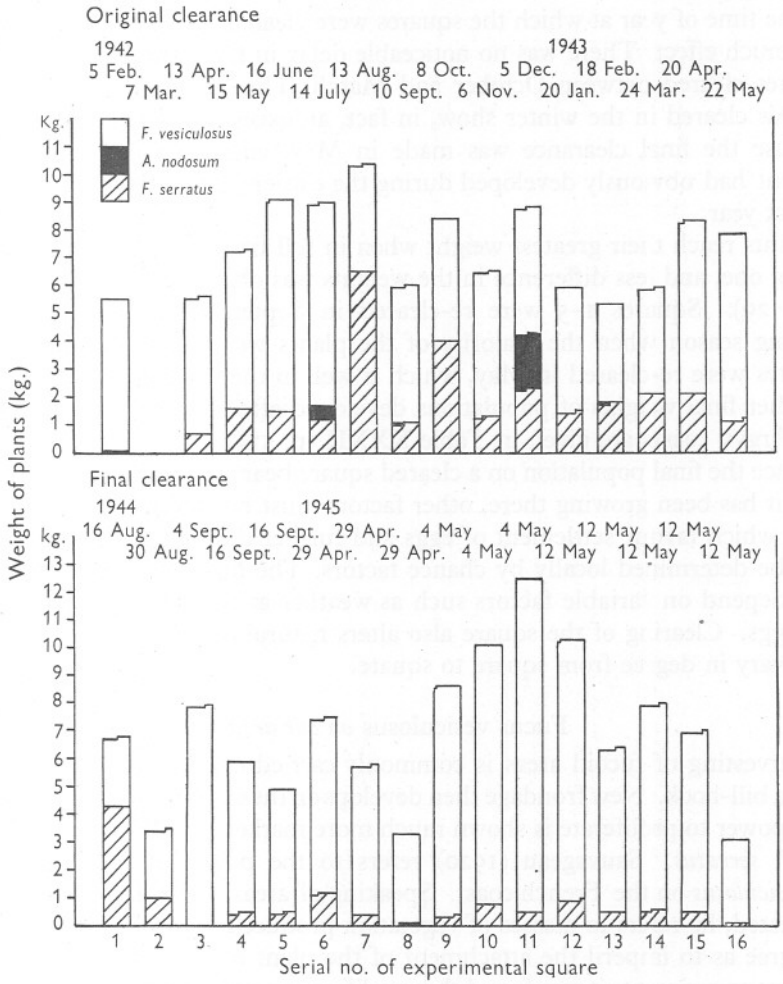

Fig. 29. The repopulation of cleared areas by *Fucus vesiculosus* on the Devon coast. Original and final weights of plants on sixteen 1-metre-square areas at Wembury.

original population. Fig. 30 shows an analysis of the plant populations in size groups at the beginning and end of the experiment. Though the total weight of the final populations is slightly less than that of the original populations, the number of plants in the final populations is much greater than in the original populations (Table I, p. 444). In grouping the plants, 27 cm. was taken as the length of a first-year plant, 55 cm. as the length of a plant at

the end of its second year, and over 55 cm. for plants older than 2 years. The lengths were based on growth-rate as determined by experiment. The increase in numbers in the final populations is due largely to the much greater number of young plants.

The time of year at which the squares were cleared does not appear to have had much effect. There was no noticeable delay in the return of germlings to squares cleared between October and March. The squares with the shorter periods cleared in the winter show, in fact, an excess of young plants, partly because the final clearance was made in May, and the young plants then present had obviously developed during the earlier part of the fruiting period of that year.

Plants reach their greatest weight when in full fruit. The fruiting period is a long one, and less difference in the weights was obtained than was expected (Fig. 29). Squares 1–5 were re-cleared in September at the end of the fruiting season when the majority of the plants were sterile; the remaining squares were re-cleared in May, which is well in the fruiting season.

Other final weights of populations developed after clearance on the Devon and Argyll coasts are given in Table XXXII (p. 513).

Since the final population on a cleared square bears no simple relation to the time it has been growing there, other factors must be considered. The conditions which favour settlement of eggs and further development of sporelings may be determined locally by chance factors. The final population may very well depend on variable factors such as weather at the time of settlement of the eggs. Clearing of the square also alters natural conditions and its effects may vary in degree from square to square.

Fucus vesiculosus *on cut areas*

Harvesting of fucoid areas is commonly carried out by cutting the fronds with a bill-hook. New frondage then develops on the cut fronds by proliferation. The power to proliferate is shown much more markedly by *F. vesiculosus* than by *F. serratus*. Sauvageau (1920) refers to the power of proliferation by *F. vesiculosus* on the French coast. Speaking of areas where *Fucus* is regularly harvested, he refers to masses of vegetation produced by proliferation to such a degree as to imperil the attachment of the plant to the substratum. In the present experiments it was found that proliferation took place only from fronds which were provided with an apical cell at the time of breakage, that is, that no proliferation will take place on frondage which had produced receptacles. The size of the proliferation-frondage depends on the age of the cut fronds. Proliferation from young frondage will produce frondage of normal size, but, with increasing age of the cut frondage, the proliferated fronds are more and more stunted and may indeed be extremely minute. Proliferated frondage from an old part of the plant has been noted, which was no longer than 2 cm. and bore minute receptacles less than 0·3 cm. long. It is obvious that in

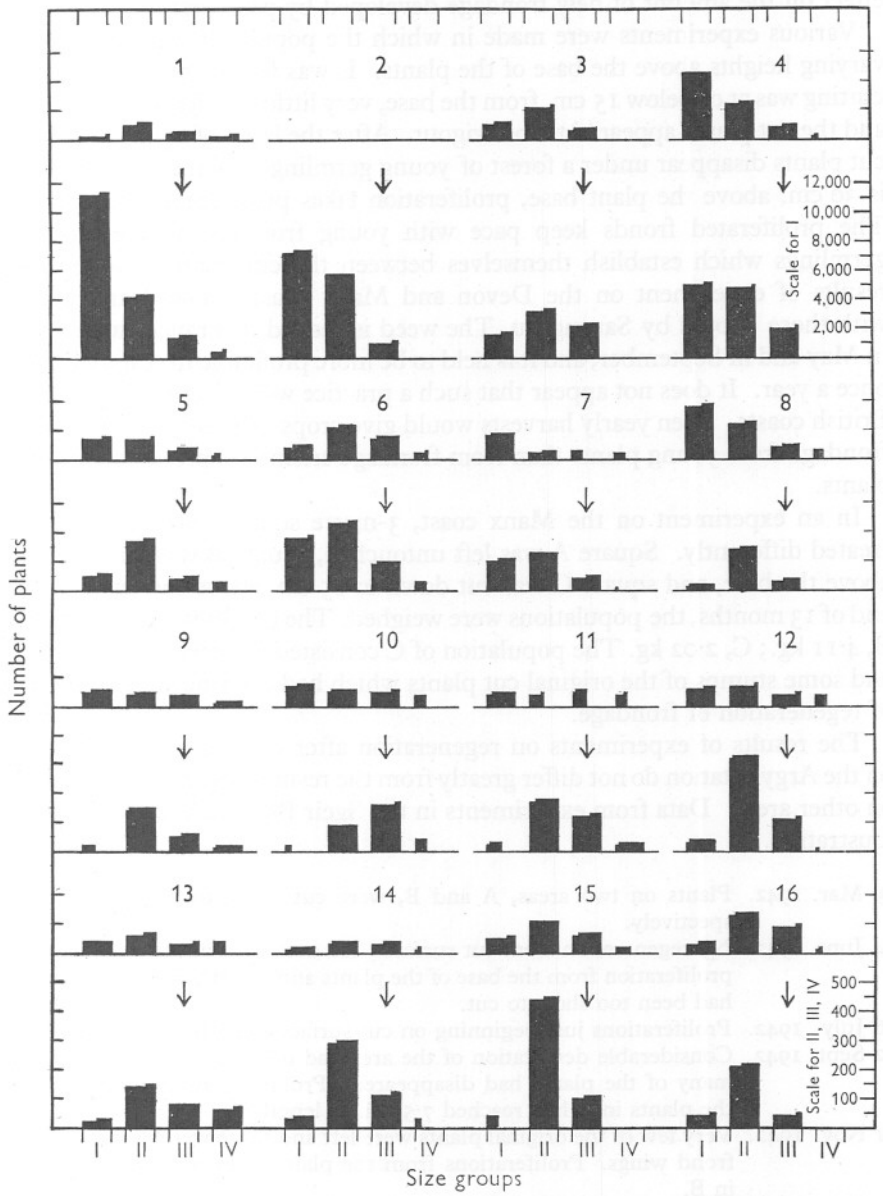

Fig. 30. The repopulation of cleared areas by *Fucus vesiculosus* on the Devon coast. Original and final numbers of plants in size-groups on sixteen 1-metre-square areas at Wembury. Size-groups as follows: I, under 10 cm. in length; II, 10–27 cm.; III, 27–55 cm.; IV, 55 and over. Scale for group I (top right corner) is reduced by a factor of 20.

reaping by cutting, the height of the cut above the base of the plant will have an effect on the amount of new frondage developed by proliferation.

Various experiments were made in which the population was cut down to varying heights above the base of the plants. It was found that, if the level of cutting was at or below 15 cm. from the base, very little proliferation took place, and the cut plants appeared to lose vigour. After the lapse of a year or two, the cut plants disappear under a forest of young germlings. If the level of cutting is 30 cm. above the plant base, proliferation takes place readily and rapidly. The proliferated fronds keep pace with young frondage arising from the germlings which establish themselves between the cut plants. None of the results of experiment on the Devon and Manx coasts showed any parallel with those quoted by Sauvageau. The weed is reaped in France twice a year, in May and in September, and it is held to be more profitable to reap twice than once a year. It does not appear that such a practice would be profitable on the British coasts. Even yearly harvests would give crops consisting of much more frondage from young plants than from frondage arising by proliferation of cut plants.

In an experiment on the Manx coast, 3-metre squares side by side were treated differently. Square A was left untouched, square B was cut to 30 cm. above the base, and square C was cut down to 15 cm. above the base. At the end of 13 months, the populations were weighed. The results were: A, 4·76 kg.; B, 4·11 kg.; C, 2·02 kg. The population of C consisted entirely of young plants and some stumps of the original cut plants which had done nothing in the way of regeneration of frondage.

The results of experiments on regeneration after cutting for *F. vesiculosus* on the Argyll station do not differ greatly from the results of similar experiments on other areas. Data from experiments in the Sgeir Bhuidhe area will serve as illustration.

19 Mar. 1942. Plants on two areas, A and B, were cut down to 8 and 15 cm. respectively.

4 June 1942. No regeneration from cut surfaces had occurred, but there was a little proliferation from the base of the plants and growth from fronds which had been too short to cut.

16 July 1942. Proliferations just beginning on cut surfaces of plants on A and B.

12 Sept. 1942. Considerable devastation of the area had occurred in the interval and many of the plants had disappeared. Proliferations from the base of the plants in B had reached 7·5 cm. in length.

11 Nov. 1942. Very few of the original plants were left and those were denuded of the frond wings. Proliferations from the plant bases had reached 15 cm. in B.

6 Feb. 1943. More deterioration had occurred in the cut population and the stumps were almost hidden under a growth of new plants.

From this point on progressive deterioration followed, and at last there were none of the original cut plants left. It is obvious that no profit would result by

cutting the population at levels less than 30 cm. above ground. In any case the great bulk of the returning population is derived from the upgrowth of new plants.

Fucus serratus *on cleared areas*

A strip, 1 m. wide, running through the entire belt of *F. serratus* was cleared at Port Erin in July 1941. In its upper levels the population of the strip was mixed *F. serratus* (dominant), *Ascophyllum* and *Fucus vesiculosus*. The middle section was pure *F. serratus* and the lower levels ran into the top of the *Laminaria digitata* zone. That part of the strip which carried a pure population of *Fucus serratus* was 9 m. long. The two uppermost squares on the strip were covered by boulders after a storm, but the rest of the strip escaped much interference.

The total weight of the plant population was initially 170 kg., of which 47 kg. was due to *Ascophyllum*. The final weight of the population was 92 kg., representing a total loss in weight of 78 kg. This deficit is in part explained by the fact that *Ascophyllum* did not regenerate itself on the cleared area during the period of the experiment. Sporelings appeared in small numbers and reached a length of a few cm., but inevitably disappeared again. Even at this date, 8 years after the original clearance, there is still no sign of the establishment of an *Ascophyllum* population. There are on an average 20 sporelings of *Ascophyllum* per m^2., the longest of which is only 13·5 cm. Fig. 31 and Table XXXIV (p. 514) show the analyses of the weights and numbers of the final and original populations. A summary of the proportions of the component algae is shown below:

	Original population (kg.)	Final population (kg.)
Total weight	170	92
F. vesiculosus	1	4
F. serratus	87	71
Ascophyllum	47	0
Laminaria	32	17

The *Fucus* population might have been expected to gain advantage by the improvement in lighting of the strip by the removal of the *Ascophyllum*; there is an increase of 3 kg. in the weight of *Fucus vesiculosus* when its competitor *Ascophyllum* was removed and failed to return, but this slight advantage is balanced by the decreased weight of *Fucus serratus* in the final population. There is no permanent population of *Laminaria* at this level on the shore, as the young plants are frequently removed and replaced. Rough weather caused considerable fluctation in the amount of *Laminaria* above L.W.N.T. *L. digitata*, 90 cm. long, was recorded at interim observations, but the long plants had all disappeared when the strip was finally cleared in April 1944. The data from a repopulation experiment from Wembury involving nineteen 1-metre squares, F.S.H. 1–3 and F.S.L. 1–16, may be used to illustrate recolonization on the

Devon coast. Figs. 32 and 33 give a comparison of weights in the original and final populations and analyses of the numbers of plants in various size groups.

A summary of the data is given below:

	Original population (kg.)	Final population (kg.)
Total weight	137·7	133·0
F. serratus	137·4	131·7
F. vesiculosus	0·3	0·5
Laminaria	—	0·8

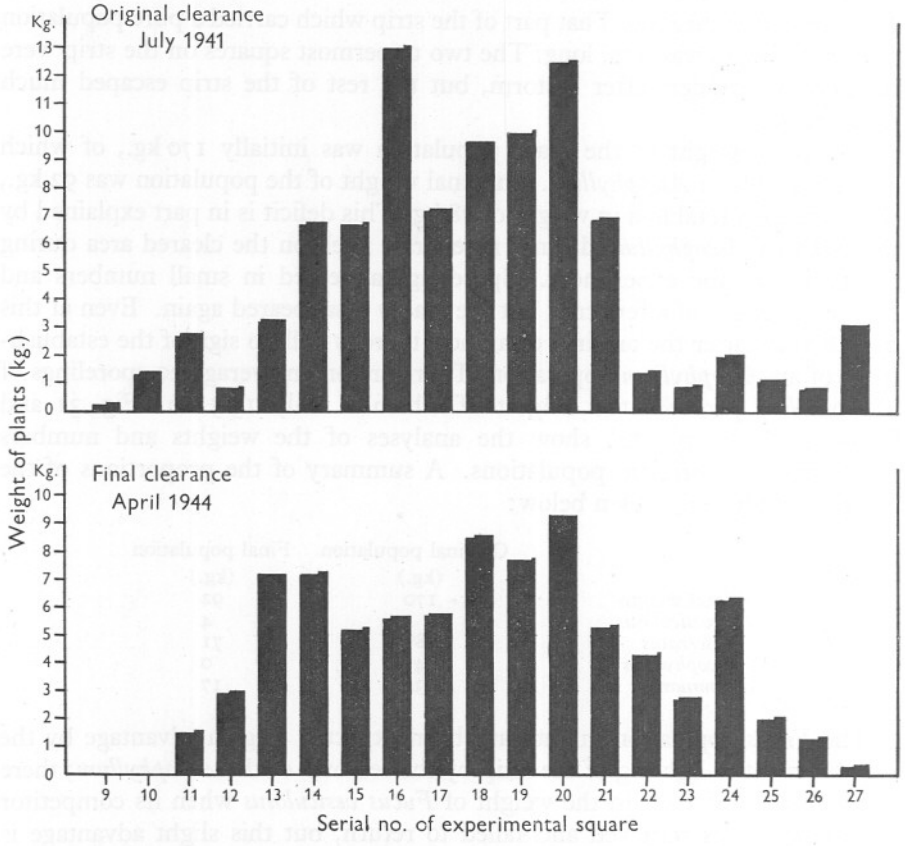

Fig. 31. The repopulation of cleared areas by *Fucus serratus* on the Manx coast. Original and final weights of plants on nineteen 1-metre-square areas at Port Erin.

The Devon population on the *Fucus serratus* squares was much more nearly a pure *F. serratus* population than that on the Port Erin station. There was no *Ascophyllum* present, and the final weight was only 4·7 kg. short of the original weight.

Other final weights of populations, developed after clearance on the Devon and Argyll coasts, are given in Table XXXII in the Appendix (p. 513).

Fucus serratus *on cut areas*

The results of experiments in which the vegetation was truncated do not differ greatly from those with *F. vesiculosus*. As with the latter species, the areas of *F. serratus* showed normal growth of apices which were too short to be cut. The removal of a large percentage of the apical cells by cutting seems to be detrimental to the tone of the plant. Denudation of the wings of the fronds

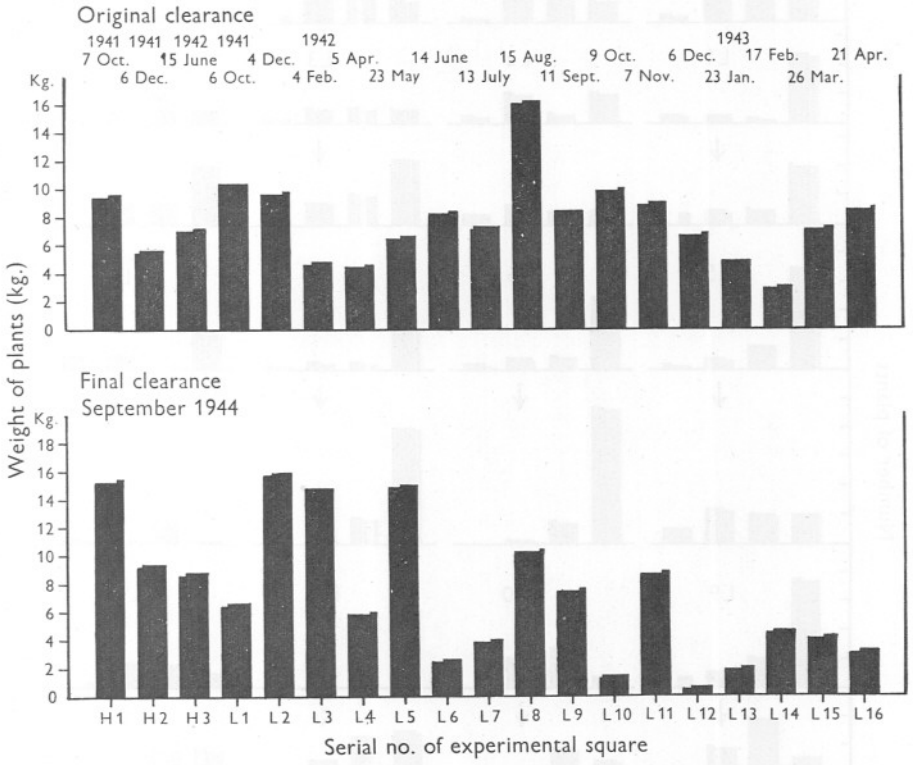

Fig. 32. The repopulation of cleared areas by *Fucus serratus* on the Devon coast. Original and final weights of plants on nineteen 1-metre-square areas at Wembury.

is marked, and the plant is readily infected by epiphytic algae. The growth of the uncut shoots keeps pace with the elongation of young plants which develop on the experimental plots if the original truncation was made at a height of 30 cm. from the base of the plant. When the level of cutting was 15 cm. from the base, the rate of elongation of uncut fronds was less than that of young plants. The explanation of the difference lies in the age of the cut frondage. Cutting at a level of 15 cm. leaves only old portions of large plants. These lower parts of the plant have much less vigour of growth than the younger distal frondage. On cut fronds of *F. serratus* it is only rare that proliferations

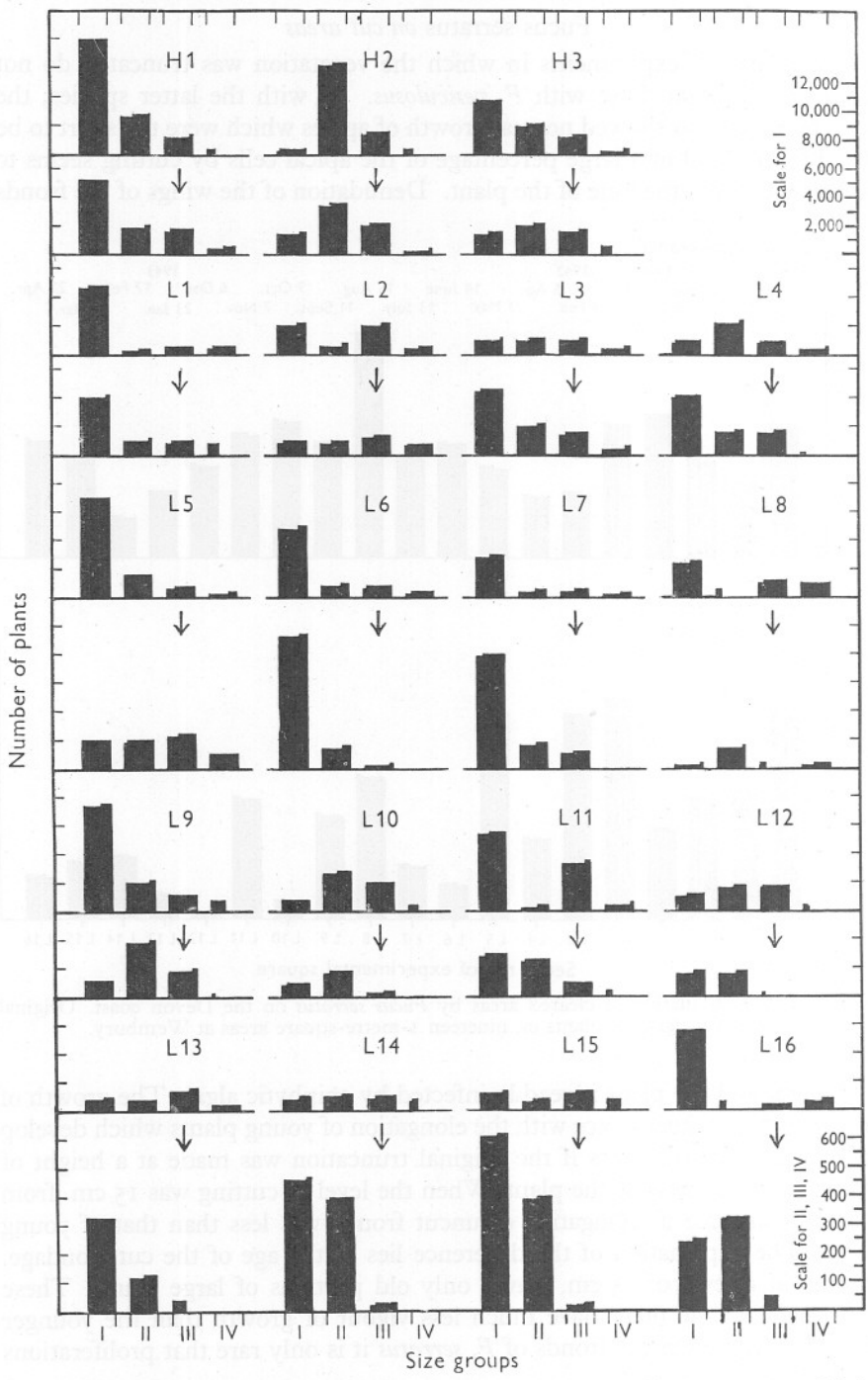

Fig. 33. The repopulation of cleared areas by *Fucus serratus* on the Devon coast. Original and final numbers of plants in size-groups on nineteen 1-metre-square areas at Wembury. Size-groups as follows: I, under 10 cm. in length; II, 10–27 cm.; III, 27–55 cm.; IV, 55 cm. and over. Scale for Group I (top right corner) is reduced by a factor of 20.

occur on the bare midribs or on the cut surfaces of the fronds. In this respect the species differs from *F. vesiculosus* which proliferates readily.

