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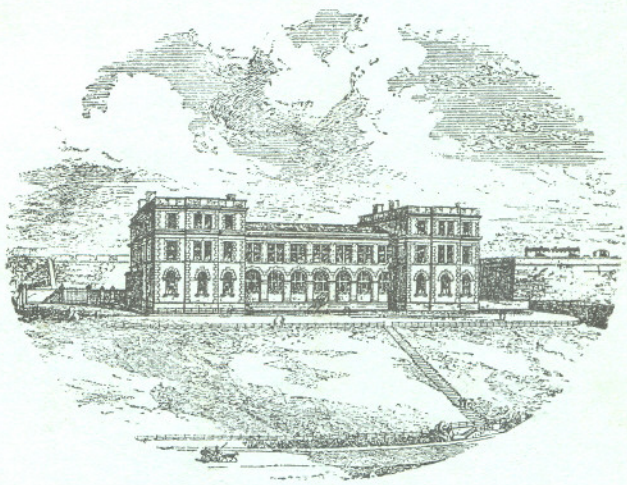

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A Preliminary Comparison of the Neon Lamp and Potentiometer Methods of Submarine Photo-Electric Photometry.

By

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With 2 Figures in the Text.

Our previous experience of submarine photometry (1925, 1926, 1928, 1929) indicated the desirability of obtaining additional information in certain directions and of speeding up the observations without sacrifice of accuracy; our aim was indeed to increase the accuracy, at the greater depths especially and in sub-surface observations. Further data upon the horizontal illumination, viz. that received by a vertical surface, were also wanted.

The above *desiderata* were sought as follows:

(*a*) To increase accuracy a more sensitive vacuum cell was obtained—a sodium cell of the Burt type, with "end-on" illumination. This had a sensitivity of 5·30 m.c. per 10^{-9} amp. as against 31·6 m.c. for the potassium vacuum cell previously used, photometer L. It was hoped that it would have been possible to use this down to bottom at Station E1, thus avoiding having recourse to a gas-filled cell; the latter has to be calibrated before and after use and the voltage change-over ratios have also to be determined, so that both on the score of accuracy and speed of operation a vacuum cell is to be preferred when possible. For several reasons, however, the Burt cell could not be used for the deeper water; firstly, owing to its smaller aperture the "end-on" is not as sensitive as the side window type, secondly, though mounted so that the aperture in the cell was close to a larger window in the new type of photometer case (described later), yet the mounting undoubtedly reduced the sensitivity somewhat, and thirdly, the plate glass, 12·5 mm. thick, reduces the middle of the solar ultra-violet somewhat, yet it is just here—at 360 mμ—that the sodium cell has its greatest sensitivity. In any case the diffusing opal glass must reduce the intensity in this region. Hen

the sensitivity of this photometer, as given above, proved to be considerably less than was expected. Furthermore, it is possible that the absorption coefficient for the light to which the sodium cell responds is greater than that for the potassium cell, the latter being of greater wave-length. This, however, remains to be tested by the measurements. A greater accuracy throughout, especially in the deeper water, was attained, however, by using photometer J, already described (1929), but maintained in its condition of maximum sensitivity by a method communicated to us by the staff of the Research Laboratories of the General Electric Co. The gas-filled potassium cell, mounted as photometer J, has its sensitivity increased by the passage of a relatively large current caused by exposure to bright light. The subsequent gradual loss of sensitivity when subjected to low illumination, implies that in deep water the cell is not as sensitive as one would expect from the voltage change-over ratio, determined at a lesser depth. For all measurements to be comparable, the sensitivity should be the same. This we formerly sought to maintain by avoiding the passage of a really large current at any time by reducing the applied voltage for bright light, the safe limit being determined by trial. A correction was also introduced, assuming the change of sensitivity to be a linear function of the time. The method, now adopted, is the reverse. The cell is momentarily connected with a voltage just sufficient to produce a glow discharge in absence of light. This leaves it in a highly sensitive state ; immediately after the glow the measurement is made at the voltage appropriate to the illumination. This is the best one can do with a gas-filled cell. A special series of tests was carried out to ascertain the accuracy thus obtainable. These are described elsewhere. (Atkins, 1931.) If the glow were allowed to continue the cell would be ruined. The method gives results which seem to be more constant than those obtained formerly, but not as constant as with a vacuum cell. With light of low illumination, however, the far greater sensitivity of the gas-filled cell outweighs this defect and the readings become more accurate, being much larger.