From such experiments in cutting which have been done in this investigation, it would appear that reaping every 2 years would give the best results. There is no advantage in waiting for plants of larger growth because the depletion rate for large plants is too high to permit of any advantage. A good uniform population of young plants develops in one year, but they are very light; the second year population has a greatly increased bulk, but the depletion rate rises. New populations grow very rapidly on cleared areas, and it does not appear that cutting off the tops of the plants rather than removing them bodily would give any advantage, especially with *F. serratus*.

From records which are available it seems that the cutting of fucoids is usually annual, and on the coast of France weed is reaped twice in the year. Whether that is done because there is a better total yield from areas treated in this way or because the weed is needed every year is not stated. The reaping referred to in the literature is probably a mixed crop of *Ascophyllum* and the two species of *Fucus*. No mention is made of how much of the area is reaped at one time. It would appear from the results of the present experiments that the best yield might be gained by reaping alternate areas at intervals of 18 months to 2 years.

Sauvageau (1920) makes reference to the view held by the French weed-cutters that weed reaped in the spring is of greater value as a fertilizer than weed reaped in the autumn. There is no reference to which component of the weed is meant in this statement. In the spring, both *F. vesiculosus* and *Ascophyllum* would be fruiting and might be considered to be in a state of greatest vigour, but this could not apply to *Fucus serratus*. Further research is obviously needed into the seasonal change of chemical content of the weed at various ages, and especially changes related to the onset and development of the reproductive stages.

Conclusion

Concentration on details of seasonal behaviour of two species of marine algae over an extended period of time has revealed some facts which were not known before. The interest of the records lies not only in their novelty, but also in the speculation to which they may give rise.

One is familiar with the alternation of reproductive and vegetative phases in land plants, but with the two species of *Fucus* under discussion, the seasonal rhythms stand opposed to one another; the vegetative season of one coincides with the reproductive season of the other species. The actual physical components of the environment which control the onset of reproduction are as yet unascertained.

It is also somewhat surprising to find that the familiar monopodial and sympodial branching of land plants have their counterparts in the sea; and

that something very like an axial gradient is shown by the basipetally increasing latency of apices in *F. serratus*.

The degree of apical control on subperipheral frondage is also well marked. Apical controls are exerted on the stature of proliferations from various levels in the plant body, and on the arrest of necrosis of tissue following reproduction, at a point where one arm of a dichotomy is still provided with an apical cell. In the development of receptacles an antithesis between vegetative elongation and reproduction is shown by the fact that in *F. vesiculosus* gametangia are not laid down in the receptacle until the apical cell has ceased to function and the apical groove has flattened out.

It is interesting to reflect that in the course of a long evolution in the sea, such relatively 'simple' marine plants as these two species of *Fucus* have developed growth rhythms, habits of branching, controlled defoliation after fruiting, and apical control of remote parts of subtending tissue, in a degree comparable to that shown by land plants with an entirely different history.

Summary

A certain variation in level of the fucoid zone with latitude is demonstrated. The belt of *Fucus vesiculosus* and *F. serratus* lies lower on the Devon coast than on either the Manx or the Argyll coast.

The conditions for the optimum germination of fertilized eggs are dissimilar to those for maximum rate of frond-extension.

Normal growth-rates have been established for both species for the first 3 years of life. In *F. vesiculosus* the average rate of elongation per week is 0·48 cm. on the Devon coast, 0·45 cm. on the Manx coast and 0·68 cm. on the Argyll coast. In *F. serratus* the average rate of elongation per week is 0·49 cm. on the Devon coast, 0·68 cm. on the Manx coast and 0·85 cm. on the Argyll coast. The rate of growth is shown to vary with the conditions of the environment. Shelter from rough water tends to enhance growth-rate, and there is an indication that greater stature is achieved by the plants from the Argyll station than from either of the other stations.

Growth-rate in the second and subsequent years shows a rhythm induced by alternating emphasis on receptacle-formation and frond-extension.

The rate of forking is shown to be encouraged by conditions of exposure, but is unaccountably greater on the Devon coast for both species.

The existence of a morphological rhythm showing latent superiority of growth-potential by one arm of a dichotomy, alternating from side to side of the thallus at each successive dichotomy has been demonstrated.

Continued frond-extension in *F. serratus* has been shown to proceed by a kind of relay-system. Distal frondage becomes largely receptacular and further elongation of the plant is brought about by the renewed activity of subperipheral apices.

Frond-extension in *F. vesiculosus* is due to continued elongation of primary and secondary leaders which may produce reproductive fans in pseudo-lateral positions but always maintain one peripheral leader.

The range of variation shown by *F. vesiculosus* in number and position of vesicles is illustrated and its significance discussed.

The sequence of stages in receptacle-formation is defined. The incidence of fruiting is compared for the two species and for various stations. *Fucus serratus* is shown to have a wider range of fruiting time in relation to geographical locality.

The excision of depleted receptacular frondage is achieved by necrosis of tissue, working basipetally until stopped at a dichotomy, one arm of which is still under the control of a functional apex, however distant.

Depopulation brought about by accidental removal of plants in rough weather is shown to be considerable.

Repopulation in relation to the time factor is discussed on data from the three stations.

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APPENDIX

TABLE IX. GROWTH-RATE BY MARKED PLANTS OF *FUCUS VESICULOSUS* AT WEMBURY

Square 14 on strip

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Increase in no. of tips	Growth-rate per week (cm.)
A 1	287	26·0	7	517	0·69
2	364	36·0	9	628	0·71
3	512	27·0	9	218	0·36
4	377	40·0	12	1761	0·74
5	338	19·0	9	625	0·36
6	157	19·5	5	—	0·87
7	186	23·5	8	521	0·88
B 1	32	4·5	2	—	1·0
2	32	3·5	1	—	0·75
3	58	6·5	1	—	0·78
4	383	27·0	10	—	0·49
5	58	4·5	4	—	0·52
6	165	8·5	2	—	0·31
C 1	32	7·0	0	—	1·55
2	191	13·0	5	—	0·46
3	58	9·5	2	—	1·14
4	221	7·0	3	—	0·22
5	235	6·0	6	—	0·17
6	134	8·0	1	—	0·41
7	105	3·5	2	—	0·23
8	193	11·5	5	—	0·40

Average elongation-rate, 0·62 cm. per week.

TABLE X. GROWTH-RATE BY MARKED PLANTS OF *FUCUS VESICULOSUS* AT WEMBURY

Square 16A on strip

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Growth-rate per week (cm.)
1	810	34·0	11	0·29
2	249	19·0	7	0·53
3	633	34·0	17	0·37
4	664	33·0	13	0·34
5	810	56·5	21	0·48
6	563	40·0	10	0·49
7	371	21·5	4	0·40

Average elongation rate, 0·41 cm. per week.

TABLE XI. GROWTH-RATE BY MARKED PLANTS OF *FUCUS VESICULOSUS* AT WEMBURY

Fucus vesiculosus, areas 1 and 2

Plant no.	Length (cm.)			No. of dichotomies		Duration of exp. in days	Growth-rate per week (cm.)
	Initial	Final	Increase	Initial	Final		
Area 1: 725	34·0	31·0 F.	−3·0	9	9	931	—
		48·0 M.	14·0	9	12	461	0·21
727	36·0	54·0	18·0	9	26	688	0·18
284	9·0	35·0	26·0	2	13	654	0·26
705	46·0	71·0	15·0	18	24	546	0·32
710	22·0	35·5	13·5	6	11	490	0·19
726	16·0	27·5	11·5	5	8	385	0·20
740	26·0	55·0	29·0	6	20	654	0·31
707	44·0	51·0	7·0	16	15	210	0·23
708	24·0	31·5	7·5	10	18	325	0·16
720	45·0	56·0	11·0	17	23	210	0·36
724	22·0	32·5	10·0	5	9	325	0·21
728	43·0	62·5	19·5	11	21	268	0·50
742	29·0	33·0	4·0	5	10	325	0·08
743	48·0	72·0	24·0	11	24	414	0·40
744	38·0	55·0	17·0	14	20	325	0·36
750	44·0	59·5	15·5	18	25	268	0·40
150	18·0	20·5	2·5	3	4	210	0·08
151	14·5	17·8	3·3	1	1	182	0·12
Area 2: 1	82·0	96·0	14·0	32	37	309	0·29
8	71·0	81·0	10·0	21	24	183	0·38
11	76·5	79·0	2·5	27	29	94	0·17
16	67·0	70·0	3·0	24	24	94	0·22
17	71·5	85·0	13·5	18	21	183	0·51
72	13·0	28·5	15·5	3	8	324	0·33
82	25·0	46·0	21·0	6	16	385	0·38
86	46·0	54·0	8·5	12	17	309	0·17
88	26·5	51·0	24·5	7	15	324	0·52
4	49·5	87·0	37·5	15	26	619	0·42
5	37·0	66·0	29·0	14	25	619	0·32
22	50·0	66·0	16·0	15	22	619	0·18
14	75·0	103·0	28·0	19	32	493	0·39
13	104·0	114·5	10·5	33	41	124	0·59
64	19·5	67·0	47·5	4	20	619	0·53
65	61·0	99·0	38·0	19	33	493	0·53
66	38·5	82·0	43·5	6	22	619	0·49
77	28·0	43·0	15·0	9	14	428	0·24
83	19·5	31·0	11·5	4	9	435	0·18
90	69·0	75·0	6·0	20	19	156	0·26
91	59·0	91·0	32·0	14	31	588	0·38
3	38·0	73·0	35·0	13	24	543	0·45
9	73·0	81·5	8·5	22	27	183	0·32
20	59·0	63·5	4·5	21	22	94	0·33
63	34·5	61·5	27·0	8	16	566	0·33
21	47·0	51·5	4·5	14	17	222	0·14
80	30·0	49·0	19·0	7	17	320	0·41

Average elongation rate, 0·31 cm. per week.

TABLE XII. GROWTH-RATE BY MARKED PATCHES OF *FUCUS VESICULOSUS* AT WEMBURY

Square 16 A on strip, patches 1–3. December 1941 to April 1943

	Date ...	1941 4 Dec.	1942 2 Feb.	3 Apr.	13 May	15 June	15 July	16 Aug.	12 Sept.
1.	Length (cm.)	<1·0– 8·0	<1·0–11·2	<1·0–13·5	<1·0–17·5	<1·0–20·2	—	<1·0–32·0	<1·0–35·0
	No. of dichotomies	0–1	0–4	0–4	0–5	0–6	—	0–8	0–8
2.	Length (cm.)	<1·0–10·0	1·0–12·5	1·0–13·0	<1·0–16·7	<1·0–19·0	<1·0–20·5	<1·0–28·0	<1·0–31·0
	No. of dichotomies	0–4	0–5	0–4	0–5	0–6	0–6	0–8	0–10
3.	Length (cm.)	<1·0–18·0	<1·0–23·0	<1·0–16·0	<1·0–19·5	<1·0–23·0	<1·0–26·0	<1·0–29·0	<1·0–35·0
	No. of dichotomies	0–7	0–10	0–4	0–5	0–7	0–7	0–8	0–8

	Date ...	1942 13 Oct.	9 Nov.	12 Dec.	1943 22 Jan.	19 Feb.	3 Mar.	4 Apr.
1.	Length (cm.)	<1·0–37·0	<1·0–39·5	<1·0–42·0	<1·0–38·5	<1·0–40·0	<1·0–42·0	—
	No. of dichotomies	0–9	0–11	0–10	0–8	0–11	0–10	—
2.	Length (cm.)	<1·0–34·0	<1·0–35·0	<1·0–36·5	<1·0–27·0	<1·0–36·0	<1·0–40·0	<1·0–42·5
	No. of dichotomies	0–11	0–12	0–12	0–13	0–11	0–12	0–11
3.	Length (cm.)	<1·0–36·0	<1·0–33·0	<1·0–45·0				
	No. of dichotomies	0–12	0–10	0–9				

TABLE XIII. GROWTH-RATE BY MARKED PATCHES OF *FUCUS VESICULOSUS* AT WEMBURY

Fucus vesiculosus area, patches 1–4. December 1941 to April 1943

	Date ...	1941 16 Dec.	1942 5 Feb.	18 Apr.	15 May	16 June	14 July	13 Aug.	10 Sept.
1.	Length (cm.)	0·5– 3·0	<1·0– 5·2	<1·0– 7·0	<1·0–13·0	<1·0–13·0	<1·0–18·0	<1·0–22·0	<1·0–25·0
	No. of dichotomies	0–1	0–1	0–1	0–2	0–2	0–4	0–6	0–5
2.	Length (cm.)	0·5– 5·0	<1·0– 6·0	<1·0–10·0	<1·0–11·0	<1·0–14·8	<1·0–19·0	<1·0–20·5	<1·0–26·5
	No. of dichotomies	0–1	0–2	0–2	0–3	0–3	0–5	0–4	0–8
3.	Length (cm.)	<1·0–11·5	<1·0–11·5	<1·0–15·5	<1·0–18·5	<1·0–20·0	<1·0–21·5	<1·0–23·0	<1·0–26·0
	No. of dichotomies	0–3	0–3	0–3	0–4	0–6	0–7	0–7	0–7
4.	Length (cm.)	<1·0– 9·5	<1·0–13·5	<1·0–17·0	—	<1·0–24·5	<1·0–28·0	2·0–34·0	2·5–35·0
	No. of dichotomies	0–2	0–2	0–4	—	0–5	0–6	0–10	0–9

	Date ...	1942 8 Oct.	6 Nov.	5 Dec.	1943 5 Jan.	2 Feb.	21 Mar.	20 Apr.
1.	Length (cm.)	<1·0–27·5	<1·0–27·0	<1·0–23·0	<1·0–23·5	<1·0–32·0	<1·0–33·5	<1·0–38·0
	No. of dichotomies	0–7	0–8	0–7	0–7	0–9	0–8	0–12
2.	Length (cm.)	<1·0–29·5	<1·0–32·0	<1·0–34·0	<1·0–34·0	<1·0–35·5	<1·0–35·5	<1·0–40·0
	No. of dichotomies	0–9	0–11	0–12	0–13	0–12	0–11	0–13
3.	Length (cm.)	<1·0–25·5	<1·0–29·0	<1·0–27·0	<1·0–30·0	<1·0–34·5	<1·0–30·0	<1·0–32·0
	No. of dichotomies	0–7	0–8	0–9	0–10	0–11	0–12	0–14
4.	Length (cm.)	6·5–40·0	5·5–41·0	6·0–42·5	7·0–49·0	1·0–51·5	7·0–52·0	13·0–55·0
	No. of dichotomies	0–9	0–9	0–8	0–12	0–12	0–12	0–11

TABLE XIV. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD AT WEMBURY

Metre squares 1–16

Square no.	Period of exp. (years + days)	Growth-rate for 1 year (cm. per week)	Growth-rate for whole period (cm. per week)
1	2 y. 193 d.	0·59	0·54
2	2 y. 175 d.	0·46	0·41
3	2 y. 144 d.	0·28	0·39
4	2 y. 126 d.	0·51	0·42
5	2 y. 92 d.	0·53	0·54
6	2 y. 289 d.	0·41	0·42
7	2 y. 259 d.	0·46	0·40
8	2 y. 200 d.	0·25	0·32
9	2 y. 208 d.	0·37	0·53
10	2 y. 179 d.	0·38	0·57
11	2 y. 150 d.	0·42	0·51
12	2 y. 112 d.	0·43	0·48
13	2 y. 83 d.	0·49	0·56
14	2 y. 49 d.	0·42	0·53
15	2 y. 22 d.	0·49	0·48
16	2 y. 10 d.	0·41	0·47

Average elongation-rate for 1 year, 0·43 cm. per week.
Average elongation-rate for whole period, 0·47 cm. per week.

TABLE XV. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD IN THE ISLE OF MAN

Port Erin, strip 1

Square no.	Length of plants (cm.) 1941 Aug.	1942 Jan.	Apr.	Aug.	Dec.	1943 Apr.	Growth-rate per week (cm.) 1st year	1 yr. 9 months
−7	Cleared	12·0	19·0	27·5	31·0	34·5	0·51	0·40
−5	Cleared	9·0	14·3	26·0	33·5	42·5	0·48	0·49
−2	Cleared	3·0	11·5	20·0	30·5	41·5	0·37	0·48
−1	Cleared	10·5	15·5	25·0	35·0	43·0	0·46	0·49
1	Cleared	4·5	11·0	18·0	25·0	37·0	0·34	0·43
2	Cleared	10·5	14·0	19·0	28·5	39·5	0·37	0·46
3	Cleared	5·0	10·0	14·5	21·0	27·0	0·39	0·31
4	Cleared	5·0	11·0	14·5	20·5	29·0	0·29	0·33
5	Cleared	7·0	17·5	24·5	31·5	42·5	0·45	0·49
10	Cleared	16·0	28·5	39·0	43·5	49·5	0·74	0·57

Average elongation-rate, 0·45 cm. per week.

TABLE XVI. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD IN ARGYLL. SGEIR BHUIDHE AND LOBSTER POND

Station: Sgeir Bhuidhe (exposed locality)

Length in cm.

1942					1943					1944	
Mar.	June	July	Sept.	Nov.	Feb.	Apr.	June	Aug.	Oct.	Feb.	Sept.
Cleared	—	2·1	7·0	11·0	16·0	19·0	23·5	22·0	24·0	32·5	41·0

Station: Lobster Pond (sheltered locality)

Length in cm.

1942				1943		1944	
Feb.	June	Sept.	Nov.	Feb.	Aug.	Feb.	Sept.
Cleared	3·0	7·0	20·0	29·0	46·0	58·0	77·0

TABLE XVII. GROWTH-RATE OF *FUCUS VESICULOSUS* BY CLEARED AREA METHOD IN ARGYLL. ASCOPHYLLUM ROCK

West strip	Duration of exp. (days)	Increase in length (cm.)	Growth-rate per week (cm.)
Upper level	969	100	0·72
Middle level	969	119	0·86
Low level	969	90	0·65
Area 3	569	68	0·83
East Strip	819	110	0·93
Square AH1	495	28	0·28
Square AH2	495	36	0·51

Average growth-rate for the area is 0·68 cm. per week.

TABLE XVIII. GROWTH-RATE BY MARKED PLANTS OF *FUCUS SERRATUS* AT WEMBURY

Square 15 on strip

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Increase in no. of tips	Growth-rate per week (cm.)
A 1	221	17·5	6	305	0·55
2	273	19·0	5	86	0·50
3	532	36·5	12	1639	0·48
4	532	39·0	11	1929	0·51
5	243	16·0	5	373	0·46
6	348	30·5	10	—	0·61
7	253	13·0	3	156	0·36
					Av. 0·50
B 1	199	23·5	7	256	0·83
2	59	5·8	1	31	0·68
3	59	6·5	1	7	0·77
4	570	19·5 max.	7	499	0·24
5	257	18·0 unbroken	4	379	0·49
6	119	12·0	2	83	0·70
7	550	17·0	7	46	0·21
8	246	16·0 unbroken	6	52	0·37
9	30	3·0	0	—	0·70
					Av. 0·55
C 1	59	5·0	2	75	0·49
2	59	5·0	0	17	0·49
3	29	1·5	1	—	0·36
4	539	45·5	11	1696	0·59
5	119	13·0	2	77	0·76
6	217	15·5	3	51	0·50
7	495	31·0	10	488	0·44
8	539	45·5	11	1908	0·59
					Av. 0·53
D 1	155	16·5	3	47	0·74
2	59	2·5	1	15	0·29
3	549	7·5	4	575	0·09
4	257	12·5 unbroken	4	260	0·34
5	296	4·0	3	—	0·09
6	199	6·0	2	—	0·18
7	59	2·5	0	17	0·29
8	227	21·0	5	173	0·61
9	199	22·0 unbroken	4	—	0·74
10	270	15·0	6	181	0·38
11	199	16·0 unbroken	4	137	0·56
12	199	20·5	4	275	0·71
					Av. 0·42
E 1	298	7·5	2	−18	0·13
2	228	17·5 unbroken	3	34	0·40
3	518	38·5	10	152	0·52
4	313	27·5 unbroken	7	261	0·64
5	149	14·5	4	185	0·68
6	518	22·5	10	140	0·30
7	270	19·0 unbroken	7	156	0·49
8	417	18·0	5	51	0·30
9	270	27·5	9	225	0·71
10	228	24·0	6	546	0·73
11	518	45·0	12	416	0·57
12	383	16·5	6	41	0·35
					Av. 0·49
F 1	143	16·5	7	272	0·80
2	193	17·5	4	164	0·63
3	59	7·0	1	10	0·83
4	544	60·0	14	419	0·77
5	291	6·5	1	15	0·15
6	544	38·5	12	1386	0·49
7	544	35·5	10	409	0·45
8	544	34·5	13	220	0·44
					Av. 0·57

Average elongation rate, 0·50 cm. per week.

TABLE XIX. GROWTH-RATE BY MARKED PLANTS OF *FUCUS SERRATUS* AT WEMBURY

Square 21 on strip

Plant no.	Length (cm.)			No. of dichotomies		Duration of exp. (days)	Growth-rate per week (cm.)
	Initial	Final	Increase	Initial	Final		
1	14·0	51·0 F.	37·0	6	23	989	0·26
		52·0 M.	38·0	—	—	727	0·36
2	28·0	80·0	52·0	9	25	989	0·36
3	13·5	61·0	47·5	6	23	989	0·33
4	8·0	70·0	62·0	3	25	989	0·43
5	14·0	62·5	45·5	5	21	989	0·32
6	13·5	51·5	38·0	6	20	606	0·44
7	25·0	36·5	11·5	9	12	338	0·23
8	9·5	12·0	2·5	4	6	281	0·06
9	13·0	42·0	29·0	4	12	309	0·65
10	12·0	32·5	20·5	3	10	309	0·42
11	36·0	64·0	28·0	11	16	309	0·63
12	14·0	28·5	14·5	6	12	212	0·47
13	20·0	40·0	20·0	6	15	338	0·41
14	11·0	31·0	20·0	4	9	311	0·45
15	8·0	27·0	19·0	3	8	254	0·52
16	10·0	14·2	4·2	5	8	163	0·18
17	10·5	30·8	20·3	3	8	254	0·56
18	11·5	34·0	22·5	2	8	281	0·56
19	7·5	41·0	33·5	2	13	415	0·56
20	9·0	27·5	18·5	5	11	254	0·50
21	14·5	39·5	25·0	4	10	338	0·51
22	14·0	40·0	26·0	4	11	338	0·53
23	7·5	37·0	29·5	3	12	338	0·61
24	6·0	34·0	28·0	2	10	373	0·52

Average elongation-rate, 0·43 cm. per week.

TABLE XXI. GROWTH-RATE BY MARKED PLANTS OF *FUCUS SERRATUS* AT WEMBURY

Square 16 on strip

Plant no.	Length (cm.)			No. of dichotomies		Duration of exp. (days)	Growth-rate per week (cm.)
	Initial	Final	Increase	Initial	Final		
165	12·5	39·0	26·5	5	16	824	0·22
303	8·0	45·0	37·0	3	17	764	0·33
288	13·5	66·0	52·5	6	26	943	0·39
301	9·5	48·0	38·5	3	15	635	0·42
167	10·0	59·5	49·5	3	21	855	0·40
160	14·0	39·5	25·5	5	14	372	0·48
168	14·5	19·5	5·0	5	8	303	0·11
171	14·0	38·5	24·5	5	14	372	0·46
173	11·0	38·0	27·0	4	11	372	0·48
175	17·0	38·5	21·5	8	13	271	0·55
294	9·0	27·5	18·5	3	9	253	0·51
297	12·0	28·5	16·5	5	10	253	0·45
298	10·5	33·5	23·0	5	12	372	0·44
304	10·5	44·0	33·5	6	15	635	0·36
305	6·0	17·0	11·0	2	10	532	0·14
307	7·5	29·5	22·0	2	11	342	0·45
308	6·0	30·0	24·0	1	10	342	0·49
438	7·5	26·0	18·5	2	9	253	0·51
170	17·0	31·0	14·0	6	11	222	0·44

Average elongation-rate, 0·40 cm. per week.

TABLE XX. GROWTH-RATE BY MARKED PLANTS OF *FUCUS SERRATUS* AT WEMBURY

Square 21 *a* on strip

Plant no.	Length (cm.)			No. of dichotomies		Duration of exp. (days)	Growth-rate per week (cm.)
	Initial	Final	Increase	Initial	Final		
196	25·0	40·5	15·5	7	13	314	0·33
197	20·0	37·0	17·0	8	13	369	0·32
335	12·0	19·5 F.	7·5	4	10	989	0·05
		21·0 M.	9·0	4	7	504	0·11
336	9·0	45·5	36·5	3	14	534	0·47
337	10·0	29·0	19·0	5	12	369	0·35
338	10·5	47·0	36·5	4	16	534	0·47
339	14·9	57·0	43·0	4	16	608	0·49
340	16·0	31·5	15·5	6	10	806	0·13
342	14·0	43·5	29·5	5	14	899	0·22
343	12·0	22·5	10·5	3	6	193	0·37
346	11·5	69·0	57·5	5	22	945	0·42
347	11·0	63·0	52·0	3	19	989	0·36
348	8·0	44·0	32·0	3	17	989	0·22
349	8·0	61·0	53·0	3	19	989	0·37
450	7·5	48·5	41·0	2	16	945	0·30
651	36·0	50·5	14·5	9	18	669	0·15
654	39·0	68·0	25·0	4	19	256	0·68
657	63·0	78·0	15·0	16	28	324	0·32
661	44·0	63·0	19·0	12	21	504	0·26
662	51·0	70·0	19·0	14	22	441	0·30
664	37·0	71·0	34·0	10	21	534	0·44
27	29·0	56·5	27·5	11	19	669	0·28
28	35·5	49·0	13·5	10	15	282	0·33
29	36·5	42·0 F.	6·5	12	15	799	0·05
		58·0 M.	21·5	12	18	222	0·67
34	79·0	92·0	13·0	18	26	256	0·35
35	28·0	64·5	36·5	9	23	608	0·42
36	64·0	77·0	13·0	14	20	256	0·35
41	45·0	56·5	11·5	18	21	256	0·31
42	41·0	48·0	7·0	11	13	256	0·19
43	71·0	89·0 F.	19·0	14	22	256	0·52
		90·0 M.	18·0	14	21	369	0·34
45	53·0	71·5 F.	18·5	14	19	256	0·50
		75·0 M.	22·0	14	22	560	0·27
46	40·0	54·0 F.	37·5	12	27	945	0·27
		77·5 M.	14·0	12	20	416	0·23
48	39·0	52·5 F.	21·0	14	20	608	0·23
		60·0 M.	13·5	14	18	324	0·29
200	24·0	70·0	46·0	8	20	608	0·53
201	11·5	42·5	31·0	5	14	608	0·35
202	22·0	61·5	39·5	8	18	560	0·43
203	20·5	25·5	15·5	6	9	282	0·38
205	16·0	75·0	59·0	5	23	945	0·43
206	20·0	47·0	27·0	6	12	728	0·26
209	20·5	14·5	4·0	6	12	369	0·07
210	22·5	51·0	28·5	8	14	534	0·37
212	25·5	61·0	35·5	10	20	504	0·49
213	20·0	29·5	9·5	6	10	369	0·17
215	33·0	61·0	28·0	10	14	369	0·53
216	35·5	58·0	22·5	12	19	369	0·42
217	31·0	68·0	37·0	11	18	608	0·42
218	32·0	60·0	28·0	12	17	504	0·38
220	33·0	50·0	17·0	10	14	369	0·32
221	27·0	44·5	17·5	11	16	343	0·36
222	25·0	48·5	23·5	10	17	534	0·30
223	26·0	50·0	24·0	10	16	416	0·40
224	29·0	49·0	20·0	11	16	669	0·21
225	24·5	55·0	30·5	7	17	638	0·33
227	38·0	73·0	35·0	8	19	560	0·53
230	25·0	56·0	31·0	9	17	369	0·58
234	29·0	53·5	24·5	9	19	324	0·43
236	20·5	32·5	12·0	7	10	369	0·22
239	20·0	35·0	15·0	6	11	369	0·28
241	23·0	64·0	41·0	8	21	638	0·45
242	17·0	60·0	43·0	6	20	669	0·45
244	21·5	52·5	31·0	7	17	608	0·35
245	12·5	39·5	27·0	6	15	369	0·51
247	21·0	42·5	21·5	8	15	416	0·35
249	12·0	19·0	7·0	5	7	416	0·11
250	13·0	61·0	48·0	5	21	989	0·34

F., final. M., maximum.

Average elongation-rate, 0·35 cm. per week.

TABLE XXII. GROWTH-RATE BY MARKED PATCHES OF *FUCUS SERRATUS* AT WEMBURY

Square 16 on strip, patches 1–4. December 1941 to April 1943

Date ...	1941 22 Dec.	1942 2 Feb.	3 Apr.	13 May	14 June	15 July	15 Aug.	12 Sept.
1. Length (cm.)	0·2– 1·0	1·2– 2·0	4·0– 6·0	5·0– 8·5	1·0–10·5	1·0–12·5	1·0–20·0	1·0–20·5
No. of dichotomies	0	0	0–1	1–2	0–3	0–4	0–5	0–7
2. Length (cm.)	<1·0– 3·5	<1·0– 3·8	1·0– 9·0	<1·0–11·5	<1·0–15·5	<1·0–16·0	<1·0–20·0	<1·0–21·0
No. of dichotomies	0–1	0–2	0–3	0–4	0–6	0–6	0–6	0–7
3. Length (cm.)	1·0– 5·0	1·0– 8·0	1·0–12·0	1·0–14·5	1·0–15·5	1·5–19·5	1·0–24·5	1·0–26·0
No. of dichotomies	0–1	0–3	0–5	0–5	0–5	0–7	0–7	0–8
4. Length (cm.)	1·0– 9·0	1·0–11·2	1·0–15·5	1·0–20·0	1·0–23·0	1·0–20·5	1·0–27·0	1·0–31·0
No. of dichotomies	0–2	0–4	0–6	0–8	0–7	0–7	0–8	0–8

Date ...	1942 13 Oct.	12 Nov.	12 Dec.	1943 22 Jan.	7 Feb.	21 Mar.	22 Apr.
1. Length (cm.)	1·0–21·0	<1·0–22·0	<1·0–22·0	<1·0–32·0	<1·0–23·5	<1·0–34·0	<1·0–25·0
No. of dichotomies	0–7	0–8	0–8	0–9	0–8	0–11	0–9
2. Length (cm.)	<1·0–22·0	<1·0–22·0	<1·0–20·5	<1·0–21·5	<1·0–21·5	<1·0–24·5	<1·0–28·5
No. of dichotomies	0–8	0–8	0–8	0–9	0–9	0–8	0–7
3. Length (cm.)	2·0–29·5	1·0–30·0	1·0–34·0	1·0–37·0	1·0–38·5	1·0–39·5	1·0–43·0
No. of dichotomies	0–9	0–10	0–11	0–12	0–11	0–11	0–13
4. Length (cm.)	1·0–33·8	1·0–35 5	1·0–36·0	1·0–33·5	1·0–35·5	1·0–35·5	1·0–37·0
No. of dichotomies	0–9	0–10	0–11	0–10	0–12	0–11	0–12

TABLE XXIII. GROWTH-RATE BY MARKED PATCHES OF *FUCUS SERRATUS* AT WEMBURY

Square 21 on strip, patches 1–3. December 1941 to April 1943

Date ...	1941 4 Dec.	1942 2 Feb.	5 Apr.	16 May	15 June	15 July	15 Aug.	12 Sept.
1. Length (cm.)	0·5– 1·5	1·4– 2·0	3·0– 5·0	1·0–10·0	1·0–11·2	1·0–15·5	1·0–20·0	1·0–21·5
No. of dichotomies	0	0	0–1	1–2	1–3	0–4	0–5	0–5
2. Length (cm.)	0·5– 1·5	1·6– 2·2	1·0– 6·5	1·0– 9·0	1·0–10·5	1·0–13·5	1·0–20·0	1·0–25·0
No. of dichotomies	0	0	0–2	0–3	0–3	0–4	0–6	0–9
3. Length (cm.)	1·0– 9·0	1·0– 9·0	1·0–12·0	—	1·0–19·5	1·0–23·0	1·0–31·0	1·0–31·0
No. of dichotomies	1–2	2–3	0–3	—	0–6	0–8	0–8	0–8

Date ...	1942 9 Oct.	11 Nov.	12 Dec.	1943 21 Jan.	18 Feb.	21 Mar.	22 Apr.
1. Length (cm.)	1·0–25·0	1·0–26·5	1·0–31·5	1·0–27·5	1·0–29·5	1·0–31·0	1·0–22·0
No. of dichotomies	0–7	0–7	0–8	0–8	0–9	0–10	0–7
2. Length (cm.)	1·0–25·0	1·0–25·5	1·0–28·0	1·0–28·5	1·0–26·0	1·0–25·5	1·0–23·0
No. of dichotomies	0–9	0–9	0–9	0–9	0–9	0–9	0–9
3. Length (cm.)	1·0–33·5	1·0–35·0	1·0–38·0	1·0–38·0	1·0–38·0	1·0–38·0	1·0–44·0
No. of dichotomies	0–10	0–11	0–12	0–13	0–11	0–13	0–13

TABLE XXIV. GROWTH-RATE BY MARKED PATCHES OF *FUCUS SERRATUS* AT WEMBURY

Square 22 on strip. December 1941 to April 1943

Date ...	1941 12 Dec.	1942 4 Feb.	2 Apr.	16 May	15 June	15 July	15 Aug.	12 Sept.
Length (cm.)	0·2– 2·4	1·0– 3·1	1·0– 5·5	1·0– 8·0	1·0–11·0	1·0–15·5	1·0–19·0	1·0–21·5
No. of dichotomies	0	0	0–1	0–2	0–4	0–5	0–5	0–6

Date ...	1942 9 Oct.	9 Nov.	12 Dec.	1943 23 Jan.	18 Feb.	13 Mar.	22 Apr.
Length (cm.)	1·0–24·5	1·0–29·0	1·0–32·5	1·0–31·0	1·0–33·0	1·0–32·0	1·0–36·0
No. of dichotomies	0–10	0–9	0–9	0–10	0–10	0–12	0–12

TABLE XXV. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD AT WEMBURY

Metre squares H 1–3, L 1–16

Square no.	Period (days)	Growth-rate per week (cm.)	Period (days)	Growth-rate per week (cm.)	Total period (years + days)	Growth-rate per week (cm.)
H 1	372	0·57	728	0·51	2 y. 331 d.	0·56
2	365	0·49	733	0·82	2 y. 287 d.	0·51
3	367	0·46	725	0·55	2 y. 97 d.	0·60
L 1	368	0·57	755	0·44	2 y. 346 d.	0·50
2	368	0·70	727	0·64	2 y. 309 d.	0·62
3	379	0·60	735	0·60	2 y. 226 d.	0·56
4	381	0·34	733	0·40	2 y. 179 d.	0·45
5	373	0·60	728	0·62	2 y. 142 d.	0·57
6	371	0·34	729	0·42	2 y. 100 d.	0·41
7	383	0·39	724	0·55	2 y. 78 d.	0·46
8	353	0·44	738	0·57	2 y. 35 d.	0·63
9	356	0·47	749	0·57	—	—
10	387	0·52	711	0·43	—	—
11	358	0·60	683	0·65	—	—
12	360	0·23	656	0·32	—	—
13	356	0·74	616	0·67	—	—
14	357	0·54	583	0·55	—	—
15	353	0·43	553	0·62	—	—
16	370	0·46	516	0·58	—	—

Average elongation-rate: Plants approximately 1 year old, 0·50 cm. per week.
Plants 1–2 years old, 0·55 cm. per week.
Plants 2–3 years old, 0·53 cm. per week.

TABLE XXVI. GROWTH-RATE OF *FUCUS SERRATUS* AND *FUCUS VESICULOSUS* BY CLEARED AREA METHOD AT WEMBURY

Square 19 on strip

	F. vesiculosus		*F. serratus*	
Date	Length	No. of dichotomies	Length	No. of dichotomies
5. iv. 42	Rock surface removed			
28. iv. 42	No repopulation			
13. v. 42	0·5– 1·0	0	0·5– 1·0	0
17. vi. 42	0·1– 4·0	1	0·1– 4·0	1
15. vii. 42	0·1– 4·0	1	0·1– 4·0	1
14. viii. 42	0·1– 4·0	1	0·1– 4·0	1
13. ix. 42	0·1– 7·0	2	0·1– 7·0	1
14. x. 42	0·1–12·0	2	0·1– 9·2	4
26. x. 42	0·1–14·5	4	—	—
12. xi. 42	0·1–16·3	3	—	—
8. xii. 42	0·1–20·5	5	0·1–12·0	4
21. i. 43	0·1–17·5	4	0·1–16·6	6
18. ii. 43	0·1–15·5	4	0·1–15·0	6
21. iii. 43	0·1–19·0	4	0·1–20·0	6
22. iv. 43	0·1–20·0	6	0·1–24·5	7
22. v. 43	0·1–24·3	6	0·1–23·0	5
16. vi. 43	0·1–26·5	5	0·1–30·5	9
31. vii. 43	0·1–32·0	5	0·1–35·5	9
1. ix. 43	0·1–36·0	6	0·1–36·0	11
3. x. 43	0·1–42·5	8	0·1–40·0	11
1. xi. 43	0·1–45·0	11	0·1–47·5	13
9. xii. 43	0·1–49·0	10	0·1–49·0	10
10. i. 44	0·1–47·0	10	0·1–47·0	12
9. ii. 44	0·1–43·0	12	0·1–52·0	12
14. iii. 44	0·1–46·5	16	0·1–53·0	13
9. iv. 44	0·1–49·0	16	0·1–55·0	14
11. v. 44	0·1–50·0	9	0·1–60·0	16
7. vi. 44	0·1–46·5	13	0·1–64·0	16
6. vii. 44	0·1–58·0	13	0·1–62·5	14
22. viii. 44	0·1–62·0	17	0·1–72·0	16

Average elongation-rate over a period of 2 years 129 days: *F. vesiculosus*, 0·50 cm. per week. *F. serratus*, 0·58 cm. per week.

TABLE XXVII. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD AT WEMBURY

Square 19A 2 on strip

Date	Length (cm.)		No. of dichotomies	
	Plants on rock	Plants on edge of pool	Plants on rock	Plants on edge of pool
9. ix. 41	Rock surface scraped			
6. x. 41	<1– 2·0			
8. x. 41	Rock surface removed			
17. xi. 41	No repopulation			
4. xii. 41	No repopulation			
30. iii. 42	<1– 2·0	—	0	—
13. v. 42	1– 5·0	—	1	—
15. vi. 42	1– 8·0	—	2	—
15. vii. 42	1–12·5	1–20·5	3	5
14. viii. 42	1–14·0	1–23·0	7	7
13. ix. 42	1–16·0	1–26·0	6	7
14. x. 42	1–17·7	1–31·0	7	8
9. xi. 42	1–23·5	1–32·5	6	8
12. xii. 42	1–29·0	1–36·0	10	8
21. i. 43	1–24·0	1–38·0	7	9
18. ii. 43	1–34·0	1–37·0	8	9
21. iii. 43	1–31·0	1–34·0	9	9
24. iv. 43	1–30·0	1–43·0	9	10
22. v. 43	1–36·0	1–45·0	10	10
16. vi. 43	1–38·0	1–50·0	10	9
5. viii. 43	1–45·0	—	10	—
1. ix. 43	1–46·0	1–55·0	12	12
3. x. 43	1–48·0	—	8	—
1. xi. 43	1–52·0	—	15	—
9. xii. 43	1–49·0	—	14	—
10. i. 44	1–50·0	—	16	—
12. ii. 44	1–55·0	—	16	—
9. iv. 44	1–60·0	—	16	—
11. v. 44	1–54·0	—	17	—
7. vi. 44	1–56·0	—	16	—
6. vii. 44	1–72·0	—	19	—
22. viii. 44	1–76·0	—	20	—

Average elongation-rate over period of 2 years 348 days: 0·49 cm. per week.
Average elongation-rate of plants near pool over period of 722 days: 0·53 cm. per week.

TABLE XXVIII. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD IN THE ISLE OF MAN

Port Erin Bay, strips 1–3

Strip 1. August 1941 to September 1944

Square no.	Length of plants (cm.) 1941 5 Aug.	1942 2 Jan.	19 Apr.	7 July	1943 10 Dec.	16 Apr.	20 Sept.	1944 1 Jan.	15 Apr.	Rate of growth per week (cm.)
10	Cleared	8·0	16·0	28·5	30·5	38·0	—	—	—	0·43
11	Cleared	8·5	15·0	26·0	38·5	44·5	53·5	—	76·0	0·63
12	Cleared	3·0	11·5	19·0	32·0	41·0	45·0	—	68·0	0·56
13	Cleared	7·5	12·5	14·0	39·5	50·0	41·0	38·0	64·0	0·53
14	Cleared	11·0	14·5	20·5	27·5	31·0	45·0	45·0	69·0	0·57
15	Cleared	9·0	16·0	25·0	28·0	29·0	32·0	50·0	73·0	0·60
16	Cleared	7·5	18·5	25·0	30·0	36·5	60·5	65·0	60·5	0·50
17	Cleared	11·0	20·5	29·5	31·5	37·0	51·0	57·0	73·0	0·60
18	Cleared	13·5	19·0	36·0	42·0	36·5	50·0	61·0	78·0	0·64
19	Cleared	14·5	19·5	30·0	39·0	43·0	59·0	66·5	77·5	0·64
20	Cleared	11·5	20·0	30·5	34·0	38·0	58·0	63·0	75·5	0·64
21	Cleared	6·5	16·0	31·0	38·5	43·0	62·5	50·0	78·5	0·65
22	Cleared	14·0	22·0	31·5	40·0	50·0	48·5	57·0	71·0	0·58
23	Cleared	10·0	21·0	31·0	37·5	48·0	42·0	54·5	61·5	0·51
24	Cleared	8·5	16·0	27·0	32·5	37·0	43·0	55·0	76·0	0·63
25	Cleared	3·0	6·0	16·0	25·0	34·5	—	—	64·0	0·53
26	Cleared	7·5	15·5	37·5	45·0	43·0	—	—	72·0	0·59
27	Cleared	—	1·0	17·0	29·0	36·5	—	—	56·0	0·46

Average elongation-rate, 0·57 cm. per week.

Strip 2. April 1942 to September 1944 (843 days)

Square no.	Av. length of 10 longest plants (cm.)	Rate of growth per week (cm.)
11	65·5	0·53
12	70·0	0·56
13	73·0	0·59
14	78·0	0·63

Average elongation-rate, 0·58 cm. per week.

Strip 3. August 1942 to September 1944 (762 days)

Square no.	Av. length of 10 longest plants (cm.)	Rate of growth per week (cm.)
13	75·5	0·69
14	76·4	0·70
15	71·8	0·65
16	73·1	0·67

Average elongation-rate, 0·68 cm. per week.

Table XXIX. Growth-rate of *Fucus serratus* by Cleared Area Method in the Isle of Man

Port St Mary and Castletown

Port St Mary

Square no.	Length of plants (cm.) 1943 12 Apr.	7 Aug.	31 Dec.	1944 17 Apr.	Growth-rate per week (cm.)
1	0	14·0	25·0	34·0	0·64
2	0	15·5	27·0	37·2	0·70
3	0	17·5	31·5	45·0	0·85
4	0	11·0	22·5	31·0	0·58
5	0	10·5	23·5	47·8	0·90

Average elongation-rate, 0·73 cm. per week.

Scarlet Point, Castletown

Square no.	Length of plants (cm.) 1943 13 Apr.	9 Aug.	31 Dec.	1944 18 Apr.	Growth-rate per week (cm.)
1	0	15·0	26·5	39·5	0·74
2	0	17·5	30·5	42·5	0·80
3	0	19·0	32·5	49·0	0·90
4	0	15·5	27·0	39·0	0·74
5	0	17·5	33·5	55·5	1·04

Average elongation-rate, 0·84 cm. per week.

Table XXX. Growth-rate of Marked Plants of *Fucus serratus* in Argyll. Serratus Rock

Plant no.	Duration of exp. (days)	Increase in length (cm.)	Increase in no. of dichotomies	Growth-rate per week (cm.)
A 1	1044	74·0	10	0·50
2	245	22·5	4	0·64
3	496	68·0	10	0·93
4	308	43·0	4	0·97
5	308	30·5	5	0·69
6	248	26·5	6	0·75
7	248	19·0	3	0·53
8	192	35·0	4	1·27
B 1	520	74·0	8	0·99
2	248	32·5	2	0·91
3	248	38·0	7	1·07
4	248	39·0	5	1·10
5	190	30·5	3	1·12
6	248	44·5	5	1·82
7	248	47·0	6	1·32
C 1	248	35·0	5	0·98
2	248	32·0	5	0·90
3	248	38·0	6	1·07
4	443	24·5	2	0·38
5	443	47·0	6	0·74
6	248	32·5	5	0·91
7	520	11·5	2	0·15
8	248	31·0	5	0·87

Average elongation-rate, 0·90 cm. per week.

TABLE XXXI. GROWTH-RATE OF *FUCUS SERRATUS* BY CLEARED AREA METHOD IN ARGYLL

Serratus Rock

Square no.	Duration of exp. (days)	Growth-rate per week (cm.)
E 1	315	0·88
E 2	315	1·06
E 3	315	1·08
A 1	385	0·83
A 2	385	0·72
B and C	385	1·10
D	385	0·90
1	982	0·78
2	238	0·91
3	178	0·82

Average elongation-rate for area, 0·91 cm. per week.

Ascophyllum Rock

Square no.	Duration of exp. (days)	Length of plant (cm.)	Growth-rate per week (cm.)
West strip: 3	1031	70·0	0·47
5 and 6	1031	90·0	0·66

Average elongation-rate for area, 0·57 cm. per week.