To sum up, for accuracy and speed of work down to moderate depths the Burt cell (photometer M) or the potassium vacuum cell (photometer L) may be used, but for the greater depths the potassium gas-filled cell (photometer J) must be used. What these depths actually are depends upon the clearness of the water at the time.

(*b*) Observations immediately above and below the water surface are obviously desirable because owing to the shadow of the ship the light just above the water is always less than that as measured on the deck-house roof. Measurements in the latter position serve, however, to detect any change in general illumination. The shadow error is not a constant. The stern of the ship is always kept pointing towards the sun, so that with a

bright sun—say $\beta=3$—the shadow is relatively unimportant, since only a percentage of the diffuse light is cut off. With overcast sky, $\beta=1$, this loss becomes the same percentage of the total light.

As the photometer is lowered through the water the shadow error increases at first and then decreases. It is obvious, however, that it is soon rendered insignificant by the absorption of the water, so though it may affect the percentage values of the illumination at the lesser depths it will have but little effect on the absorption coefficients calculated from them.

The difference between the measurements just above and just below the water surface denotes the loss due to irregular surface reflections, the submarine photometer—even when in air—having a few millimetres of water over its opal disc. Formerly we allowed 15 per cent to cover these shadow and reflection losses and took it that the sub-surface light was 85 per cent of that on the deck-house roof, on an average.

Under calm weather conditions with diffuse light and opal disc over photometer it is quite possible to obtain tolerably good measurements just above and just below the water, using the potentiometer method of measuring the photo-electric current. (See Series 48.) As a rule, however, the conditions render such measurements impossible, because the photometer swings too much, the wave motion is too great at the surface, and the sunlight just below the surface is naturally very variable.

For such measurements the neon lamp method described by J. H. J. Poole (1928) has many advantages, since it gives a measure of an integrated current over any convenient period of time. The measurements made with it in Lower Lough Bray have already been described (J. H. J. and H. H. Poole, 1930). Photometer M was used for this work. The neon lamp outfit taken to sea was the same one that had been at Lough Bray. Since its serviceableness on ships and small boats is great, while its cost and weight are low, an outline of the principle upon which it works is given further on. The fact that the method integrates the current makes it immaterial whether the latter varies irregularly, provided that over the period of the measurements the mean current remains constant. In other words the general illumination must not change—or if it does a series of integration measurements must be performed and an average taken, just as in the potentiometer method. By the help of the neon lamp method measurements were obtained just above and just below the water surface and at depths down to 5 m.; concordant measurements are not easily obtained at depths less than 5 m., using the potentiometer method.

(*c*) Series relating to the horizontal light intensity and the intensity of light travelling upwards have already been given (1928, 1929). These refer to light received on a photometer window placed vertically, or

inverted. Williams (1929) has since made similar measurements with a projecting tube to ensure that only light at 90° to the vertical should enter. Further measurements appeared desirable and as a new case to contain the Burt cell had to be made, it was so designed as to be better adapted for being slung with window vertical. This could most