TABLE XXXII. WEIGHTS OF FUCOID POPULATIONS IN DEVON AND ARGYLL

Experimental area	No. of months of growth	Species present on areas *F.v.*	*F.s.*	*A.*	Wt. in kg. per m.²
Devon. Wembury strip 3 m. wide					
Square 4:	Original population	−	+	+	15·6
East	36	+	+	−	14·8
Middle	36	+	+	+	14·3
West	36	+	+	+	15·7
Square 8	36	−	+	−	15·6
Square 14:	16	+	+	−	7·9
High level	28	+	+	−	16·0
Low level	28	+	+	−	9·2
Square 15:	Original population	−	+	+	9·1
(*a*)	34	−	+	−	11·5
(*b*)	34	−	+	−	12·3
Square 16	36	−	+	−	22·9
Square 19	Original population	−	+	−	9·7
	28	+	+	−	17·0
Square 19*a*: South	31	−	+	−	20·0
North	31	−	+	−	7·5
Square 21	Original population	−	+	−	12·4
	36	−	+	−	22·2
Square 21*a*	36	−	+	−	9·2
Argyll					
Ascophyllum Rock:					
West strip 1	33	−	+	+	13·0
2	33	+	+	+	4·6
3	33	−	+	+	9·9
4	33	−	+	−	42·4
East strip	33	−	+	−	2·1
Area 3	16	+	+	+	23·3
Serratus Rock:					
1	Original population	−	+	−	13·1
	33	−	+	−	13·3
2	Original population	−	+	−	27·9
	33	−	+	−	25·5
Lobster Pond	Original population	+	−	−	6·8
	27	+	−	+	6·7
Sgeir Bhuidhe	27	+	−	−	6·7

F.v. = *F. vesiculosus; F.s.* = *F. serratus; A.* = *Ascophyllum.*

Table XXXIV. Analysis of Population in Size Groups. Port Erin

Metre sq. no.	Total no. plants	Under 10 cm.	10–29 cm.	29–59 cm.	Over 59 cm.
Strip. 1. *Fucus vesiculosus* and *Fucus serratus*. Original population					
1	124	51	43	20	10
2	847	802	28	14	3
3	962	902	30	27	3
4	332	235	50	42	5
5	788	729	37	20	2
6	660	319	301	38	2
7	310	305	5	—	—
8	1166	1154	10	2	—
9	2168	2151	12	5	—
10	421	394	17	8	2
11	393	326	46	15	6
12	243	202	20	18	3
13	597	560	21	14	2
14	907	835	41	25	6
15	957	843	43	59	12
16	876	713	39	86	38
17	904	762	77	45	20
18	1258	801	380	37	40
19	755	665	25	30	35
20	1150	1008	45	63	34
21	433	344	46	29	14
22	636	589	31	16	—
23	720	645	61	14	—
24	381	314	43	24	—
25	14	3	3	8	—
26	27	26	1	—	—
27	47	14	15	18	—
Strip 2. Original population					
11	68	27	28	12	1
12	12	0	7	3	2
13	3132	3095	19	16	2
14	981	943	38	—	—
15	2977	2945	10	19	3
16	1637	1597	7	26	7
17	4615	4535	14	53	13
Strip 2. Final population. *F. vesiculosus*					
11	214	183	20	4	7
12	188	41	41	69	37
13	614	518	38	44	14
14	981	943	18	13	7
15	—	—	—	—	—
16	98	64	32	—	—
17	218	177	21	20	—
Strip 2. Final population. *F. serratus*					
11	125	58	37	24	6
12	305	160	57	77	9
13	481	281	78	103	19
14	700	391	177	106	26
15	626	470	109	47	—
16	1194	750	273	133	38
17	1114	670	249	175	20
Strip 3. Final population. *F. serratus*					
13	1248	390	423	393	42
14	866	192	320	296	58
15	1110	114	536	414	46
16	1212	536	453	176	47

TABLE XXXIII. SEQUENCE OF REPRODUCTIVE STAGES THROUGH THE YEAR IN *FUCUS VESICULOSUS* ON THE DEVON COAST AS SHOWN BY A NUMBER OF INDIVIDUAL PLANTS

Occurrence of different stages in receptacle development and maturation. Stages 1–9 (see p. 474). S indicates whole plant sterile

Size of plants Area I, Dec. 1941 Area II, Dec. 1942		1942								1943										1944						
Length (cm.)	No. of dichotomies	Mar.	Apr.	June	July	Aug.	Sept.	Oct.	Nov.	Jan.	Feb.	Mar.	Apr.	May	June	July	Oct.	Nov.	Dec.	Jan.	Mar.	Apr.	May	June	July	Aug.
9·0	2	S	S	S	S	S	S	S	S	—	1	3, 4	6	6	6	7–9	9, S	9, S	9, S	Gone	—	—	—	—	—	—
16·0	5	S	S	S	S	S	S	S	S	2	2	—	—	—	9, S	9, S	9, S	9, S	9, S	9, S	9, S	Gone	—	—	—	—
22·0	6	4	6	6, 7	7, 8	7, 8	8	9, S	9, S	3, 4, 9	2, 4, 9	4, 6, 9	4, 6, 9	6–9	6–9	9, S	Gone	—	—	—	—	—	—	—	—	—
24·0	10	4, 9	5, 9	6, 7, 9	7, 8, 9	8, 9	8, 9	9, S	9, S	Gone	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
26·0	6	S	6	6	7, 8	7, 8	8	9, S	9, S	2–4, 9	1, 4, 9	4, 6, 9	—	6–9	6–9	7–9	8, 9	Gone	—	—	—	—	—	—	—	—
34·0	9	5	6, 7	7	8	8	8	9, S	9, S	—	1, 3, 6, 9	4, 6, 9	6, 9	7–9	7–9	7–9	9, S	1, 9	9, S	9, S	9, S	9, S	9, S	9, S	9, S	Gone
36·0	9	5, 9	5, 9	6, 7, 9	6–9	8, 9	8, 9	9, S	9, S	1, 4, 9	1, 4, 9	4, 6, 9	4, 6, 9	6, 9	6–9	7–9	8, 9	9, S	1, 9	1, 3, 9	6, 9	Gone	—	—	—	—
44·0	16	5, 9	6, 9	6, 7, 8, 9	7–9	7–9	8, 9	9, S	9, S	3, 4, 9	Gone	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
44·0	18	5, 9	6, 9	7, 9	7–9	—	8, 9	9, S	9, S	2, 3, 9	2, 4, 9	4, 6, 9	6, 9	4, 6–9	6–9	7–9	9, S	1, 9	1, 2, 9	1, 3, 9	Gone	—	—	—	—	—
46·0	18	5, 9	6, 9	6, 7, 9	6–9	7–9	8, 9	9, S	9, S	—	2, 5, 9	4, 6, 9	6, 9	6, 9	6–9	7–9	9, S	Gone	—	—	—	—	—	—	—	—
48·0	11	5, 9	6, 9	6, 7, 9	7–9	7–9	8, 9	9, S	9, S	3, 4, 9	2, 5, 9	Gone	—	—	—	—	—	—	—	—	—	—	—	—	—	—
19·5	4	—	—	—	—	—	—	—	—	S	S	S	S	S	S	S	S	1	1, 2	1, 4	2, 5	1, 5	3, 6	6, 8	6–8	6–9
19·5	4	—	—	—	—	—	—	—	—	S	S	S	S	S	S	S	S	1	2, 4	1, 4	1, 5	3, 5	6	6–8	7, 8	8, 9
25·0	6	—	—	—	—	—	—	—	—	S	S	S	S	1(1 tip)	—	6	9, S	1, 9	1, 9	1–5, 9	Gone	—	—	—	—	—
26·5	7	—	—	—	—	—	—	—	—	1 (few)	2, 3	4	4, 6	5, 6	8	8	9, S	1, 9	1–3, 9	Gone	—	—	—	—	—	—
28·0	9	—	—	—	—	—	—	—	—	—	1, 3	4, 6	4, 6	5, 6	6	7	9, S	1, 2, 9	—	—	3, 4, 9	4, 5, 9	6, 9	6–9	7–9	7–9
33·5	11	—	—	—	—	—	—	—	—	S	1	2, 3	—	4, 6	5, 6	7	9, S	1, 9	2, 9	1, 3, 9	3, 4, 9	1, 4, 9	3, 6, 9	6–9	Gone	—
34·5	8	—	—	—	—	—	—	—	—	1, 2	1, 3	2, 5	—	4, 6	6	6, 7	8, 9	1, 9	1, 9	1, 3, 9	2, 4, 9	1, 5, 9	4, 6, 9	6–9	6–9	Gone
37·0	14	—	—	—	—	—	—	—	—	1 (few)	2, 3, 4	2–5	4, 6	5, 6	6	6–8	8, 9	1, 9	1, 9	1–4, 9	2, 4, 9	1, 5, 9	4, 6, 9	4–6, 9	6–9	6–9
38·0	13	—	—	—	—	—	—	—	—	1, 3	2, 4	3, 6	4, 6	4, 6	3, 4, 6	6–8	9, S	9, S	1, 2, 9	1, 2, 9	1, 4, 9	3, 5, 9	1, 5, 9	4, 6, 9	4, 6, 9	6–9
38·5	6	—	—	—	—	—	—	—	—	1 (few)	1, 3	2, 6	4, 6	3, 4, 6	6, 7	8	1, 2, 9	1, 3, 9	1, 4, 9	1, 6, 9	1, 6, 9	3, 6, 9	6–9	6–9	7–9	7–9
40·0	14	—	—	—	—	—	—	—	—	1, 3, 9	1–4, 9	3–6, 9	6, 9	5, 6, 9	5, 6, 9	6, 9	7–9	1, 9	1, 2, 9	1, 4, 9	2–5, 9	1, 5, 9	3, 6, 9	6–9	6–9	7–9
46·0	12	—	—	—	—	—	—	—	—	1, 2	—	3, 6	4, 6	5, 6	4, 6	6, 7, 8	8, 9	9, S	1, 3, 9	Gone	—	—	—	—	—	—
47·0	14	—	—	—	—	—	—	—	—	1, 2, 9	1, 3, 9	3, 5, 9	3, 4, 6, 9	3, 4, 6, 9	4, 6	6, 7	7–9	1, 9	1, 9	1, 3, 9	2, 4, 9	1, 5, 9	4, 6, 9	6–9	6–9	Gone
49·5	15	—	—	—	—	—	—	—	—	1 (few)	1, 3	1, 6	4, 6	4, 6	4, 6	7	9, S	9, S	9, S	Gone	—	—	—	—	—	—
50·0	15	—	—	—	—	—	—	—	—	1, 2, 9	1, 2, 3, 9	1, 5, 9	6, 9	5, 6, 9	3, 4, 6, 9	6, 9	6–9	8, 9	1, 9	1, 3, 9	1, 4, 9	1, 5, 9	4, 5, 6, 9	6–9	6–9	7–9
59·0	14	—	—	—	—	—	—	—	—	1, 3, 9	—	1, 5, 9	4, 6, 9	5, 6, 9	6, 9	6–9	8, 9	1, 9	1, 2, 9	1, 3, 9	1, 6, 9	1, 6, 9	3, 6, 9	4–9	6–9	9, S
59·0	21	—	—	—	—	—	—	—	—	1, 3, 9	2, 4, 9	2, 6, 9	4, 6, 9	4, 6, 9	4, 6, 9	9, S	9, S	9, S	9, S	1, 3, 9	2, 9	4, 9	4, 6, 9	7, 9	8, 9	8, 9
61·0	19	—	—	—	—	—	—	—	—	1, 2, 9	1, 5, 9	1, 6, 9	4, 6, 9	5, 6, 9	6, 9	6–9	7–9	1, 9	1, 2, 9	1, 4, 9	1, 6, 9	1, 6, 9	3, 6, 9	6, 9	Gone	—
66·0	23	—	—	—	—	—	—	—	—	1, 3, 9	2, 3, 9	2, 6, 9	4, 6, 9	4, 6, 9	4, 6, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
67·0	24	—	—	—	—	—	—	—	—	1, 2, 9	1–4, 9	2, 6, 9	4, 6, 9	5, 6, 9	6, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
69·0	20	—	—	—	—	—	—	—	—	2, 4, 9	1, 5, 9	2, 6, 9	4, 6, 9	5, 6, 9	6–9	7–9	1, 8, 9	1, 2, 9	1, 4, 9	1, 5, 9	2, 6, 9	9, S	9, S	9, S	9, S	9, S
69·0	31	—	—	—	—	—	—	—	—	2, 4, 9	2, 6, 9	3, 6, 9	6, 9	6, 9	3, 6, 9	6–9	6–9	1, 3, 9	1, 3, 9	Gone	—	—	—	—	—	—
71·0	21	—	—	—	—	—	—	—	—	1, 3, 9	1, 5, 9	2–6, 9	4, 6, 9	5, 6, 9	6, 7, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
71·5	18	—	—	—	—	—	—	—	—	1, 2, 9	2, 4, 9	3–6, 9	4, 6, 9	4, 6, 9	4, 6, 9	6–9	Gone	—	—	—	—	—	—	—	—	—
73·0	22	—	—	—	—	—	—	—	—	1, 3, 9	1, 4, 9	1, 6, 9	4, 6, 9	5, 6, 9	6, 8, 9	7–9	8, 9	1, 9	1, 2, 9	1, 4, 9	2, 5, 9	1, 5, 9	3, 6, 9	Gone	—	—
75·0	19	—	—	—	—	—	—	—	—	1, 3, 9	2, 5, 9	3, 6, 9	6, 9	3, 4, 6, 9	2, 3, 6–9	3, 4, 9	7–9	1, 9	1, 2, 9	1, 5, 9	3, 6, 9	1, 6, 9	6, 9	6, 7, 9	7–9	9, S
77·0	25	—	—	—	—	—	—	—	—	2, 4, 9	1, 4, 9	2, 6, 9	4, 6, 9	4, 6, 9	6, 9	7–9	8, 9	8, 9	9, S	1, 9	1, 2, 9	1, 4, 9	3, 5, 9	6, 9	6–9	7–9
82·0	32	—	—	—	—	—	—	—	—	1–4, 9	2–6, 9	2–6, 9	4, 6, 9	5, 6, 9	4–9	6–9	6–9	8, 9	1, 9	Gone	—	—	—	—	—	—
89·0	31	—	—	—	—	—	—	—	—	1, 2, 3, 9	2–4, 9	3, 6, 9	4, 6, 9	5, 6, 9	6, 9	6–9	8, 9	8, 9	9, S	Gone	—	—	—	—	—	—
95·0	37	—	—	—	—	—	—	—	—	1, 3, 9	2–4, 9	4, 6, 9	4, 6, 9	4, 6, 9	6, 9	Gone	—	—	—	—	—	—	—	—	—	—
105·0	33	—	—	—	—	—	—	—	—	2, 4, 9	2, 5, 9	1, 6, 9	4, 6, 9	4, 6, 9	6, 7, 9	7–9	9, S	9, S	9, S	9, S	9, S	9, S	9, S	9, S	9, S	9, S

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

THE ANNELID PHOSPHAGEN: WITH A NOTE ON PHOSPHAGEN IN ECHINODERMATA AND PROTOCHORDATA

By E. Baldwin and W. H. Yudkin

Proc. Roy. Soc. B, Vol. 136, 1950, pp. 614–31

A new, arginine phosphate-like phosphagen is present in annelid and gephyrean worms.

A second phosphagen, possibly identical with creatine phosphate, has also been found in certain annelids but not so far in gephyreans. This second phosphagen sometimes co-exists with the first, but is found alone in some species.

The distribution of these two phosphagens does not appear to be correlated with physiological activity or with environmental factors.

Arginine could not be isolated from either of two annelid or one gephyrean species; a new base is, however, present in the guanidine fraction and has been isolated as the picrate. It has not yet been identified.

The significance of these observations is discussed in relation to the taxonomic status of the Annelida and Gephyrea. It is indicated that there exists a close relationship between these groups.

The new 'annelid phosphagen' is, apparently, confined to the Annelida and Gephyrea, which are thus chemically distinguishable from the Arthropoda and Mollusca.

Some new data are presented concerning the distribution of arginine and creatine phosphates in Echinodermata and Hemichordata, and the evidence concerning these two groups is reviewed with special reference to the echinoderm-hemichordate theory of vertebrate ancestry.

It is concluded that existing data support this theory, and that the new information concerning the phosphagens of the annelids serves to emphasize the wide divergence that exists between the segmented invertebrates and the true Chordata.

E.B.

The Effect of Temperature on the Electrical Activity of the Giant Axon of the Squid

By A. L. Hodgkin and B. Katz

Journ. Physiol., Vol. 109, 1949, pp. 240–9

The giant nerve fibre of *Loligo* provides excellent material for measurements of the electrical characteristics of the surface membrane. The present paper contains an account of experiments dealing with the effect of temperature on the action potential. It is shown that the absolute magnitude of the action potential decreases with increasing temperature but that the resting potential remains practically constant over the range 0–20° C. The time course of the spike is greatly accelerated by a rise in temperature. The rate of decline of the spike appears to have a higher temperature coefficient than the rate of rise.

A.L.H.

The Effect of Calcium on the Axoplasm of Giant Nerve Fibres

By A. L. Hodgkin and B. Katz

Journ. Exp. Biol., Vol. 26, pp. 292-4, 1949

It is well known that a rod of axoplasm can be obtained by extruding the contents of a giant nerve fibre, and that if this is done in sea water, the axoplasm disperses rapidly. The present paper contains a brief account of experiments dealing with the effect of ions on this phenomenon. It is shown that dispersal of axoplasm from the giant axon of *Loligo* depends upon the presence of small concentrations of calcium. No dispersal occurs in isotonic calcium-free solutions of sodium or potassium chloride.

A.L.H.

The Effect of Sodium Ions on the Electrical Activity of the Giant Axon of the Squid

By A. L. Hodgkin and B. Katz

Journ. Physiol., Vol. 108, 1949, pp. 37–77

In recent years physiologists at Plymouth and at Woods Hole have made an intensive study of the giant nerve fibre of *Loligo*. One of the most interesting results of this work has been the finding that the action potential of a nerve fibre is associated with a reversal of potential difference across the surface membrane. For some time no satisfactory way of accounting for this effect

could be found, but it now appears that it may have an interesting explanation in terms of permeability and ionic concentration. Chemical studies have shown that potassium is concentrated in the interior of a nerve fibre whereas sodium is relatively dilute. Experiments described in the present paper suggest that the surface membrane is able to alter its ionic permeability in a remarkable manner during activity. In the resting nerve fibre the membrane appears to be more permeable to potassium than to sodium, and this has the effect of making the inside of the nerve fibre negative with respect to the outside. During activity the membrane does not break down, as was formerly supposed, but reverses the resting condition by becoming highly and specifically permeable to sodium. This change allows sodium to enter the nerve fibre faster than potassium can leave it, with the result that the inside of the nerve fibre becomes positive with respect to the outside. This state of affairs must be transitory, and it is suggested that the rise in sodium permeability is short-lived and that the membrane potential is restored to its resting level by an outward migration of potassium ions.

The 'sodium hypothesis' is supported by the following observations: (i) conduction of impulses is impossible in sodium-free media; (ii) the potential difference across the active membrane varies with the external concentration of sodium in the manner predicted by the hypothesis; (iii) the rate of depolarization of the nerve membrane can be varied over a wide range by altering the external concentration of sodium. A.L.H.

Internode Lengths in the Nerves of Fishes

By P. Kynaston Thomas and J. Z. Young

Journ. Anat., Vol. 83, 1949, pp. 336–50

Measurements of internodal distance and diameter were made on isolated nerve fibres dissociated in glycerin after formalin fixation and osmic acid staining. Several marine fishes were investigated, including *Raia clavata*, *Scyliorhinus canicula*, *Torpedo ocellata* and *Conger conger*.

In the lateral line nerves of the ray and conger eel, the distance between the nodes may reach 8 mm. on the largest fibres. In mammals the corresponding value is 1·5 mm. Internode length increases more rapidly with diameter in the lateral line branch of the vagus than in the branchial branches, and more rapidly in the lateral line nerves of larger than of smaller fishes. In lateral line nerves from fishes of different lengths the ratio of the maximum internode length to the length of the animal is approximately constant. There is not, therefore, a fixed internode length for each fibre diameter, the correlation between the variables being due to the fact that both are correlated with growth.

There is a sharply defined minimum internodal distance of about 0·2 mm. in the various fishes studied, and this is also found in other animal groups.

The conditions in fishes and other vertebrates are consistent with the view that internode length is determined when the nodes are first formed, possibly by surface tension, and later by the amount of growth in length of the nerve. When medullation takes place internode length is short, and is the same for all fibres. As growth proceeds, a relationship between internode length and diameter appears, such that the larger fibres have longer and the smaller shorter internodes. There is little change in the number of nodes after medullation; as the nerves elongate so, too, do the internodes. The occurrence of longer internodes on the larger fibres would be explained if the ultimately larger fibres became myelinated earliest. P.K.T.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1949–50

The Council has to record with deep regret the deaths of Prof. Walter Garstang, formerly a member of the Scientific Staff of the Association's laboratories at Plymouth and at Lowestoft, and later a Vice-President and an Honorary Member; Mr R. A. Todd, also an early member of the Scientific Staff contemporary with Prof. Garstang; Prof. August Krogh, For.Mem.R.S., an Honorary Member of the Association; and Dr Robert Gurney, a Founder of the Association.

The Council and Officers

Four ordinary meetings of the Council were held during the year, three in the rooms of the Royal Society, and one at the Plymouth laboratory. At these the average attendance was sixteen. The Association is indebted to the Council of the Royal Society for the use of their rooms, and to the Council of the Linnean Society for the use of their rooms for the Annual General Meeting.

During the year Dr J. E. Smith was appointed as Governor representing Cambridge University in place of Dr C. F. A. Pantin, F.R.S.; and Mr Harrison S. Edwards representing the Fishmongers' Company in place of Mr A. R. Wagg.

The Plymouth Laboratory

All the major war damage repair and rebuilding having now been completed, attention has been devoted to the equipment of the buildings with furnishings and fittings.

A 15-in. Colchester lathe and tools for sheet metal work have been installed in the workshop; an additional electric power line has been laid. An old doorway in the passage connecting the north and south buildings has been renewed and opened up to give easy access to the main workshop.

The full equipment of both the main workshop and the physiology workshop has added greatly to the scope of the work of the laboratory, enabling the development of many new types of apparatus for research at sea.

The Aquarium

The aquarium has proved as popular as ever, particularly with summer visitors, and many parties of school children have attended with their teachers. The stock of fishes and invertebrates in the tanks has been maintained at capacity.

The display has been much improved by the addition of a number of

coloured drawings illustrating the animals in the tanks. These have been painted by students of the Plymouth City School of Art, and thanks are due to the Principal, Mr L. Duckett, M.C., A.R.C.A., and to the students themselves, especially Miss Jenefer Peter and Mr H. Williams.

Dr D. P. Wilson has recorded in Vol. XXVIII, No. 2, of the *Journal* some observations on the lives and habits of a variety of species living in the aquarium. Among these is the record of a *Sabella* which has lived in one of the tanks for over ten years.

Research Ships

The research vessels *Sabella* and *Sula* have worked regularly throughout the year. As reported last year, the *Sula* has proved to be a most efficient and useful little ship and has made it possible for the *Sabella* to undertake extended cruises to more distant waters both up and down Channel.

By the beginning of this year deterioration of the underwater metal sheathing of the *Sabella* had reached a point where it became necessary either to remove it altogether or to make extensive renewals of the metal. By permission of the Admiralty the sheathing has been removed. To carry out this work *Sabella* was placed in dry dock during the first fortnight in June.

All the necessary requirements having now been completed the *Sula* has been accepted for classification by Lloyds.

The motor-boat *Gammarus* has, as usual, worked regularly throughout the year, apart from brief periods for normal maintenance of hull and engines.

In December 1948 permission was obtained from H.M. Treasury to incur costs necessary for the preparation of plans and specifications for a proposed new research vessel to replace *Sabella*. In co-operation with Messrs Graham and Woolnough, a Liverpool firm of Naval Architects, these have been completed and have formed the basis of tenders from selected firms for the construction of the vessel.

The Staff

Mr N. A. Holme was appointed to the staff in the grade of Scientific Officer in April 1949.

Dr J. A. C. Nicol was appointed to the staff in the grade of Senior Scientific Officer in June 1949.

Dr J. S. Alexandrowicz was appointed to the staff in the grade of Temporary Senior Scientific Officer on 1 January 1950.

Mr D. K. Hill resigned from the post of Physiologist on the staff on 30 September 1949, to take up an appointment to direct a new Department of Biophysics at the British Post-graduate Medical School at Hammersmith.

Mr F. S. Russell, Dr H. W. Harvey and Mr P. G. Corbin attended the thirty-seventh meeting of the International Council for the Exploration of the Sea in Edinburgh in October 1949.

Occupation of Tables

The following one hundred and nine workers have occupied tables at the Plymouth laboratory during the year:

B. C. ABBOTT, London (Physiology of dogfish muscle).
Miss E. B. ALBRECHT, London (Behaviour of *Arenicola ecaudata*).
Dr A. A. ALEEM, London and Alexandria (Littoral diatoms).
Dr X. M. AUBERT, London and Louvain (Physiology of dogfish muscle).
T. BAGENAL, Cambridge (Identification of fishes).
R. BAINBRIDGE, Oxford (Plankton interrelationships).
Dr ELIZABETH J. BATHAM, Cambridge (Nerve net of sea anemones).
A. C. G. BEST, London (Histology of marine animals).
G. BOLSTER, Oxford (General zoology).
Dr ANNA M. BIDDER, Cambridge (Library).
Dr HANS BOREI, Stockholm (General).
Dr P. BUFFA, Oxford (Effects of sodium fluoracetate on marine animals).
Miss E. M. BROWN, London (Parasitic Dinoflagellates).
B. C. BROWNE, Cambridge (Geology and geophysics of ocean bed).
Prof. S. F. BUSH, Natal (Laboratory organization).
H. W. CHANG, Academia Sinica, Shanghai (Biology of *Callionymus*).
Dr G. CHAPMAN, London (Mesogloea of *Calliactis*).
Dr P. N. J. CHIPPERFIELD, I.C.I., Brixham (Library).
K. U. CLARKE, London (General zoology).
Miss E. CLAY, I.C.I., Brixham (Algal cultures).
Dr & Mrs N. E. COLLIAS, Wisconsin (Littoral fauna).
F. R. COOMBE, Plymouth (Physical properties of sand grains).
R. A. COX, National Institute of Oceanography (Oceanographical methods).
Dr D. J. CRISP, I.C.I., Brixham (Library).
Dr D. R. CROFTS, London (Mollusc embryology).
R. I. CURRIE, National Institute of Oceanography (Chemistry of sea water).
Prof. J. F. DANIELLI, London (Nucleus transplantation in *Echinus* eggs).
E. J. DENTON, Aberdeen (Nerve fibres in *Carcinus*).
Miss E. DRESEL, Cambridge (Excretion in Isopods and Amphipods).
J. E. ELGOOD, London (General zoology).
D. ETHERINGTON, London (Sporozoan parasite in *Phascolosoma minutum*).
G. R. FISH, Colonial Office (Culture of phytoplankton).
J. E. FORREST, London (Nudibranchs).
G. R. FORSTER, D.S.I.R. (Biology of prawns).
H. C. FOUNTAIN, Torpoint (Marine Acarines).
Dr VERA FRETTER, London (Ecology and structure of *Cerithiopsis* and *Triphora*).
T. GASCOYNE, London (Biology of *Tritonia*).
Prof. J. GRAY, F.R.S., Cambridge (Locomotion of fishes).
Miss U. M. GRIGG, D.S.I.R. (Biology of Trochids).
Surg. Lieut. D. O. HAINES, R.N., H.M.S. *Challenger* (General).
Dr J. E. HALE, London (Chlorocruorin haem in *Sabella*).
R. E. HALL, Southampton (Marine Chironomids).
R. HAMOND, Holt, Norfolk (Hydroids and Polyzoans).
Dr J. P. HARDING, British Museum (Nat. Hist.) (Colour photography of Entomostraca).
Miss M. B. HARLEY, Durham (Feeding in *Nereis diversicolor*).
Dr T. J. HART, National Institute of Oceanography (Ice diatoms; hake).

M. N. HILL, Cambridge (Geology and geophysics of ocean bed).
A. L. HODGKIN, F.R.S., Cambridge (Neurophysiology).
Prof. SVEN HÖRSTADIUS, Uppsala (Nucleus transplantation in *Echinus* eggs).
W. R. HOWELLS, Aberystwyth (Intertidal ecology).
O. D. HUNT, Newton Ferrers (Fouling organisms).
Prof. E. G. HUTCHINSON, Yale (Mineral inclusions in marine animals).
A. F. HUXLEY, Cambridge (Neurophysiology).
P. H. JELLINEK, Cambridge (Marine ecology).
Dr M. W. JEPPS, Glasgow (Life history of *Polystomella*).
R. JOHNSTON, Aberdeen (Chemistry of sea water).
F. R. HARDEN JONES, Colonial Office, (General; swim bladder in fishes).
W. C. JONES, Cambridge (Orientation of sponge spicules).
K. A. JOYSEY, London (Echinoderms).
Dr B. KATZ, London (Neurophysiology).
Dr G. Y. KENNEDY, Sheffield (Pigments of *Branchiomma* and *Aplysia*).
R. D. KEYNES, Cambridge (Neurophysiology).
Prof. W. B. R. KING, F.R.S., Cambridge (Geology and geophysics of ocean bed.)
Dr F. G. W. KNOWLES, Marlborough College (Control of pigment movement in Crustaceans).
Miss P. KOTT, Australia (Colonial Tunicates).
G. KRISHNAN, Manchester (Physiology of sinus gland in crabs).
Dr MARIE V. LEBOUR, Cawsand (Decapod Crustaceans).
Dr P. R. LEWIS, Cambridge (Neurophysiology).
Dr H. W. LISSMAN, Cambridge (Locomotion of fishes).
Dr JOAN I. LORCH, London (Nucleus transplantation in *Echinus* eggs).
Dr A. G. LOWNDES (Entomostraca).
Dr SIDNIE M. MANTON, F.R.S., London (Locomotion of Arthropods and Polychaetes).
Dr L. HARRISON MATTHEWS, Bristol (Locomotion of fishes).
M. D. MENON, Madras (Biology of *Gadus luscus* and *G. minutus*).
M. N. MISTAKIDIS, Conway (Library).
Miss V. MOYLE, Cambridge (Excretion in Isopods and Amphipods).
Prof. LILY NEWTON, Aberystwyth (Library).
V. NOVAK, Cambridge (Sinus gland hormones of Crustaceans).
Dr T. OUANG, Amoy (Hatching gland of dogfish embryo).
Dr C. F. A. PANTIN, F.R.S., Cambridge (Nerve net of sea anemones).
Prof. R. A. PETERS, F.R.S., Oxford (Effect of sodium fluoracetate on marine animals).
W. T. W. POTTS, Cambridge (Microanalytical methods for inorganic ions).
Dr R. D. PURCHON, Cardiff (Rock-boring Lamellibranchs).
Dr JEANETTE L. RAYMENT, Edinburgh (Radioactive tracers and algae).
Dr. T. D. M. ROBERTS, Glasgow (Electrophysiology of Cephalopod eye).
Dr J. D. ROBERTSON, Glasgow (Microanalysis of inorganic ions in *Sepia*).
G. A. ROBINSON, Development Commission (Phytoplankton).
M. ROESSINGH, Leiden (Plankton).
Dr E. S. RUSSELL, Hastings (Decapod Crustaceans).
Dr L. SILÉN, Stockholm (Biology of Polyzoans. Fixation of *Phoronis*).
Dr E. W. SIMON, Oxford (Toxicity studies in *Echinus* eggs).
B. W. SPARROW, Newton Ferrers (Fouling organisms).
Miss F. A. STANBURY, Plymouth (Library).
Miss M. F. SUTTON, London (Regeneration in *Ciona*).
J. SWALLOW, Cambridge (Geology and geophysics of ocean bed).
R. V. TAIT, London (General).

Prof. R. V. TALICE, Uruguay (General).
A. G. TAYLOR, Freetown (General).
Dr HAROLD THOMPSON, Australia (General).
D. VAUX, Lowestoft (Physical oceanography).
P. R. WALNE, Conway (Chemistry of sea water).
I. M. WATT, Exeter (Underwater photography).
Dr J. E. WEBB, Nigeria (General zoology).
Dr G. WEDDELL, Oxford (Staining of corneal nerve fibres).
Dr S. WEIDMANN, Berne (Neurophysiology).
G. P. WELLS, London (Behaviour of *Arenicola ecaudata*).
Dr E. WESTBLAD, Stockholm (Turbellarians).
Dr W. H. YUDKIN, Cambridge (Phosphagens in Polychaetes).
Dr E. ZANDER, Oxford (Staining of corneal nerve fibres).

A very large number of short visits have been made by research workers wishing to see the work of the laboratory or to discuss their problems with individual members of the staff. Among these the following have come from overseas: Dr Nazir Ahmad, E. Pakistan; Miss L. M. Angel, Adelaide; H. C. Aslyng, Denmark; Prof. and Mrs G. P. Baerends, Groningen; R. Bassindale, Achimota College, Gold Coast; Prof. and Mrs L. R. Blinks, Pacific Grove; Señora Bonilla, Uruguay; D. F. Bumpus, Woods Hole; Dr C. Lalor Burdick, New York; Dr B. Kullenberg, Göteborg; Miss D. F. McCarthy, Adelaide; Dr M. F. E. Nicolai, Leiden; Dr K-G. Nyholm, Uppsala; Prof. T. Park, Chicago; Dr W. Rodhe, Uppsala; W. F. Royce, Woods Hole; E. F. Scott, New Zealand; Miss N. G. Sproston, Shanghai; Dr E. A. Thomas, Zurich; E. C. Zimmerman, Honolulu; J. Pericot and J. Baca, Barcelona.

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin, and were attended by forty-five students from the following Universities and University Colleges: Oxford, Cambridge, Glasgow, Aberdeen, Dublin, Durham, London, Sheffield, Cardiff, Exeter, Hull, Leicester, Southampton, and from Chelsea Polytechnic, Middlesex Hospital, and Plymouth Technical College.

Also during the Easter Vacation Mr P. H. F. White brought nine boys from Harrow School, and Miss M. E. Morris five from the Bec School, London.

Scientific Work of the Plymouth Laboratory Staff

With the increasing number of visiting workers, and especially of younger scientists preparing for posts at home and abroad, much of the time of the scientific staff has inevitably been taken up in giving help and advice. This is an important side of the work of the laboratory which is contributing to the efficiency of the post-war expansion in marine biological investigations.

Physics and Chemistry of Sea Water

Last year's report described in some detail the work on the measurement of daylight in air and under water which is being carried out by Dr W. R. G.

Atkins in collaboration with Dr H. H. Poole, Mr F. J. Warren and Miss P. G. Jenkins. This work has been continued and is being prepared for publication. Special attention has been given to the re-standardization of photocells and to the examination of new ones. The determination of the vertical extinction coefficient of natural waters by the photoelectric balance by depth seems to be a simple method which is scarcely affected by sudden fluctuations in the intensity of daylight. Dr Atkins worked with Dr Poole in the Royal Dublin Society's laboratory during parts of May and June.

Much time has been devoted to the study of the scattering of light in the Tyndall beam, using the R.C.A. electron multiplier cell, the sensitivity of which is vastly greater than that of any cell previously available for use, even with high amplification. Attempts are being made to ascertain the effects due to the different sized particles suspended in the water.

Dr Atkins also continued work on the copper cycle in the sea. The new plastic-lined closing water-bottle made it possible to deal with other than surface samples. As with several other minor constituents the deeper layers are less rapidly depleted than the surface.

Optical methods for the study of suspended matter are being supplemented by chemical analyses and the deposits, algal and inorganic, have been further examined by Dr Atkins and Mr F. A. J. Armstrong.

Dr H. W. Harvey has continued, in collaboration with Mr Armstrong, an investigation of the phosphate and total phosphorus in the waters off Plymouth. The results of this survey, commenced in 1947, will shortly be published. It is thought that this study of the phosphorus cycle in the sea has allowed the water masses passing through the area to be distinguished the one from the other, simply, and at any time of year, in terms of their potential fertility. There is evidence indicating that this potential is rather closely related to the actual productivity of the water mass and to the survival of young fish. This study required some knowledge of the quantity of plants and of pelagic and benthic animals in the area. From information supplied by colleagues and friends and from observations on plant population made during the past year, Dr Harvey has been able to arrive at rough tentative estimates of the average population density of the main ecological groups, and of their food requirements. Since these estimates and their interrelations are of wider interest than that for which they were originally made, an account will be published in the *Journal*.

Dr L. H. N. Cooper has continued to re-assess and correlate earlier work in the English Channel, Celtic Sea and the adjacent waters of the Atlantic Ocean. In collaboration with Mr David Vaux he has dissected one thread from the pattern of events, the effects of winter cooling of the water south-west of Ireland. In some winters this may become heavier than the adjacent oceanic surface water. It then tends to flow westward over the shelf to the edge of the slope where it may sink until it meets water of similar density. In this way shelf water may be carried down to a depth of 600 m. or more. This

'cascaded' water may be recognized by its high oxygen content. The results have been published in Vol. XXVIII, No. 3, of the *Journal*, together with further developments and applications to the hydrography of the Celtic Sea.

Amongst the hydrographical records obtained south-west of Ireland between 1910 and 1913 by the Irish Fisheries Service, there were a number which suggested that heavy water overlaid lighter. Often these anomalous records were internally consistent so that it seems very doubtful whether they should be dismissed as due to errors of observations. If they are accepted as correct and indicating a density inversion, it becomes possible to follow for 90 miles along the side of the continental slope water which had flowed from the Celtic Sea as a winter cascade. The course of this water is predicted by applying Rossby's wake stream theory to the oceanic water lying off the slope. It would seem likely that Rossby's theory may be widely applied in the Atlantic Ocean south-west of the British Isles and will provide a valuable working hypothesis for unravelling the complex water movements which occur.

Dr Athelstan Spilhaus has observed density inversions in the neighbourhood of the New England continental slope, although the operative causes may there be different. Dr Cooper is maintaining close contact with Dr Spilhaus.

Mr F. A. J. Armstrong has continued the monthly hydrographic cruises to the Station E 1, ten miles beyond the Eddystone, and has carried on the routine phosphate estimations begun by Dr Atkins in 1923. He has also been engaged on improving existing methods of analysis of nitrate, and has applied Dr Harvey's absorptiometer for the estimation of iron with 2:2'-dipyridyl. Experiments are being made to test whether storage of sea water in glass vessels leads to leaching of iron from the walls and precipitation of ferric hydroxide.

Mr Armstrong has collaborated with Dr Harvey in work on the phosphorus cycle, making many analyses of total phosphorus. A short paper by him on corrections in the method for phosphate determination and reproducibility of results has been published in Vol. XXVIII, No. 3, of the *Journal*.

Plankton

Mr F. S. Russell has completed his monograph on the Medusae of the British Isles and the manuscript and the many coloured plates and line drawings have now gone to the Cambridge University Press for printing.

The weekly half-hour oblique hauls with the 2 m. stramin ring-trawl have been continued during the year. Preliminary inspection of the catches by Mr P. G. Corbin shows no marked change from the very low level of production of young fish observed in 1948.

A study of the small coloured flagellate and non-motile forms present in the sea water off Plymouth has been started by Dr Mary Parke. The first stage in the work, now in progress, is the study of the different marine types to be found in these waters so that in any later quantitative work a quick recogni-

tion and classification of single individuals can be made. This study of the different types is being done by the cultivation of the organisms present in samples of sea water taken at intervals during the year. The observations that have been made during the last year for inshore waters suggest that, although most classes are represented throughout the year, there is a rise and fall in the numbers of some classes with the time of the year; for example, the flagellate forms belonging to the Chrysophyceae are most abundant from November to May, while those belonging to the Cryptophyceae (mainly with red pigment) are most common from June to October. In addition to many mixed cultures of these new organisms twenty-five pure cultures of new organisms, started from clones, have been obtained. These cultures include representatives from the following classes: Chlorophyceae, Chrysophyceae, Bacillariophyceae, Cryptophyceae, Dinophyceae, Euglenineae, Myxophyceae and possibly Xanthophyceae.

The stock cultures of marine diatoms and flagellates have been maintained throughout the year, and subcultures have been sent to other institutions for research and teaching purposes.

Arising from the studies on the relation between the phosphorus available in the water and the animal populations, Dr H. W. Harvey is investigating the accuracy of sampling of zooplankton in water of moderate depth by means of vertical net hauls. Meters have been constructed which register the flow of water past them. Provided the ratio of the filtering area of the net to the size of its mouth exceeded a limiting value, substantially the same flow of water was registered when the net was hauled through the same distance of water, irrespective of the position of the meter in the mouth. This allows the use of these meters for measuring the quantity of water filtered by a net. It has been found that a conical net acts as an aerofoil, causing a negative pressure in its wake which assists the passage of water through the net.

A meter, fitted with a device to stop the vanes revolving when the net is lifted from the water, has been supplied to the Fisheries Laboratory at Lowestoft, and has now been in frequent use in a Hensen net for several months. A similar meter has been supplied to the Scottish Fishery Board.

Observations have been made with nets of different sizes and types to determine the nature or degree of patchiness of zooplankton. The aim is to arrive at the simplest means of obtaining a sample truly representative of an area. The workshop facilities have made possible this development of apparatus for a special purpose.

Fauna and Flora of the Sea Floor

Dr D. P. Wilson's experiments on the settlement reactions of *Ophelia bicornis* larvae were continued during the summer-breeding season. Taking, as a starting-point, the result of a single test in 1948 which was not readily interpreted on the assumption that physical size and shape of the sand grains

is the only factor in promoting metamorphosis, a set of experiments was devised which have shown that there is at least one other factor involved, and one which may have an even greater influence. Sand from the nearby Salthouse Lake re-graded to resemble the natural Bullhill sand, in which the adult worms live, repels the larvae more strongly than the slightly greater angularity and roughness of the grains would appear to merit. It was found that when this sand is sprinkled into water in a dried condition most of it will float, whereas the Bullhill sand sample used in the experiments, when similarly treated, almost all sinks. The Salthouse Lake sand becomes readily wettable, and therefore sinkable, after heating to a high temperature; larvae will then settle in it and metamorphose. Extraction of the sand by ether, alcohol or acetone did not destroy its flotability and neither did treatment with aqua-regia; the sand was not made any more attractive to the larvae by the use of these reagents. Contact with finely powdered activated charcoal reduced the flotability of Salthouse Lake sand, but not completely as did heating. The larvae, nevertheless, settled very readily in the sand after this treatment, and a big proportion at once proceeded to metamorphose. Treatment of Bullhill sand with activated charcoal increased its attraction and speeded the onset of metamorphosis. Activated charcoal treatment did not, however, induce larvae to metamorphose in a calcareous sand of similar grade to the quartz sand of the Bullhill Bank. Experiments with the smallest sizes of sand grains after treatment with activated charcoal indicate that size can still be regarded as an important factor in influencing settlement. Work is still in progress and no definite conclusions from this year's results have yet been drawn.

During the year Dr Wilson has published in Vol. XXVIII, No. 2, of the *Journal* an account of the decline of *Zostera* at Salcombe and its effects on the shore. A comparison of old and recent photographs of the eastern shore of the harbour, taken at comparable states of the tide, indicate that at the lower levels the shore has been lowered 2 or 3 ft. as a result of the washing away of sand formerly bound by the roots and rhizomes of the *Zostera*. At the same time, sand has been piling up at high-water mark; some of this must have come from the old *Zostera* beds, but more has accumulated from farther afield.

The fauna near low-water mark is changing in character; it is not as rich as it used to be, particularly in those commensal species for which the Salcombe *Zostera* beds were notable.

Dr Mary Parke is collecting together the data for the second paper on the British Laminariaceae dealing with *Laminaria digitata* (L.) Lamour. So far most of the calculations for the growth of the frond have been made but they have not yet been analysed.

Additions have been made to the collection of preserved specimens of marine algae being built up at the laboratory; the most interesting of these are the very rare algae *Atractophora hypnoides* Crn. and *Gigartina teedii* Lamour., which are new records from the Plymouth area, and *Mesogloia lanosa* Crn. and

Myriocladia loveni J. Ag.? which have not previously been recorded for the Devon coast. The *Myriocladia* may have to be placed in a new species. Further information has been accumulated on the occurrence, distribution and reproduction of the marine algae of the Plymouth area.

Mr G. M. Spooner has continued his work on *Gammarus* and other Amphipoda, and a paper on the occurrence of *G. zaddachi oceanicus* is in preparation. Examination of collections of Amphipoda in general from Plymouth and elsewhere shows how imperfect our knowledge still is of even the species present. *Stenothoë valida* and *Apherusa henneguyi* are new records for the Plymouth area and for Britain. The latter appears to be well established on offshore grounds and to be regularly eaten by *Gadus minutus*. Unrecognized species of *Stenothoë*, *Leucothoë*, *Ampelisca* and *Monoculodes* have also been observed.

In September 1949, Mr Spooner, assisted by Mr N. A. Holme, made a preliminary survey of the fauna of the Helford estuary.

Dr H. G. Vevers has continued his work on the breeding biology of the Plymouth echinoderms. The occurrence in the gonads of *Asterias rubens* of the parasitic ciliate, *Orchitophrya stellarum*, suggests that only rich and well-fed starfish populations are attacked. The parasite has been found in starfishes south of the Eddystone and also in Plymouth Sound, but not in the intermediate Rame-Eddystone Grounds. An attempt is now being made to estimate the density of starfishes and other epifaunal invertebrates by means of photographs taken underwater with an apparatus developed in the laboratory. Photographs have already been taken at depths down to 70 m., but their quality is not yet wholly satisfactory and modifications are being made which should give better definition. The apparatus takes a series of forty to forty-five photographs at each descent, the area covered by each photograph being 1 m. square. A number of such series have now been taken on sand, muddy sand and gravel bottoms near Plymouth. They show a high density of the ophiuroid, *Ophiothrix fragilis*, with smaller numbers of *Asterias rubens* and other echinoderms as well as *Chlamys opercularis*, polyzoan colonies and worm casts. At the depths worked the natural light is quite insufficient to allow an adequate exposure and all lighting is, therefore, done by photofloods worked from the electric mains of R.V. *Sabella*.

Mr N. A. Holme has been continuing his work on techniques for quantitative investigation of the bottom fauna. Using the new bottom sampler, described in Vol. XXVIII, No. 2, of the *Journal*, two series of twenty hauls have been made in Bigbury Bay and Whitsand Bay, with the object of determining the number of samples necessary for a fairly accurate determination of the biomass.

In addition a new type of core sampler is being tested in which the coring tube is made to penetrate more deeply by producing a suction at the top of the tube. The suction is provided by opening a chamber of air at atmospheric pressure under water, the chamber being attached to the top of the coring tube. With this apparatus it is hoped to take cores of 1/50 m.^{2} area and of 30 cm.

depth. Observations on land indicate that suction greatly increases the penetration of a coring tube into sand, but preliminary experiments at sea have not produced cores longer than 15 cm. This may be due to a number of causes, among which is the suggestion, supported by results obtained by Mr M. N. Hill with a free-falling core sampler, that the depth of sand overlying rock in the Plymouth area is less than 30 cm. in many places. It is also possible that the apparatus is not sufficiently weighted, since the buoyancy of the air chamber seriously diminishes its weight under water.

A considerable amount of data has now been collected on the ecology and systematics of the genus *Ensis*. There appear to be three British species: *E. ensis* (L.), *E. siliqua* (L.) and *E. arcuatus* Jeffreys. Examination of named specimens from various collections, however, has revealed the considerable difficulty experienced in identification, particularly in regard to *E. arcuatus* (Jeffreys). The three species inhabit different types of soil: *E. ensis* occurs in fine gravel, *E. siliqua* in clean sand, and *E. arcuatus* in muddy sand. The latter is the least common and most localized of the three species.

Physiology of Marine Organisms

Mr D. K. Hill, who left the staff in October 1949, has continued work with the 200 μ nerve fibre of *Sepia*. The statement made in the last Report, to the effect that it is possible to measure a small increase in diameter of the fibre as the result of stimulation, has been substantiated. This amounts to about 0·2 μ increase in diameter for 10,000 impulses. It appears, however, that the effect is not—as was previously stated—largely due to the difference in volume between the hydrated sodium and potassium ions which are known to exchange across the membrane during activity. It now seems more likely that only about 6 % of the change can be accounted for in this way, and the greater part of the swelling is probably due to an increase in the osmotic pressure of the interior of the fibre brought about by the entry of equivalent amounts of sodium and chloride ions. There is evidence that the fibre undergoes a very small *decrease* in volume initially. This shows up at the start of a period of high-frequency stimulation, but after a few seconds the main phase of swelling supervenes. The maximum shrinkage is about 0·02 μ in diameter. It is only possible to speculate on the cause of this phenomenon.

The kinetics of the penetration of water into the giant fibres of *Loligo* and *Sepia* in response to a change in the external osmotic pressure have been investigated: the results were needed in connexion with the work described above. It was found that the length of a nerve fibre changes when it swells or shrinks: the tension determines which way it goes. When the fibre is under low tension swelling gives an increase in length; if the fibre is put under higher tension the length decreases. In the work on the kinetics of water penetration this change of length was used to follow the volume change; it is a much more sensitive indicator than is the diameter of the fibre.

Work has been continued in connexion with the change in the opacity to white light of a crustacean nerve trunk which is brought about by repetitive stimulation. It was found that the opacity is very sensitive to changes in fibre diameter which follow alterations in the osmotic pressure of the external solution. The response to stimulation is of the right order of magnitude to be attributable to changes in fibre diameter.

Dr J. A. C. Nicol has continued his studies of the nervous system of polychaetes with the intention of concentrating on sensory mechanisms in marine animals. An investigation of photosensitivity in the sabellid *Branchiomma vesiculosum* is now in progress. This has been made possible through the co-operation of Dr Atkins and Mr Warren who have assisted with photoelectric apparatus and measurements. By using the giant axon reflex of *Branchiomma* as an indicator of responsiveness, information has been collected on the sensitivity to changes in light intensity. There is considerable individual variation, but by studying groups of individuals it has been possible to gather statistical data for representative populations. The animals can detect very small decrements in intensity. A relatively greater intensity change is required to evoke a response at low initial intensities than at higher intensities. The animals respond to intensity changes throughout the visual spectrum but appear to be less sensitive to longer wave-lengths. In addition to responding to sudden decreases in intensity, the animals also react to a moving intensity change (i.e. progression of a shadow) across the visual field. Sensitivity to a moving stimulus is much higher than to sudden and uniform decreases in light intensity, and adaptation to the latter does not affect response to a moving stimulus. Various lines of evidence indicate that adaptation occurs neither on the efferent nor on the afferent sides of the reflex pathway, but takes place rather in central correlation areas. *Branchiomma* is unique among non-arthropods in the possession of a primitive form of compound eye. The separate parts of this eye probably facilitate detection of movements.

Dr J. S. Alexandrowicz has continued researches, interrupted by the war, on the nervous system of invertebrates, with special attention to the peculiar innervation of some muscle fibres in Crustaceans. By means of methylene-blue staining these were more closely examined in *Homarus vulgaris* and *Palinurus vulgaris*, and it was found that in the dorsal part of the abdomen there are ganglion cells, four in each segment, which send numerous short richly ramifying processes to the muscles and a long process, one from each cell, to the abdominal ganglionic chain. The muscle bundles in which the short processes terminate show a certain independence and a somewhat different structure from the neighbouring muscles, while the nerve fibres ending in them, besides the cell-processes mentioned above, seem to be also independent in their peripheral course from other nerves running to the muscles. Several ganglion cells of the same kind were also found in the thoracic region.

In the Gastropod *Aplysia punctata* the nerves of the digestive organs were investigated by means of methylene-blue staining. A rich nervous plexus could be seen in the oesophagus, stomach and intestine with a different arrangement of the nervous elements in each of these parts. Nerve cells of various shapes have been found; the bipolar cells, which may be regarded as sensory elements, send one process towards the lumen of the alimentary canal and the other from the opposite side into the nerve-plexus; other cells of unipolar and multipolar appearance and of various sizes are scattered in the walls of the digestive organs or form small groups. In the region where the oesophagus joins the gizzard the nervous elements are arranged in the form of an irregular ring and the ganglion cells are especially abundant at this place.

The results of some exploratory tracer experiments with seaweeds by Mr G. M. Spooner have been published in Vol. XXVIII, No. 3, of the *Journal*. These concern the uptake of the elements strontium and yttrium.

Radioactive strontium is extracted from sea water by the brown seaweeds, in particular by *Fucus serratus*. It is held that this effect is simply a result of ionic exchange, and that the algae regularly contain many times as much strontium in their cell fluids as exists in sea water. On the ionic exchange hypothesis, it appears that *F. serratus* has about 40 times as much strontium as sea water, *F. vesiculosus* about 30, *Ascophyllum nodosum* about 20, and *Laminaria digitata* about 14. By contrast, red algae and green algae such as *Ulva* extract 'active' strontium only to a small or negligible extent. On the above hypothesis, in *Gigartina* the strontium is concentrated by a factor of about 2, while in *Rhodymenia* it may be less than in the sea.

Radioactive yttrium is heavily taken up by the red algae (*Rhodymenia*, *Gigartina*, *Chondrus*) and by the green alga *Ulva*, even to the extent of depleting the water of this element, or very nearly so. The yttrium, however, is not usually heavily taken up by the brown algae, and may, as with a sample of *Fucus vesiculosus* var. *evesiculosus*, be taken up only to quite a small degree.

The diatom *Nitzschia* takes up 'active' yttrium very heavily.

The extraction of yttrium appears to be a matter partly of ionic exchange and partly of *adsorption* on surfaces. It is suggested that both processes may be important with red algae, the former primarily with brown algae, and the latter primarily with *Nitzschia*.

From the 'decay' characteristics of mounted pieces of frond of the red algae and *Ulva*, estimates of the true half-life of Y^{90} were made. The value derived is 63·4 hr. (or 2·642 days).

Fish and Fisheries

During the year Mr G. A. Steven completed a report on the mackerel fishery in the south-west of England with special reference to spawning, feeding and 'fishermen's signs'. This report has been published in Vol. XXVIII, No. 3, of the *Journal*. In last year's Report the importance of 'yellow water'

was mentioned. Further study of mackerel catches from waters of different kinds has provided what appears to be a simple and straightforward explanation of Allen's generalization that the catches of mackerel in May in the Newlyn deep sea fishery are to some extent affected by the amount of sunshine in the same region in February and March.

Data bearing upon the difficult problem of age and growth rate in mackerel are now being worked up. It is found that the otoliths, if carefully cleaned and examined by direct illumination under water against a black background, can be read, though not always with ease even in the younger fish and often not at all in older fish. Age determination by scale readings is also possible, but the scales are so small that the difficulty of obtaining uncontaminated scale samples from large numbers of fish is almost unsurmountable. An additional difficulty is that only a very small proportion of the scales show recognizable growth markings. Nevertheless, a sufficient number has been collected to show that they give readings in agreement with those of the otoliths. The use of otoliths has therefore been adopted as being less tedious and more satisfactory than scales. No skeletal structure has been found that carries reliable indications of annual growth increments.

Because of the difficulty of reading and interpretation in both scales and otoliths much doubt has surrounded the growth and age of mackerel. In 1914, Nilsson published the following figures relating to their growth in Swedish waters:

Length at end of	cm.
1st year	Up to 21·0
2nd year	21·5–28·0
3rd year	28·5–31·0
4th year	31·5–33·0
5th year	33·5–35·0

By contrast, Le Gall, in 1938, gives the following figures for mackerel in the English Channel and Celtic Sea:

Length at end of	cm.
1st year	8–11
2nd year	18–21
3rd year	26–28
4th year	30–32
5th year	About 35

The wide divergence between the results of those two workers for fishes of the two younger year-classes cannot be attributed to differences in locality, especially as preliminary results derived from data collected in 1936 and 1937 in the English Channel and Celtic Sea provided results in agreement with those of Nilsson. Those tentative sizes published in 1939 were:

Length at end of	Up to about
2nd year	27·0 cm.
3rd year	31·5 cm.
4th year	33·5 cm.
5th year	35·0 cm.

Data concerning the length of 1-year-old fish had not then been fully analysed. Further data for the years 1938, 1939, 1940, 1948 and 1949 are now being worked up. The results so far obtained confirm the previous observations and are still in agreement with those of Nilsson, a length of well over 20 cm. often being reached by the end of the first year of life. A report on this work is now being prepared.

Mr P. G. Corbin has continued work on the Ammodytidae. Considerable numbers of the smooth sand-eel, *Gymnammodytes semisquamatus* (recorded as *Ammodytes circerellus* in the Reports of Council for 1947–48 and 1948–49), have been caught in the Plymouth area. It has thus been possible to compare the vertebral numbers of the Plymouth population with that of specimens from Scottish waters. Further comparison of this species with samples of the Mediterranean smooth sand-eel, *G. cicerelus*, and the South African species *G. capensis*, is the subject of a note for the *Journal*. The distribution of the post-larval Ammodytidae in Scottish waters is also being studied. This has been made possible by the courtesy of Dr C. E. Lucas, Director of the Marine Laboratory of the Scottish Home Department at Aberdeen, where extensive collections were made available to Mr Corbin for examination.

Mr M. D. Menon, Indian State Scholar, has studied the biology of *Gadus minutus*. In its post larval stages *G. minutus* feed entirely on copepods, mainly *Pseudocalanus elongatus*. The O-group feeds on small decapods, amphipods, copepods, isopods and polychaetes. The adolescent and adult groups feed on larger decapods like *Processa canaliculata*, *Galathea* sp. and *Portunus* sp., fish, polychaetes and amphipods. The feeding of the fish shows a seasonal fluctuation depending on spawning and growth.

The age and growth rate of the fish have been computed from the supra-occipital crests, which show alternating opaque and transparent zones. The males and females grow at the same rate in the first year; but in the succeeding years the males grow more slowly than the females. The spawning period is from February to May with the height of spawning in March and April. The majority of males reach maturity at *ca.* 11 cm. and the females at *ca.* 13 cm. Most of the fish spawn in their second spring. The results of this work are being published in Vol. XXIX, No. 1, of the *Journal*.

Mr H. W. Chang, British Council Scholar from the Academia Sinica, has been working on the biology of the dragonet, *Callionymus*. He has found that in addition to the two species *C. lyra* (L.) and *C. maculatus* (Rafin), a third species *C. fasciatus* (C. & V.), previously unrecorded off Plymouth, also occurs.

Both the otoliths and radials of the pectoral girdle can be used for age determination in these three species, but the latter are far more satisfactory than the otoliths. It has been found that the male *C. lyra* may reach 5 and the female 7 years of age, while no *C. maculatus* nor *C. fasciatus* has been found over 3 years old.

In the male *C. lyra* the onset of sexual maturity may take place in the third year, or it may be delayed until the fish is in its fourth or fifth years. Sexually mature fish have not been found less than about 20 cm. in total length. During the most intense period of the breeding season, April and May, nearly 80% of the males above 20 cm. are fully mature. The percentage of mature males falls abruptly in July and August, and it is less than 5 % in the winter. It is, therefore, probable that most of the male *C. lyra* die after one breeding season. Whether or not the female survives more than one spawning has not yet been determined.

Observations are also being made on the change in form and coloration in the male in relation to sexual maturity, *Callionymus* being remarkable for its sexual dimorphism.

The Library

The thanks of the Association are again due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association. Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated. To Prof. A. V. Hill, F.R.S., we are grateful for the gift of 18 volumes of *Harvey Lectures*, which cover the years 1924–47. Among other acquisitions, by purchase out of the Browne Bequest Fund, may be mentioned specially: William Scoresby, *An Account of the Arctic Regions, and the Journal of a voyage to the Northern Whale-Fishery*, 3 volumes; Sowinsky, *Amphipoden des Baikal Sees*, text and plates; Weber and Beaufort, *The Fishes of the Indo-Australian Archipelago*, 8 volumes; Lang, *Monographie der Harpacticiden*, 2 volumes; Harvey, *Phycologia Australica*, 5 volumes; and 3 volumes of the *Harriman Alaska Expedition Reports*.

Published Memoirs

Vol. XXVIII, No. 1, of the *Journal* was published in June 1949, No. 2 in October, and No. 3 in December.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ALEEM, A. A., 1950. A fungus in *Ectocarpus granulosus* C. Agardh near Plymouth. *Nature*, Vol. 165, p. 119.

AL-HUSSAINI, A. H., 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: Anatomy and Histology. *Quart. Journ. Micr. Sci.*, Vol. 90, pp. 109–39.

AL-HUSSAINI, A. H., 1949. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits: Cytology and Physiology. *Quart. Journ. Micr. Sci.*, Vol. 90, pp. 323-54.

BACCI, GUIDO, 1949. Ricerche su *Asterina gibbosa* (Penn.). I. La migrazione delle gonadi. *Arch. Zool. Ital.*, Vol. XXXIV, pp. 23–9.

BACCI, GUIDO, 1949. Ricerche su *Asterina gibbosa* (Penn.). II. L'ermafroditismo in una popolazione di Plymouth. *Arch. Zool. Ital.*, Vol. XXXIV, pp. 47–74.

BALDWIN, E. & YUDKIN, W. H., 1950. The annelid phosphagen: with a note on phosphagen in Echinodermata and Protochordata. *Proc. Roy. Soc. Lond.*, B, Vol. 136, pp. 614–31.

BROWN, C. H., 1950. Quinone tanning in the animal kingdom. *Nature*, Vol. 165, p. 275.

GRAHAM, ALASTAIR, 1949. The molluscan stomach. *Trans. Roy. Soc. Edinb.*, Vol. LXI, pp. 737–78.

HODGKIN, A. L. & KATZ, B., 1949. The effect of temperature on the electrical activity of the giant axon of the Squid. *Journ. Physiol.*, Vol. 109, pp. 240–9.

HODGKIN, A. L. & KATZ, B., 1949. The effect of calcium on the axoplasm of giant nerve fibres. *Journ. Exp. Biol.*, Vol. 26, pp. 292–4.

HODGKIN, A. L. & KATZ, B., 1949. The effect of sodium ions on the electrical activity of the giant axon of the Squid. *Journ. Physiol.*, Vol. 108, pp. 37–77.

INSTITUTION OF CIVIL ENGINEERS: Discussion on Maintenance of Maritime Works. Introductory Notes: (1) Timber Structures (by F. V. M. BELL); (2) Reinforced Concrete (by G. L. HARGREAVES); (3) Steel (by E. L. BROWNING). Maritime and Waterways Engineering Division, 1948–49, 1949.

JØRGENSEN, C. BARKER, 1949. Feeding-rates of Sponges, Lamellibranchs and Ascidians. *Nature*, Vol. 163, p. 912.

KNOWLES, FRANCIS G. W., 1950. The control of retinal pigment migration in *Leander serratus*. *Biol. Bull.*, Vol. 98, pp. 66–80.

KRISHNAN, G., 1950. Sinus gland and tyrosinase activity in *Carcinus maenas*. *Nature*, Vol. 165, pp. 364–5.

LOWENSTEIN, OTTO and ROBERTS, T. D. M., 1949. The equilibrium function of the otolith organs of the Thornback Ray. *Journ. Physiol.*, Vol. 110, pp. 392–415.

NICOL, J. A. C., 1948. The giant axons of Annelids. *Quart. Rev. Biol.*, Vol. 23, pp. 291–323.

NICOL, J. A. C., 1948. The function of the giant axon of *Myxicola infundibulum* Montagu. *Canad. Journ. Res.*, Vol. 26, D, pp. 212–22.

NICOL, J. A. C., SMYTH, C. N. & WHITTERIDGE, D., 1947. Conduction velocity in relation to axon diameter in *Myxicola infundibulum*. *XVII Int. Physiol. Congr.*, Oxford, 1947, pp. 243–4 (Abstract).

REES, W. J., 1950. On a giant Squid, *Ommastrephes caroli* Furtado, stranded at Looe, Cornwall. *Bull. Brit. Mus.* (*Nat. Hist*), *Zool.*, Vol. 1, pp. 31–41.

RUSSELL, F. S., 1939. Chaetognatha. Fiches d'identification du Zooplancton. No. 1, *Int. Cons. Explor. Mer*, Copenhague, 1949.

RUSSELL, F. S., 1939. Hydromedusae. Family: Tubulariidae. Fiches d'identification du Zooplancton. No. 2, *Int. Cons. Explor. Mer*, Copenhague, 1949.

SEXTON, E. W., 1949. The multiform species *Jassa falcata* (Montagu 1808) Crustacea, Amphipoda. *Proc. Linn. Soc.*, Vol. 161, 1948–49, pp. 144–5. (Abstract of Exhibit by Dr Isabella Gordon, Linn. Soc., General Meeting, April 1949.)

THÉODORIDÈS, JEAN, 1949. Quelques publications récentes (1939–48) sur la biologie des Coléoptères des Iles Britanniques. *L'Entomologiste*, Vol. V, pp. 68–72.

THOMAS, P. KYNASTON & YOUNG, J. Z., 1949. Internode lengths in the nerves of fishes. *Journ. Anat.*, Vol. 83, pp. 336–50.

TRIPATHI, YOGENDRA R., 1949. Some new Myxosporidia from Plymouth with a proposed new classification of the order. *Parasitology*, Vol. 39, pp. 110–18.

WILSON, D. P., 1949. Animals of the sea. *Photogr. Journ.* A, pp. 195–9.

Membership of the Association

The total number of members on 31 March 1950 was 543, being 38 more than on 31 March 1949; of these the number of life members was 75 and of annual members 468. The number of Associate members is now five, Mr R. A. Todd having died during the year.

During the year Prof. H. U. Sverdrup and Prof. Hans Pettersson were elected Honorary Members.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledge the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s*.), Leeds (£20), Durham (£10. 10*s*.), Manchester (£10. 10*s*.), Nottingham (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), Hull (£10. 10*s*.), Southampton (£10. 10*s*.), Sheffield (£5), and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1950–51:

President

Prof. JAMES GRAY, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Sir SIDNEY F. HARMER, K.B.E., Sc.D., F.R.S.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
The Rt. Hon. TOM WILLIAMS, M.P.
G. P. BIDDER, Sc.D.
W. T. CALMAN, C.B., D.Sc., F.R.S.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S.
H. G. MAURICE, C.B.
E. S. RUSSELL, O.B.E., D.Sc.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., Sec. R.S.
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.
A. T. A. DOBSON, C.B., C.V.O., C.B.E.

COUNCIL

To retire in 1951

Miss ANNA M. BIDDER, Ph.D.
Prof. F. W. ROGERS BRAMBELL, D.Sc., F.R.S.
J. N. CARRUTHERS, D.Sc.
O. D. HUNT
Prof. J. E. HARRIS, Ph.D.

To retire in 1952

MICHAEL GRAHAM, O.B.E.
C. E. LUCAS, D.Sc.
L. HARRISON MATTHEWS, Sc.D.
J. D. H. WISEMAN, Ph.D.
Prof. V. C. WYNNE-EDWARDS

To retire in 1953

G. E. R. DEACON, D.Sc., F.R.S.
E. FORD
F. C. FRASER, D.Sc.
F. GROSS, D.Sc.
Prof. C. M. YONGE, D.Sc., F.R.S.

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

F. S. RUSSELL, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
P. D. H. DUNN, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Major E. G. CHRISTIE-MILLER
HARRISON S. EDWARDS
Prof. A. C. HARDY, D.Sc., F.R.S. (Oxford University)
J. E. SMITH, Ph.D. (Cambridge University)
Prof. H. GORDON JACKSON, D.Sc.(British Association)
H. G. MAURICE, C.B. (Zoological Society)
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1950

	£ s. d.	£ s. d.
CAPITAL RESERVE ACCOUNT:		
As at 31st March 1949		32688 8 2
SURPLUS ACCOUNT:		
As at 31st March 1949	2122 15 11	
Add: Excess of Income over Expenditure for the year ...	2217 9 9	
Transfer from Bequest Funds for purchase of Assets	308 2 10	
Donation for purchase of special apparatus	31 4 0	
	4679 12 6	
		37368 0 8
AQUARIUM SINKING FUND:		
As at 31st March 1949	169 17 1	
Add: Donations for rebuilding Aquarium Tanks	26 17 5	
	196 14 6	
	£ s. d.	
E. T. BROWNE BEQUEST FUNDS:		
Building Fund, as at 31st March 1949 ...	50 7 1	
Less: Expenditure on Extension of Workshops transferred	25 0 0	
	25 7 1	
Library Fund, as at 31st March 1949 ...	1204 11 6	
Add: Interest on Investment	36 2 11	
	1240 14 5	
Less: Transfer to Surplus Account	87 0 0	
	1153 14 5	
Special Apparatus Fund, as at 31st March 1949	2650 18 8	
Add: Interest on Investment	79 11 7	
	2730 10 3	
Less: Transfer to Surplus Account	221 2 10	
	2509 7 5	
Scientific Publications Fund, as at 31st March 1949	2043 7 2	
Add: Interest on Investment	61 6 4	
	2104 13 6	
		5793 2 5

	£ s. d.	£ s. d.
FIXED ASSETS, at valuations as estimated by the Director at 31st March 1950:		
Boats and Equipment:		
F.V. 'Sula'	11000 0 0	
Motor Boat 'Gammarus'	200 0 0	
Nets, Gear and General Equipment	100 0 0	
	11300 0 0	
Laboratory Apparatus, Equipment and Machinery ...	7090 0 0	
		18390 0 0
Library at valuation of Mr Ridgill Trout in January 1941, plus additions at cost		17100 0 0
Additions during year from Bequest Funds and Donations, at cost:		
Library	87 0 0	
Special Apparatus	252 6 10	
		339 6 10
		35829 6 10
STOCKS ON HAND as valued by the Director:		
Specimens	600 0 0	
Chemicals	250 0 0	
Journals	400 0 0	
		1250 0 0
GENERAL FUND INVESTMENT at Book Value £352. 2s. 3d. 2½ % Treasury Stock ... ... (Market value £239. 8s. 9d.) (Last year £281. 13s. 10d.)		232 7 10
E. T. BROWNE BEQUEST FUND INVESTMENTS, at cost: £5901. 8s. 7d. 3 % British Transport Stock ... ... (Market value £5252. 5s. 3d.) (Last year £5989. 19s. 0d.)		5795 3 6
COMPOSITION FEES FUND INVESTMENTS, at cost:		
£18. 8s. 6d. 2½ % Treasury Stock	15 15 0	
£730. 12s. 2d. 3 % British Transport Stock	715 3 2	
(Market value £662. 15s. 2d.) (Last year £685. 7s. 8d.)		730 18 2
VESSELS HIRE AND CAPITAL EXPENDITURE FUND INVESTMENT:		— —

COMPOSITION FEES FUND:					
As at 31st March 1949			667 18 2		
Add: Fees received			94 10 0		
				762 8 2	
BUILDINGS RECONSTRUCTION FUND:					
As at 31st March 1949			763 1 4		
Add: Grants received			2333 14 6		
Compensation received during year from War Damage Commission			917 6 9		
Transfer from E. T. Browne Bequest Building Fund			25 0 0		
			4039 2 7		
	£	s. d.			
Less: Expenditure during year					
Rebuilding East Wing	3333	14 6			
Equipment for East Wing	278	17 6			
			3612 12 0		
				426 10 7	
SUNDRY CREDITORS:					
Accrued Expenses			1050 4 3		
Subscriptions and Grant received in advance			183 5 0		
				1233 9 3	
				£45780 5 7	

SUNDRY DEBTORS:					
Sales of Specimens, etc.					738 10 9
PREPAYMENTS					103 18 4
VESSELS HIRE AND CAPITAL EXPENDITURE FUND:					
As at 31st March 1949			4532 16 10		
Less: Recovered during year:					
	£	s. d.			
Grant	4517	4 10			
Profit on sale of Investment	15	6 7			
Transfer from General Fund		5 5			
			4532 16 10		— —
BALANCES AT BANKS AND CASH IN HAND:					
Coutts & Co.			555 11 10		
Lloyds Bank Ltd. Plymouth			480 3 9		
Cash in Hand (Cr.)			64 4 7		
					1100 0 2
					£45780 5 7

O. D. HUNT
L. HARRISON MATTHEWS } *Members of the Council.*

REPORT OF THE AUDITORS TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion and to the best of our information and according to the explanations given to us, the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31st March 1950, and of the excess of income over expenditure for the year ended on that date.

We have obtained all the information and explanations which to the best of our knowledge and belief were necessary for our audit. In our opinion the Association has kept proper books of account and the above mentioned accounts, which are in agreement therewith, give in the prescribed manner the information required by the Companies Act, 1948.

Prudential Buildings, George Street, Plymouth.
18th May 1950.

PRICE, WATERHOUSE & Co.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1950

	£ s. d.	£ s. d.
To SALARIES, including Association's contributions to Superannuation Scheme and National Insurance		15558 1 9
,, LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance		12786 6 9
,, UPKEEP OF LIBRARY		584 8 6
,, SCIENTIFIC PUBLICATIONS, *less* Sales		1202 5 3
,, UPKEEP OF LABORATORIES AND AQUARIUM:		
Buildings and Machinery	785 11 8	
Electricity, Oil, Gas, Coal and Water	556 5 4	
Chemicals and Apparatus	917 13 1	
Insurances, Tithe, Ground Rent and Rent of Store ...	134 13 5	
Travelling Expenses	588 19 3	
Audit Fee	10 10 0	
Stationery, Postages, Telephone, Carriage and Sundries	576 14 9	
Specimens	180 6 2	
		3750 13 8
,, MAINTENANCE AND HIRE OF BOATS:		
Petrol, Oil, Paraffin, etc	604 17 6	
Maintenance and Repairs to Nets, Gear and Apparatus	1884 0 2	
Boat Hire, Collecting Expenses and Upkeep of Truck	143 0 6	
Insurances	668 6 0	
Hire of R.V. 'Sabella'	1380 0 0	
		4680 4 2
,, ENTERTAINMENT EXPENSES		32 17 3
,, BANK CHARGES		26 9 3
,, BALANCE, being Excess of Income over Expenditure for the year		2217 9 9
		£40838 16 4

Note: No provision is made for replacement of Fixed Assets.

	£ s. d.	£ s. d.
By GRANTS AND TABLE RENTS:		
Ministry of Agriculture and Fisheries grant from Development Fund	34000 0 0	
Fishmongers' Company	500 0 0	
Miscellaneous (including British Association £50, Royal Society £50, Physiological Society £30, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s.* 0*d.*, Leeds £20, Durham £10. 10*s.*0*d.*, Exeter £10. 10*s.*0*d.*, Leicester £10. 10*s.*0*d.* Manchester £10. 10*s.* 0*d.*, Nottingham £10. 10*s.* 0*d.*, Southampton £10. 10*s.* 0*d.*, Hull £10. 10*s.* 0*d.*, Sheffield £5, Imperial College £10, Ministry of Works £104.)	1276 0 3	
		35776 0 3
,, SUBSCRIPTIONS (excluding subscriptions received in advance)		472 11 10
,, FEES FOR TESTS OF MATERIALS		12 12 0
,, SALES:		
Specimens	2520 8 7	
Fish	361 6 8	
	£ s. d.	
Nets, Gear and Hydrographical Apparatus	1389 14 2	
Less: Cost of Materials	1164 14 3	
	224 19 11	
		3106 15 2
,, INTEREST ON INVESTMENTS		29 1 6
,, SALE OF DR M. V. LEBOUR'S BOOK		7 17 3
,, SALE OF 'PLYMOUTH MARINE FAUNA'		9 10 0
,, AQUARIUM:		
Admission Fees	1565 0 7	
Sale of Guides and Postcards	96 4 0	
	1661 4 7	
	£ s. d.	
Less: Maintenance of Buildings	37 12 4	
Printing Tickets	4 9 5	
Food	101 0 6	
Wages	93 14 0	
	236 16 3	
		1424 8 4
, TRANSFER FROM BIOLOGICAL INVESTIGATIONS ON ALGAE FUND		— — —
		£40838 16 4

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1950

GOVERNORS

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The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 48 *Fenchurch Street, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
The Prime Warden. (**Council**, 1886→)
Edwards, Harrison S., *Westhumble Lacey, nr Dorking, Surrey*. (**Council**, 1950→)
Christie-Miller, Major E. G., 38 *Hyde Park Street, W.* 2. (**Council**, 1941→; **Hon. Treasurer**, 1941→)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, *St Stephen's House, Victoria Embankment, S.W.* 1
Bayly, Robert (the late). (**Council**, 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council**, 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council**, 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner, Hills Road, Cambridge*. (**Council**, 1899→; **President**, 1939–45; **Vice-President**, 1948→)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President**, 1929; 1939–45; **President**, 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary.) (**Council**, 1895–1942; **Secretary**, 1895–1936; **Hon. Governor**, 1937–42)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall*, 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.* 2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council**, 1884–92; **Hon. Treasurer**, 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary**, 1884–90; **President**, 1891–1929)
1884 Lord Masham (the late)

1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road*, *Bournemouth West*
1888 The Worshipful Company of Drapers, *Drapers' Hall*, *E.C.* 2
1889 The Worshipful Company of Grocers, *Grocers' Hall*, *Princes Street*, *E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., M.Inst.C.E., 32 *Thornhill Road*, *Plymouth*, *Devon*
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square*, *S.W.* 1. (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc., (the late). (**Council**, 1932–5)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens*, *W.* 8
1920 Lord Buckland of Bwlch (the late)
1920 Llewellyn, Sir D. R. (the late)
1921 Harmer, F. W. (the late)
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1925 The Institution of Civil Engineers, *Great George Street*, *Westminster*, *S.W.* 1
1925 Discovery Committee
1927 Bidder, Miss Anna M., Ph.D., *Cavendish Corner*, *Hills Road*, *Cambridge*. (**Council**, 1948→)
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co., Ltd., P.O. Box* 331, *Alexandria*, *Egypt*. (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W., *Sharvells*, *Milford-on-Sea*, *Hants*

MEMBERS

* Life Members

1949 Abbott, B. C., *Biophysics Research Unit*, *University College*, *Gower Street*, *London*, *W.C.* 1
1939 Abercrombie, M., *Department of Anatomy*, *University College*, *Gower Street*, *London*, *W.C.* 1
1945 Aberdeen University Library, *The University*, *Aberdeen*

1947 Achimota College, *Department of Zoology, Achimota, Gold Coast Colony*
1934 Adam, Mrs K. M. G., 84 *Lasswade Road, Edinburgh* 9
1940 Adrian, Prof. E. D., O.M., M.D., D.Sc., LL.D., F.R.S., *St Chad's*, 48 *Grange Road, Cambridge*
1947 Affleck, R. J., 45 *Sherwood Avenue, London, S.W.* 16
1949 Aleem, A. A., Ph.D., *Faculty of Science, Farouk I University, Moharram Bey, Alexandria, Egypt*
1950 Alexandrowicz, J. S., Ph.D., M.D., *The Laboratory, Citadel Hill, Plymouth, Devon*
1949 Allen, Mrs M. E., 18 *Killieser Avenue, Streatham Hill, London, S.W.* 2
*1927 Amirthalingam, C., Ph.D., 2 *Dickmans Path, Colombo, Ceylon*
1932 Aquario Vasco da Gama, *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1944 Ashby, D. G., *P.O. Avondale, Salisbury, S. Rhodesia*
1947 Astill, D. R. D., *Newball and Mason, Ltd., Beech Avenue, Nottingham*
*1911 Viscount Astor, 3 *Elliot Terrace, Plymouth, Devon.* (**Vice-President**, 1911→)
*1929 Atkins, Miss D., D.Sc., *Oak Cottage, Chichele Road, Oxted, Surrey*
*1939 Atkins, W. R. G., O.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S., *The Old Vicarage, Antony, Torpoint, Cornwall*
*1910 Atkinson, G. T., *Gresham House, Esplanade, Lowestoft, Suffolk*
1950 Attridge, J., 44 *Windermere Road, Muswell Hill, London, N.* 10

1948 Baal, H. J., 3 *Bel Royal Villas, Jersey, C.I.*
1950 Baerends, Prof. G. P., *Zoological Laboratory, Reitemakersrijge* 14, *Groningen, Holland*
1949 Bagenal, T., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow, India*
1950 Bainbridge, R., 43 *Strathmore Avenue, Hull*
*1920 Baker, J. R., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1936 Baldwin, Prof. E., Ph.D. *Department of Biochemistry, University College, Gower Street, London, W.C.* 1. (**Council**, 1946–48)
1949 Barnard, E. E. P., 7 *Webster Gardens, Ealing, London, W.* 5
1939 Barnes, H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1930 Barrett, W. H., *Roxeth Farm, Bessborough Road, Harrow, Middlesex*
1939 Barrington, Prof. E. J. W., D.Sc., *Department of Zoology, The University, Nottingham*
1946 Barter, W. Y., 29 *Sea View Avenue, Plymouth, Devon*
1939 Bassindale, R., *University College, Achimota, Accra, Gold Coast*
1932 Bateman, J. B., Ph.D., *Physical and Chemical Division, Camp Detrick, Frederick, Ind., U.S.A.*
1946 Batham, Miss E. J., Ph.D., *Portobello Marine Biological Station, via Port Chalmers, Otago, New Zealand*
1950 Baughman, J. L., *Texas Game, Fish and Oyster Commission, Rockport, Texas, U.S.A.*
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
*1929 Bayliss, L. E., Ph.D., *Department of Physiology, University College, Gower Street, London, W.C.* 1
1934 Beadle, L. C., *Department of Biology, College of Medicine, University of Durham, Newcastle-upon-Tyne* 1, *Northumberland*

1928 Beer, G. R. de, D.Sc., F.R.S., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1950 Bell, Mrs E. B., 121 *Park Avenue, Hull, Yorks*
1947 Berrill, Prof. N. J., *Department of Zoology, McGill University, Montreal, Canada*
1947 Best, A. C. G., 6 *Station Road, Loudwater, High Wycombe, Bucks*
1948 Betts, Slade, 100 *Avondale Road, Bromley, Kent*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames, Oxon*
*1945 Bingley, F. J., *Broomhill, Herringswell, near Bury St Edmunds, Suffolk*
1925 Birkbeck College, *Fetter Lane, London, E.C.* 4
1931 Birtwistle, W., 73 *North Street, Skibbereen, Co. Cork, Eire*
1947 Bishop, M. W. H., *Meadow Farm, Waterbeach, Cambs*
1945 Black, J. A., *Ash House, Caton, near Lancaster, Lancashire*
1947 Black, Miss M. K., *c/o F. Band, High Street, Benwick, March, Cambs*
1930 Blaschko, Dr H., *Department of Pharmacology, South Parks Road, Oxford*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1936 Bogue, Prof. J. Yule, D.Sc., *Heyscroft, Hartley Road, Altrincham, Cheshire*
1932 Bolitho, Capt. R. J. B., *Gorey, Jersey, C.I.*
1945 Boney, A. D., *Ivydene, Grosvenor Road, Crownhill, Plymouth, Devon*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1947 Bossanyi, J., *Dove Marine Laboratory, Cullercoats, Northumberland*
1944 Boyd, Lt. David, R.N.V.R., 261 *Woodstock Road, Oxford*
1949 Braithwaite, E. R., *Research Department, Acheson Colloids Ltd., Prince Rock, Plymouth, Devon*
1940 Brambell, Prof. F. W. Rogers, D.Sc., F.R.S., *Department of Zoology, University College of North Wales, Bangor, Caernarvonshire.* (**Council**, 1944–47, 1948→)
1924 Brightwell, L. R., *White Cottage, Chalk Lane, East Horsley, Surrey*
1933 Bristol University, *Department of Zoology, Bristol*
1941 British Celanese Ltd., *Celanese House, Hanover Square, London, W.* 1
1948 British Cod Liver Oils (Hull and Grimsby) Ltd., *P.O. Box No.* 18, *Hull*
1939 British Ropes Ltd., *Western Avenue, Cardiff*
*1946 Brock, Mrs C. H., Ph.D., *Dept. of Agriculture, Downing St., Cambridge*
1946 Brough, Prof. James, D.Sc., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*
1928 Brown, Miss E. M., 6 *Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey*
1936 Brown, Herbert H., O.B.E., Ph.D., *Manager, Fisheries Division, Colonial Development Corporation,* 33 *Dover Street, London, W.* 1
*1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Burne, R. H., F.R.S., *Monkschester, Blue House Lane, Limpsfield, Surrey*
1948 Burrows, Mrs E. M., *Hartley Botanical Laboratories, The University, Liverpool* 3
1947 Burton, Miss J. M., 55 *Popes Grove, Twickenham, Middlesex*
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1936–39)
1947 Burton, R. F., 55 *Popes Grove, Twickenham, Middlesex*
*1949 Bush, Prof. S. F., D.Phil., *Department of Zoology, University of Natal, Pietermaritzburg, S. Africa*
1949 Butcher, A. W., *Three Salmons Hotel, Usk, Monmouthshire*

1949 Cameron, H. D., 5 *Compton Park Road, Mannamead, Plymouth, Devon*
*1950 Cameron, Prof. W. M., *Institute of Oceanography, University of British Columbia, Vancouver, Canada*
1949 Campbell, L. E., Ph.D., F.R.I.C., *British Food Manufacturing Industries Research Association, 2 Dalmeny Avenue, London, N. 7*
1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester.* (**Council**, 1927–30, 1932–34, 1937–41, 1942–45)
1950 Cant, Miss M. A., 8 *Clyde Road, Sutton, Surrey*
1950 Capstick, C. K., 24 *Kennersdene, Tynemouth, Northumberland*
1927 Carruthers, J. N., D.Sc., *Hydrographic Department, Admiralty, Cricklewood, London, N.W. 2.* (**Council**, 1948→)
1923 Carter, G. S., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1948 Carthy, J. D., *Department of Zoology, Downing Street, Cambridge*
*1931 Cattell, Dr McKeen, *Cornell University Medical College, 477 First Avenue, New York City, U.S.A.*
*1948 Cattley, J. G., *Fisheries Laboratory, Lowestoft, Suffolk*
1949 Centre de Recherches et d'Etudes Océanographiques, 1 *rue Victor Cousin, Paris (Ve), France*
*1949 Chang, H. W., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
*1949 Chapman, Garth, Ph.D., 12 *Wave Crest, Whitstable, Kent*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1947 Cheng, Prof. Chung, Ph.D., *Department of Oceanography, National Amoy University, Amoy, China*
*1947 Chidambaram, K., *Fisheries Biological Station, West Hill Post, South Malabar, India*
1946 Chipperfield, Philip N. J., Ph.D., *Hillside, Manor Road, Brixham, Devon*
1942 Christie-Miller, Major E. G., 38 *Hyde Park Street, London, W. 2.* (**Council** 1941→; **Hon. Treasurer**, 1941→)
1950 Clair, C. le, *Glebe Cottage, Cornwood, Ivybridge, S. Devon*
1947 Clarke, Miss D. H., *Gowdhurst, Chart Lane, Dorking, Surrey*
1949 Clarke, K. U., 7 *Stanley Avenue, Wembley, Middlesex*
1944 Clarke, Robert H., *'Discovery' Investigations, Queen Anne's Chambers, 41 Tothill Street, London, S.W. 1*
1936 Clothier, Peter, *Hill Close, Street, Somerset*
1939 Clowes, A. J., *Division of Fisheries, Beach Road, Sea Point, Cape Town, S. Africa*
*1886 Coates and Co. (Plymouth), Ltd., *Black Friars Distillery, Southside Street, Plymouth, Devon*
*1945 Cobham, Lt.-Cdr. A. J., R.N., *Noel Cottage, Castle Street, Portchester, Hants*
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *Cotteswold Naturalists' Field Club, City Library, Gloucester*
1933 Cole, H. A., D.Sc., *Fisheries Experiment Station, Castle Bank, Conway, Caernarvonshire*
1948 Collier, Albert, *c/o Fish and Wildlife Service, Ft Crockett, Galveston, Texas, U.S.A.*
*1885 Collier and Co., 53 *Southside Street, Plymouth, Devon*
1950 Collins, William N., 603 *Thatcher Avenue, River Forest, Illinois, U.S.A.*
1947 Collis, Miss M. M., 27 *Mowbray Road, Cambridge*
1930 Colman, J. S., *Marine Biological Station, Port Erin, Isle of Man*
1947 Cook, Miss P. M., 51 *Runnymede Crescent, Streatham, London, S.W. 16*
1940 Cook, R. H., 24 *Luard Road, Cambridge*
1939 Cooper, Major Brian, *Countess Weir House, Countess Weir, Exeter, Devon*

*1933 Cooper, L. H. N., D.Sc., F.R.I.C., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, P. G., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, Mrs P. G., Ph.D., *Dostabrook, Horrabridge, S. Devon*
1946 Corlett, John, M.Sc., *Fisheries Laboratory, Lowestoft, Suffolk*
1937 Cosway, C. A., *South Devon Technical College, Teignmouth Road, Torquay, S. Devon*
1941 Cott, H. B., D.Sc., *University Museum of Zoology, Cambridge*
1948 Council for Promotion of Field Studies, *Dale Fort Field Centre, Haverfordwest, Pembs*
1936 Crawford, G. I., 18 *East Drive, Carshalton Beeches, Surrey*
*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Usher Institute, Warrenden Park Road, Edinburgh* 9
1929 Crofts, Miss D. R., D.Sc., *Deerbank, Noisey Wood, Billericay, Essex*
*1930 Cuthbertson, Norman, 101 *Johnstone Avenue, Dartmouth, Nova Scotia, Canada*

1922 Dale, Sir Henry H., O.M., G.B.E., F.R.C.P., LL.D., F.R.S., *The Wellcome Trust*, 28 *Portman Square, London, W.* 1. (**Council**, 1922–28)
1948 Dales, R. Phillips, 67 *Westmoreland Avenue, Squirrels Heath, Essex*
1947 Dall, William, *Grace Street, Corinda, S.W.* 4, *Brisbane, Queensland, Australia*
*1919 Damant, Capt. G. C. C., C.B.E., R.N., *Thursford, Cambridge Road, East Cowes, I. of W.* (**Council**, 1928–31, 1937–40)
1939 Danielli, Prof. J. F., D.Sc., *Department of Zoology, King's College, Strand, London, W.C.* 2. (**Council**, 1944–45)
1947 Danmarks Akvarium, *Charlottenlund, Denmark*
1929 Darby, Dr H. H., *Carnegie Institution of Washington*, 5241 *Broad Branch Road, N.W., Washington* 15, *D.C., U.S.A.*
1948 Dartmouth, The Royal Naval College
1946 Das, S. M., D.Sc., *Central Marine Fisheries Research Station, West Hill P.O., Calicut, S. India*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay, S. Devon*
1931 Dawes, B., D.Sc., *Department of Zoology, University of London, King's College, Strand, London, W.C.* 2
1944 Day, Prof. J. H., D.F.C., *Department of Zoology, University, Rondebosch, Cape Town, S. Africa*
1948 Day, Lionel E., 24 *Inverness Avenue, Westcliff-on-Sea, Essex*
1948 Day, Peter R., 36 *Templeton Avenue, Chingford, London, E.* 4
1938 Deacon, G. E. R., D.Sc., F.R.S., 55 *Broadhurst, Ashtead, Surrey*. (**Council**, 1946–49, 1950→)
1939 Dennell, Ralph, *Department of Zoology, The University, Manchester* 13
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, S. Africa*
1944 Digby, P. S. B., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1948 Dodd, J. M., *Gatty Marine Laboratory, The University, St Andrews, Fife*
1942 Dollner, H., 3516 *Northcliffe, Montreal, N.D.G., Canada*
1949 Doochin, Herman D., *School of Biological Science, Stanford University, Stanford, California, U.S.A.*
1946 Douglas, Leslie, 11 *Harbour View, Seahouses, Northumberland*
1940 Dowson, Capt. W. B., *c/o Department Commerce and Industry, Freetown, Sierra Leone*
1946 Duly, S. J., 68 *Richmond Hill Court, Richmond, Surrey*
1939 Dundee University College Library, *Dundee, Forfar*

1947 Dunne, B., 53 *Headland Park, Plymouth, Devon*
1949 Dussart, B. H., *Le Paraclet par Boves (Somme), France*
1937 Dyke, Frederick Montague, *Branksome, Boreham Wood, Elstree, Herts*

*1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1933 Eastham, Prof. L. E. S., *Department of Zoology, The University, Sheffield* 10
1945 Edgell, Vice-Admiral Sir John A., K.B.E., C.B., F.R.S., 1 *Glenalmond House, Manor Fields, Putney, London, S.W.* 15. (**Council**, 1945–48, **Vice-President**, 1948→)
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
1948 Elgood, J. H., 159 *Purley Oaks Road, Sanderstead, Surrey*
1950 Elliott, Mrs J. H., 39 *Woodhaw, Egham, Surrey*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, S. Devon*
1931 Enoch, C. E. D., *Rayman Lodge, Sherborne Road, Parktown, Johannesburg, S. Africa*
*1947 Evans, Miss G. C., *Gerrans, Portscatho, near Truro, Cornwall*
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*
1942 Ewer, D. W., *Department of Zoology, Natal University College, P.O. Box* 375, *Pietermaritzburg, Natal, S. Africa*

*1929 Faouzi, Dr Hussein, *Faculty of Science (Department of Zoology), Farouk I University, Moharram Bey, Alexandria, Egypt*
1948 Faulkner, I. J., Ph.D., *I.C.I. Billingham Division, Billingham, E. Durham*
1950 Featherstone, Miss M. J., 3 *Clarence Road, Bickley, Kent*
*1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1950 Fisher, L. R., 23 *Langton Avenue, Chelmsford, Essex*
1940 Foote, Miss V. V. J., *Achimota College, Achimota, Gold Coast Colony*
1928 Ford, E., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*. (**Council**, 1950→)
1935 Ford, E. B., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1950 Forster, G. R., *The Laboratory, Citadel Hill, Plymouth, Devon*
1949 Fountain, H. C., *The Store Cottage, Polbathic, Torpoint, Cornwall*
1912 Fox, Prof. H. M., F.R.S., *Bedford College for Women, Sussex Lodge, Regent's Park, London, N.W.* 1. (**Council**, 1928–30, 1931–34, 1944–47)
1942 Foxon, G. E. H., *Department of Biology, Guy's Hospital Medical School, London Bridge, London, S.E.* 1
1950 Frampton, Cdr. R. H. C. F., R.N. (Rtd), *Ministry of Agriculture and Fisheries, Citadel Hill, Plymouth, Devon*
1924 Fraser, Miss E. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1935 Fraser, F. C., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1950→)
*1935 Fraser, James H., Ph.D., *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1939 Fretter, Miss Vera, Ph.D., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
*1930 Fritsch, Prof. F. E., D.Sc., F.R.S., 34 *Causewayside, Cambridge*. (**Council**, 1931–34, 1937–40, 1943–46)

1949 Fuller, A. S., 114 *Vale Road, Worcester Park, Surrey*
1948 Furness, W. J., *Inglewood, Abbey Park Road, Grimsby, Lincs.*

1941 Gardiner, Mrs A. C., *c/o Mrs Walter Gardiner*, 4 *Grange Road, Cambridge*
1949 Gates, J. T., 19 *Fircroft Road, Hook Rise, Surbiton, Surrey*
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Biological Laboratories, Harvard University, Cambridge* 38, *Mass., U.S.A.*
1948 Gatty Marine Laboratory, (The Principal), *The University, St Andrews, Fife*
1947 Gay, Miss M. V., *Lowerfield, Lapford, N. Devon*
1935 Gilson, H. Cary, *Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Westmorland.* (**Council**, 1940–43, 1947–50)
1945 Glasgow University, Zoology Department, *Glasgow, W.* 2
1946 Glover, R. S., *Department of Oceanography, University College, Hull*
1950 Goodley, E. F. W., 2 *Thickthorn Lane, Laleham, Staines, Middlesex*
1939 Goodrich, Dr Helen Pixell, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1943 Gourock Ropework Co., Ltd., 92 *Bay Street, Port Glasgow, Renfrew*
1931 Graham, Prof. Alastair, D.Sc., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
1949 Graham, F. G., *Trethake, Plymstock Road, Oreston, near Plymouth, Devon*
1931 Graham, Michael, O.B.E., *Fisheries Laboratory, Lowestoft, Suffolk.* (**Council**, 1931–32, 1933–36, 1943–46, 1949→)
1930 Gray, Sir Archibald M. H., C.B.E., M.D., F.R.C.P., F.R.C.S., 39 *Devonshire Place, London, W.* 1
1912 Gray, Prof. J., C.B.E., M.C., Sc.D., LL.D., F.R.S., *Department of Zoology, Downing Street, Cambridge.* (**Council**, 1920–24, 1928→; representing Cambridge University, 1928–45; **President**, 1945→)
1943 Great Grimsby Coal, Salt and Tanning Co., *Fish Dock Road, Grimsby, Lincs*
1949 Green, J., 61 *Ruskin Road, Crewe, Cheshire*
1950 Greenfield, Leonard J., 1262*E Walsh Avenue, University Branch, Miami* 46, *Florida, U.S.A.*
1948 Grigg, Miss Ursula M., *Dove Marine Laboratory, Cullercoats, Northumberland*
1948 Grove, A. V., 86 *Gowar Road, Sketty, Swansea, Glam*
1947 Guiler, E. R., *Department of Zoology, University of Tasmania, Hobart, Tasmania*
1947 Gundry, Joseph, and Co., *Bridport, Dorset*

1946 Haifa: *Sea Fisheries Research Station, P.O. Box* 50, *Haifa, Palestine*
1950 Haines, Surg.-Lieut. D. O., R.N., 217 *Cliffe Road, Strood, Rochester, Kent*
1949 Hall, Miss N. F., *Tyne Brand Products Ltd., North Shields, Northumberland*
*1946 Hamond, Richard, *Morston, Holt, Norfolk*
1947 Harbott, A. J., *Wensleydale*, 7 *Manorcrofts Road, Egham, Surrey*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford.* (**Council**, 1938–41, 1942→; representing Oxford University, 1946→)
1929 Harington, Sir Charles R., Ph.D., F.R.S., *National Institute of Medical Research, The Ridgeway, Mill Hill, London, N.W.* 7
1950 Harley, Miss M. B., *Department of Zoology, University Science Laboratories, South Road, Durham*
1946 Harling, Miss K. E., *The Arches, Looe, Cornwall*

*1885 Harmer, Sir Sidney F., K.B.E., Sc.D., F.R.S., 5 *Grange Road, Cambridge.* (**Council**, 1895–1912, 1918–23, 1925–44; representing Royal Society, 1925–44; **Vice-President**, 1934→)

1932 Harris, Prof. J. E., Ph.D., *Department of Zoology, The University, Bristol.* (**Council**, 1946–49, 1950→)

1946 Harris, T. R., 31 *All Saints Road, Wyke Regis, Weymouth, Dorset*

1939 Harrison, R. J., D.Sc., M.R.C.S., L.R.C.P., *Vinicombe, The Woodlands, Farnborough, Kent*

1947 Harrow Lower School Biology Department, *Lower School of John Lyon, Harrow, Middlesex*

1929 Hart, T. J., D.Sc., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*

1934 Hartley, P. H. T., *Edward Gray Institute of Field Ornithology*, 91 *Banbury Road, Oxford*

1924 Harvey, H. W., Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon*

1933 Harvey, Prof. L. A., *Department of Zoology, University College of the South West, Exeter, Devon.* (**Council**, 1940–43)

1950 Haswell, G. A., 23 *Russell Avenue, Hartley, Plymouth, Devon*

1939 Hayes, Dr F. R., *Dalhousie University, Halifax, N.S., Canada*

1939 Hayes, Mrs F. R., *Dalhousie University, Halifax, N.S., Canada*

1950 Hazevoet, A. C., *Vogelenzangstraat* 19-*I, Amsterdam West, Holland*

1949 Heaysman, Miss J. E. M., 69 *Brook Road, Merstham, Surrey*

1948 Hedley, Ronald H., *Armstrong House, Meadowfield, Durham*

1931 Henderson, G. T. D., D.S.C., Ph.D., *Oceanographic Laboratory*, 23 *Sandport Street, Leith, Edinburgh* 6

1939 Henry, Dr Herbert G. M., *Doune Cottage, Macduff, Banffshire*

1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W.* 1

1939 Herklots, G. A. C., Ph.D., *Vanners, Chobham, Surrey*

1950 Herring Industry Board, 1 *Glenfinlas Street, Edinburgh* 3

1939 Hewer, H. R., Assistant Professor, *Department of Zoology, Imperial College of Science, London, S.W.* 7

1926 Hickling, C. F., Sc.D., *Colonial Office, Sanctuary Buildings, Great Smith Street, London, S.W.* 1. (**Council**, 1947–50)

1926 Hill, Prof. A. V., C.H., O.B.E., Sc.D., F.R.S., 16 *Bishopswood Road, Highgate, London, N.* 6. (**Council**, 1925–29, 1930–33, 1934–37, 1938–41, 1942→; representing Royal Society, 1944→; **Vice-President**, 1948→)

*1949 Hill, D. K., *Postgraduate Medical School of London, Ducane Road, London, W.* 12

1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*

1947 Hill, M. N., 6 *St Eligius Street, Cambridge*

*1921 Hindle, E., Sc.D., F.R.S., *Zoological Society of London, Regent's Park, London, N.W.* 8. (**Council**, 1946–49)

1937 Hinton, M. A. C., F.R.S., 23 *Polworth Road, Streatham, London, S.W.* 16

1926 Hobson, Prof. A. D., *King's College, Newcastle-upon-Tyne* 1, *Northumberland*

1948 Hockley, A. R., *University College, Southampton*

1939 Hodgkin, A. L., F.R.S., *Trinity College, Cambridge*

1945 Hodson, W., *Rhodena, Penare Avenue, Prestatyn, Flints*

1947 Hollowday, E. D., F.R.M.S., 45 *Manor Road, Aylesbury, Bucks*

1948 Holme, N. A., *The Laboratory, Citadel Hill, Plymouth, Devon*

1939 Holmes, W., D.Phil., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*

1948 Holsgrove, H. E., 67 *Bridwell Road, Weston Mill Estate, Plymouth, Devon*

1933 Horne, F. R., *National Institute of Agricultural Botany, Huntingdon Road, Cambridge*

1950 Howard, G. H., 131 *Corporation Road, Grimsby, Lincs*
1948 Howe, Surg. Lt.-Cdr. (D) D. C., R.N., 607 *Dorchester Road, Broadway, near Weymouth, Dorset*
1950 Howells, D. V., 42 *Radstock Road, Reading, Berks*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1928 Hunt, O. D., *Corrofell, Newton Ferrers, S. Devon.* (**Council**, 1944–47, 1948→)
1947 Hunter, W. Russell, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
*1947 Hurrell, H. G., J.P., *Moorgate, Wrangaton, S. Devon*
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
1912 Huxley, Julian S., D.Sc., F.R.S., 31 *Pond Street, London, N.W.* 3. (**Council**, 1920–25)

1946 Iceland: *Atvinnudeild Háskólans* (*Fiskideild*), *Reykjavik*
1945 Imperial Chemical Industries Ltd., *Nobel House*, 2 *Buckingham Gate, London, S.W.* 1

1945 Jefferies, H. S., 6 *Forester Road, Bath*
1949 Jellinek, P. H., *Oakdene, Christchurch Road, London, S.W.* 14
1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1949 Jeremy, W. H. R., 38 *Barnfield Road, Exeter, Devon*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*
*1947 John, C. C., D.Sc., *The Aquarium, Trivandrum, S. India*
1934 John, D. Dilwyn, D.Sc., *National Museum of Wales, Cardiff*
*1947 Johnson, D. S., 10 *St John's Road, Cambridge*
1944 Johnson, Dr F. R., *Osu Fisheries Station, P.O. Box* 630, *Accra, Gold Coast Colony*
1948 Jones, C. Burdon, *Department of Zoology, University College of N. Wales, Bangor, Caern*
*1949 Jones, E. W. Knight, *Marine Biological Station, University College of N. Wales, Bangor, Caern*
1949 Jones, F. R. Harden, 9 *Clifton Crescent, Folkestone, Kent*
1948 Jones, J. D., *Nantyci, Llysonnen Road, Carmarthen, S. Wales*
1946 Jones, L. W. G., *Seymour House, Mount Wise, Plymouth, Devon*
1946 Jones, N. S., *Marine Biological Station, Port Erin, Isle of Man*
1949 Jones, R. J., 14 *Canning Road, Croydon, Surrey*
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*
1946 Jones, Prof. R. V., C.B., C.B.E., D.Phil., F.Inst.P., *Department of Natural Philosophy, Marischal College, Aberdeen*
1947 Jörgensen, C. Barker, *Slettevej* 8, *Copenhagen Söborg, Denmark*
1923 Judge, J. J., *Virginia House, Palace Street, Plymouth, Devon*
1950 Juniper, A. J., *The Polytechnic, Regent Street, London, W.* 1

1948 Katterns, L. B., 115 *Feltham Hill Road, Ashford, Middlesex*
1945 Katz, Max, 1915E, *Spruce Street, Seattle* 22, *Washington, U.S.A.*
1940 Keilin, Prof. D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council**, 1940–43)
1950 Keir, Ronald S., 51 *Clincort Road, Glasgow, S.* 2

1946 Kelley, D. F., 17 *Bainbridge Avenue, Hartley, Plymouth, Devon*
1949 Kennedy, G. Y., F.R.I.C., *Department of Cancer Research, University Field Laboratory, Blackbrook Road, Sheffield* 10
1946 Kenya: The Game Warden, *Game Department, P.O. Box* 241, *Nairobi*
1950 Keynes, R. D., Ph.D., *Physiological Laboratory, Cambridge*
1949 Kimmins, B. J., 19 *Cranleigh Gardens, Bristol* 9
1928 King, Mrs A. Redman, *Mixton House, Lerryn, Lostwithiel, Cornwall*
1947 Kingsbridge Modern Secondary School, *Kingsbridge, S. Devon*
1949 Kingston Technical College, *Kingston Hall Road, Kingston-upon-Thames, Surrey*
1927 Kirtisinghe, P., *Department of Zoology, University of Ceylon, Colombo* 3, *Ceylon*
1930 Kitching, J. A., O.B.E., Ph.D., *Department of Zoology, The University, Bristol*
1939 Knight, Miss Margery, D.Sc., *University Hall for Women Students, Holly Road, Fairfield, Liverpool.* (**Council**, 1943–46)
1945 Knowles, F. G. W., D.Phil., *Marlborough College, Marlborough, Wilts*
1948 Kow, Tham Ah, *c/o Fisheries Department, 4th Floor, Fullerton Building, Singapore*
1949 Kristensen, Dr Ingvar, *Zoölogisch Station, den Helder, Holland*

1950 La Rochelle, Station Océanographique, *Pavillon du Port-Le Gabut, La Rochelle* (*Charente-Maritime*), *France*
1950 Lasker, Reuben, *Marine Laboratory, Miami University, Coral Gables, Florida, U.S.A.*
*1925 Lebour, Miss M. V., D.Sc., *Kean Hill, Cawsand, near Plymouth, Devon*
1947 Leehane, J. D. B., 14 *Wyndham Street East, Plymouth, Devon*
1935 Le Mare, D. W., *Fisheries Department, Federation of Malaya and Singapore, Penang, Malaya*
1948 Letts, J. K., 183 *Windmill Lane, Greenford, Middlesex*
1948 Lloyd, A. T., *Wynona, Beacon Park Road, Plymouth, Devon*
1949 Lodge, Miss S. M., *Marine Biological Station, Port Erin, Isle of Man*
1948 Lovegrove, T., 2 *Athenaeum Place, The Hoe, Plymouth, Devon*
1926 Lowndes, A. G., Sc.D., F.R.I.C., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1931 Lucas, C. E., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen.* (**Council**, 1949→)
1930 Lumley, Adrian, *Sunnyside, Castle Gardens, Torquay, Devon*
1938 Lysaght, Miss A. M., Ph.D., 6 *Cumberland Gardens, London, W.C.* 1

1938 MacDonald, R., 112 *Antrim Road, Belfast, N. Ireland*
1935 Mackenzie, Col. W., O.B.E., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt*
1929 Mackinnon, Prof. D. L., D.Sc., 44 *St Leonard's Terrace, Chelsea, London, S.W.* 3. (**Council**, 1938–42)
1937 Mackintosh, N. A., C.B.E., D.Sc., 7 *Hinde House, Hinde Street, London, W.* 1. (**Council**, 1946–49)
1947 Macnae, William, *Department of Zoology, Rhodes University College, Grahamstown, S. Africa*
*1925 Magdalen College, *Oxford*
1945 Maitland-Adams, C. W., *The Old Rectory, Hawkwell, Hockley, Essex*
1948 Mansfield, A. W., 32 *Newton Road, Wimbledon, London, S.W.* 19

*1928 Manton, S. M., Sc.D., F.R.S. (Mrs J. P. Harding), 18 *Ennerdale Road, Richmond, Surrey*
1948 Marcotte, Alexandre, D.Sc., *Faculté des Sciences, Boulevard de l'Entente, Quebec, Canada*
1948 Mardon, Jasper, *Selwyn College, Cambridge*
1939 Marr, J. W. S., 28 *Cromwell Court, Kingston Hill, Surrey*
1949 Marshall, Douglas, M. P., *Lanwithan House, Lostwithiel, Cornwall*
*1947 Marshall, Miss S. M., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Matthews, L. Harrison, Sc.D., *Department of Zoology, The University, Bristol.* (**Council**, 1944–47, 1949→)
1937 Mayne, Dr Cyril F., O.B.E., F.R.C.S., *c/o Barclays Bank Ltd., Plymouth, Devon*
1949 McCarthy, Miss D. F., 70 *Halton Terrace, Kensington Park, Adelaide, S. Australia*
1910 McClean, Capt. W. N., 39 *Phillimore Gardens, London, W.* 8
*1929 McEwen, Mrs Lawrence, 15 *Blackett Place, Edinburgh*
1948 McIntyre, A. D., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1950 McIntyre, J. M., 75 *Harcourt Terrace, Kensington, London, S.W.* 10
*1948 Menon, M. Devidas, *Parvathi Nivas, Diwans Road, Ernakulam, United States of Cochin and Travancore, S. India*
1950 Messenger, K. G., *Uppingham School, Rutland*
1939 Metropolitan Water Board, 177 *Rosebery Avenue, London, E.C.* 1
1947 Miami University Marine Laboratory, *Coral Gables, Florida, U.S.A.*
1923 Milford Haven Trawler Owners Association, Ltd., *Milford Haven, Pembs*
1949 Millar, R. H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1946 Miller, Cyril J., 42 *Westbourne Road, Peverell, Plymouth, Devon*
1949 Millott, Prof. N., Ph.D., *Department of Zoology, University College of West Indies, Mona, Liguanea, Jamaica*
1949 Mistakidis, M. N., *Oyster Research Station, Burnham-on-Crouch, Essex*
1947 Mitchell, E. S., *Hillside, Chapel Street, Camelford, Cornwall*
1947 Mitra, G. N., *Assistant Director of Fisheries, Cuttack (Orissa), India*
1940 Moore, Hilary B., Ph.D., *Marine Laboratory, Miami University, Coral Gables, Florida, U.S.A.*
1949 Morrish, Miss C. A., *Ormdale, Woodhall Avenue, Pinner, Middlesex*
1949 Morton, J. E., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
1931 Mount Desert Island Biological Laboratory, *Salisbury Cove, Maine, U.S.A.*
1938 Mowbray, Louis L., *Curator, Bermuda Government Aquarium, Flatts, Bermuda*
1942 Moynahan, Dr E. J., *Wayside, Jordans, near Beaconsfield, Bucks*

1933 Neale, Morley H., *Chaffcombe House, Chard, Somerset.* (**Council**, 1934–36, 1939–42, 1943–46, 1947–50)
1934 Neale and West, *Trawler Owners, Wharf Street, Cardiff*
1939 Needham, Joseph, Sc.D., F.R.S., *Gonville and Caius College, Cambridge*
1947 Newell, G. E., Ph.D., 11 *Wave Crest, Whitstable, Kent*
1947 Newton, Prof. Lily, Ph.D., *Department of Botany, University College of Wales, Aberystwyth, Cardigan.* (**Council**, 1947–50)
1930 Nicholls, A. G., Ph.D., *Stowell, Hobart, Tasmania*

1950 Nicol, J. A. C., D.Phil., *Trevean, George Lane, Plympton St Maurice, S. Devon*
1947 Nisbet, R. H., 169 *Stapleton Hall Road, Finsbury Park, London, N.* 4
1948 Nobbs, Miss G. E. D., 4 *Clifton Estate, Plympton, Devon*
1949 Norris, E., *Ewdis, Priory Road, Lower Compton, Plymouth, Devon*
1950 North, J., 316 *Lee High Road, Lewisham, London, S.E.* 13
1948 Nunn, S. M., *The Laboratory, Citadel Hill, Plymouth, Devon*

1934 Oakley, Dr C. L., 58 *Cumberland Road, Bromley, Kent*
1930 Olive, G. W., *Dauntsey's School, West Lavington, near Devizes, Wilts*
1938 Oliver, James H., Ph.D., 16 *Southwark Street, London, S.E.* 1
1937 Omer-Cooper, J., *Zoological Department, Rhodes University College, Grahamstown, S. Africa*
1939 Ommanney, F. D., Ph.D., *Rowner House, Billinghurst, Sussex*
1949 Orkin, P. A., *Natural History Department, The University, Aberdeen*
1947 Orr, A. P., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1910 Orton, Prof. J. H., D.Sc., F.R.S., *Sunny Bank, Burton, Wirral, Cheshire.* (**Council**, 1945–48)
1945 Otago University Library, *Dunedin, N.* 1, *New Zealand*
*1928 Otter, G. W., *Southwood, Broadstone, Dorset*
1950 Owen, G., 5 *Jones Street, Celfynydd, Pontypridd, Glam*
1949 Owrie, Mrs Harding B., *Zoology Department, University of Miami, Coral Gables, Florida, U.S.A.*

*1939 Panikkar, N. K., D.Sc., *Central Marine Fisheries Station, Triplicane P.O., Madras, India*
*1923 Pantin, C. F. A., Sc.D., F.R.S., *Trinity College, Cambridge.* (**Council**, 1930–32, 1933–36, 1937–40, 1941–44, 1945–49, representing Cambridge University, 1946–49)
1941 Parke, Miss M. W., D.Sc., *The Laboratory, Citadel Hill, Plymouth, Devon*
1927 Parker, The Hon. John H., *Pound House, Buckland Monachorum, S. Devon*
1937 Parry, D. A., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1928 Parsons, C. W., *Zoology Department, The University, Glasgow*
*1920 Pass, A. Douglas, *Wooton Fitzpaine, Charmouth, Dorset*
1946 Paul, Mrs Vidya Vati, Ph.D., 49*B Nai Mandi, Ram Bhavan, Muzaffarnagar (U.P.), India*
1925 Pawlyn Bros., *Mevagissey, Cornwall*
1925 Pawlyn, T. A., *Mevagissey, Cornwall*
1929 Peacock and Buchan, Ltd., *Paint Manufacturers, Southampton*
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt.* (**Vice-President**, 1936→)
1948 Peiping, Institute of Zoology, National Academy of Peiping, 58 *Museum Road, Peiping* 7, *China*
1939 Pennell, V., 28 *Huntingdon Road, Cambridge*
1925 Pentelow, F. T. K., *Old Slade Lane, Iver, Bucks*
1948 Pepper, H. C., *Hastings Aquarium, George Street, Hastings, Sussex*
1929 Percival, Prof. E., *Canterbury College, Christchurch, New Zealand*
1947 Perkins, E. J., *Cross Keys, Post Office, near Hereford*
1936 Perkins, F., *Red Hand Compositions Co.,* 2 *The Firs, York Road, Ripon, Yorks*
1950 Phillipson, J., *Dove Marine Laboratory, Cullercoats, Northumberland*
1934 Picken, L. E. R., Ph.D., *Trinity College, Cambridge*
1940 Pike, R. B., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1906 Plymouth Corporation (Museum Committee), *Tavistock Road, Plymouth, Devon*

1910 Plymouth Education Authority, *Cobourg Street, Plymouth, Devon*
1906 Plymouth, Port of, Incorporated Chamber of Commerce, *Plymouth, Devon*
1924 Plymouth Proprietory Library, 1 *Alton Terrace, North Hill, Plymouth, Devon*
1929 Plymouth Public Library, *Tavistock Road, Plymouth, Devon*
1948 Pollard, D. G., 60 *Alcester Street, Stoke, Plymouth, Devon*
1947 Portsmouth Grammar School, *Biology Department, Portsmouth, Hants*
1929 Portsmouth Municipal College, *Portsmouth, Hants*
1950 Posner, Gerald S., 1262*E Walsh Avenue, University Branch, Miami* 46, *Florida, U.S.A.*
1939 Potter, Miss E. A., *Westonbirt School, Tetbury, Glos*
1950 Powell, H. T., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1950 Powell, R. R., 170 *Streatfield Road, Kenton, Middlesex*
1939 Pringle, J. W. S., *Department of Zoology, Downing Street, Cambridge*
*1947 Pryor, Thomas, D.S.O., *Westbourne House, Saltash, Cornwall*
1939 Pumphrey, Prof. R. J., Ph.D., F.R.S., *Department of Zoology, The University, Liverpool*
*1939 Purchon, R. D., Ph.D., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*

1947 Quekett Microscopical Club (W. Burrells, Hon. Sec.), 52 *Draycott Avenue, Northwick Park, Harrow, Middlesex*
1936 Queen Mary College, *Department of Zoology, Mile End Road, London, E.* 1
1939 Queen's University, *Belfast, N. Ireland*
1932 Quick, Dr H. E., F.R.C.S., 59 *Alexandra Road, Reading, Berks*
1947 Qureshi, Q. H., *Department of Zoology, Imperial College of Science and Technology, Prince Consort Road, South Kensington, London, S.W.* 7

1932 Ramalho, Dr A., *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1949 Rasmussen, E., *The Zoological Laboratory, Landbohøjskolen, Bülowsvej, Copenhagen V, Denmark*
1939 Rawlinson, Miss Ruth, 23A *Holbrook Road, Stoneygate, Leicester*
1947 Raymont, Prof. J. E. G., *Department of Zoology, University College, Southampton*
*1933 Rayner, G. W., *c/o C.S.I.R. Fisheries Division, Cronulla, N.S.W., Australia*
1949 Rees, C. B., *Oceanographic Laboratory,* 23 *Sandport Street, Edinburgh,* 6
*1936 Rees, W. J., D.Sc., 37 *Kings Road, Richmond, Surrey*
1928 Reid, D. M., *The Science Schools, Harrow-on-the-Hill, Middlesex*
1947 Rendle, H. S., 5 *Radford Park Road, Plymstock, near Plymouth, Devon*
1935 Renouf, Prof. L. P. W., *University College, Cork, Eire*
1950 Renton, K., 55 *Tavistock Road, Stoke, Plymouth, Devon*
1940 Richards, P. B., *c/o Lloyds Bank Ltd., Truro, Cornwall*
1946 Rifaat, Ahmed, *c/o Marine Laboratory, Fort Kait Bey, Alexandria, Egypt*
*1919 Ritchie, Prof. A. D., *Old College, The University, Edinburgh.* (**Council**, 1929–32, 1934–37)
1944 Ritchie, Prof. James, C.B.E., D.Sc., *Department of Zoology, The University, Edinburgh.* (**Council**, 1944–47)
1948 Robinson, G. A., *Hilton Street, Over, Cambridge*
1949 Rodhe, Dr W., *Institute of Limnology, Uppsala, Sweden*
1940 Rogers, Dr T. Howard, *Naval Research Establishment, Halifax, Nova Scotia*
1939 Ross, D. M., Ph.D., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1939 Ross, Miss Sybil S., 10 *Midmar Gardens, Edinburgh* 10

1931 Rothschild, Rt Hon. Lord G.C., Ph.D., *Merton Hall, Cambridge.* (**Council,** 1939–42)
*1932 Rothschild, The Hon. Miriam (The Hon. Mrs George Lane), *The Cottage, Ashton Wold, Peterborough, Northants.* (**Council,** 1942–45)
1945 Rowett, Miss H. G. Q., *Plymouth Technical College, Tavistock Road, Plymouth, Devon*
1924 Rudge, Chas. H., *Four Winds, Gurnick, Newlyn, Penzance, Cornwall*
1922 Russell, E. S., O.B.E., D.Sc., *Cloisters, Three Oaks, Hastings, Sussex.* (**Council,** 1927–30, 1932–35, 1936–39, 1940–43; **Vice-President,** 1948→)
1927 Russell, F. S., D.S.C., D.F.C., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon.* (**Council,** 1945→; **Secretary,** 1945→)

1946 Sagay, A. A. E., *Warri College, Warri, Nigeria*
1927 St Aubyn, Capt. The Hon. Lionel, M.V.O., *Saltram, Plympton, Devon*
*1934 Salisbury, Sir Edward J., Kt., C.B.E., D.Sc., F.R.S., 49 *Kew Green, Kew Gardens, Surrey.* (**Council,** 1934–37, 1940–43; **Vice-President,** 1948→)
1950 Samuel, J. H., 68 *Conway Road, Cardiff*
1946 Sartory, P. K., 34 *Elm Grove, Harrow Garden Village, Harrow, Middlesex*
1911 Saunders, J. T., *Christ's College, Cambridge.* (**Council,** 1930–32)
1914 Savage, R. E., *Fisheries Experiment Station, Castle Bank, Conway, Caernarvonshire*
1946 Saville, Alan, *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1945 Saville, Tom C., 31 *Mawton Crescent, Wollaton Park, Nottingham*
*1921 Scott, Peter, D.S.C., 8 *Edwardes Square, London, W.* 8
1928 Sen, B., *Vivekanada Laboratory, Baghbazar, Calcutta, India*
1946 Seshappa, G., Ph.D., *Central Marine Fisheries Research Station, West Hill P.O., Calicut, S. India*
1922 Sewell, Lt.-Col. R. B. Seymour, C.I.E., Sc.D., F.R.S., *Department of Zoology, Downing Street, Cambridge.* (**Council,** 1935–38)
1947 Shantung, National University, *Institute of Oceanography and Limnology, Tsingtao, China*
1947 Sharman, Miss M., *Royal Holloway College, Englefield Green, Surrey*
1947 Shen, Prof. C. J., *Institute of Zoology, National Academy of Peiping, 58 Museum Road, Hsi-Tzeu-Men-Wai, Peiping,* 7, *China*
1934 Sherwood, H. P., *Fisheries Experiment Station, Castle Bank, Conway, Caernarvonshire*
1935 Siam: Department of Fisheries, *Bangkok, Siam*
1940 Simpson, A. C., *Fisheries Laboratory, Lowestoft, Suffolk*
1946 Sinclair, Horace, *Paignton Zoo Aquarium, Primley, S. Devon*
*1884 Skinners, The Worshipful Company of, *Skinners' Hall, Dowgate Hill, London, E.C.* 4
1948 Slack, H. D., Ph.D., *Department of Zoology, The University, Glasgow*
1949 Smith, Major A. A. Dorrien, D.S.O., *Tresco Abbey, Isles of Scilly, Cornwall*
1948 Smith, Admiral Sir Aubrey, K.B.E., C.B., M.V.O., *Hay's Wharf and Dock, Southwark, London, S.E.* 1 (**Council,** representing Fishmongers' Company, 1937–46, **Vice-President,** 1948→)
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THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. XV (p. 735) and Vol. XXVII (p. 761) of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat and these also collect the specimens required in the Laboratory.

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All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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

CAMBRIDGE UNIVERSITY PRESS
LONDON: BENTLEY HOUSE, N.W.1
NEW YORK: 51 MADISON AVENUE
CANADA AND INDIA: MACMILLAN

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)