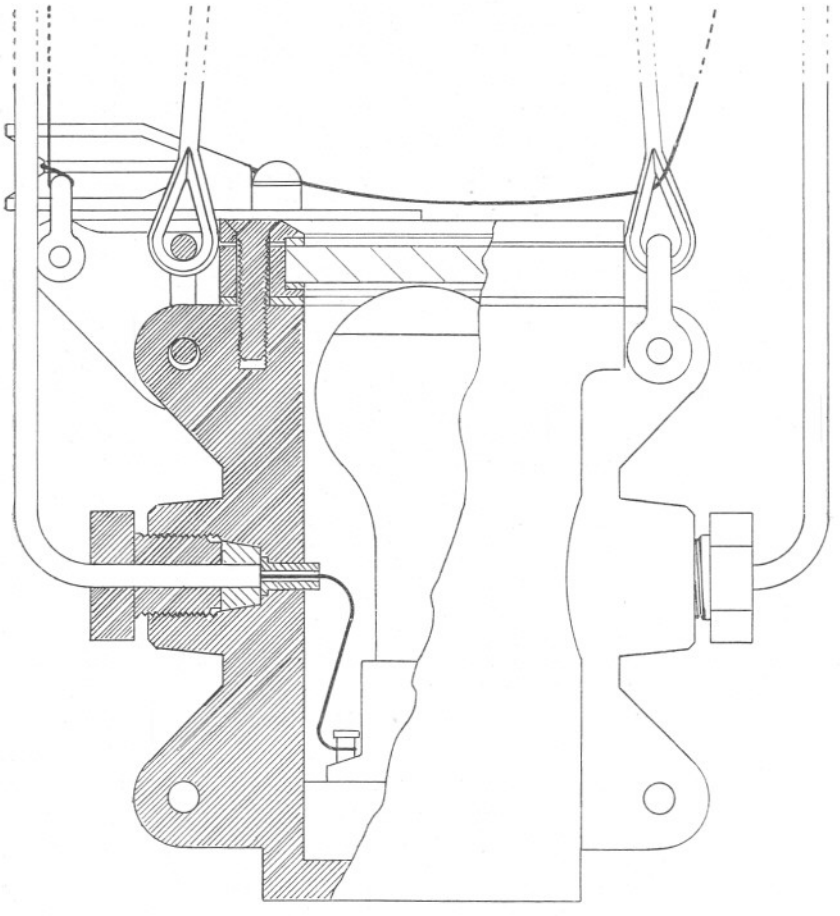

FIG. 1.—Above is shown, in part section, the new type of submarine photometer case with photo-electric cell, the height of the latter, with standard U.S.A. radio valve base, being 16 cm. Immediately over the window of the cell comes the plate glass window, 12·5 mm. thick, which is fixed as described in the lid, one screw of which is shown. The cable leads enter at the sides. Note the lower bolt-holes for lateral or inverted suspension. The photometer is shown with window cover swung clear by applying tension to the twine (full black line) on left-top corner. The twine works in the groove of the wooden projecting piece, which is a cut-away sector of a disc. It is necessary to have the twine passing through a shackle mounted on a metal flange to secure adequate leverage. The insertion of the cables has been described for the earlier type. The opal disc, attached by wax above the plate glass window, is not shown.

conveniently be done by having a cylindrical case (see figure, where the case is shown in part section) and using an "end-on" rather than a side exposure cell. This design was slung by two diametrically opposed steel wires, instead of by four—one from each corner of a box. Moreover, additional bolt-holes were placed, as indicated, near the bottom of the case so that by merely changing one suspending wire and passing its bolt through one of the side lower bolt holes one could sling the photometer with window vertical, instead of horizontal. By using both the lower bolt holes the photometer may be slung in an inverted position. In former measurements the alteration in position had to be made by lashing, with consequent delay and some uncertainty as to a precise setting of the photometer. Figure 1 shows the new type of case. It was lighter and rather easier to handle than the old one. Its greater length, however, made it more apt to tilt in the water were the ship to drift rapidly. This must have been without practical importance in the work here described.

MEASUREMENT OF THE PHOTO-ELECTRIC CURRENT.

(*a*) The Potentiometer Method.

This has been used as previously described. Occasionally with large currents the drop in potential was measured across a 40,000 ohm resistance instead of the usual 100,000 ohm.

In spite of the additional precautions described in our later work (1929) surface leakage continued to be a trouble in very damp weather. The surface of the potentiometer was coated with paraffin wax, with some effect. Nevertheless on October 15, 1929, at Station E 1, with an east wind blowing into the deck-house the leakage was so bad that operations were about to be suspended for the day. As a last resort the insulated metal box containing the H.T. batteries and connected to the negative pole, as shown in the figure facing page 301 (1929), was earthed to a nut on the iron tube carrying the steering chain on the port side of the deck. All troubles ceased immediately. A "dark current" was, however, found again on October 21, but this was traced to photometer M, which on opening was found to have leaked around the window. The internal fittings and cell were washed in distilled water and thoroughly dried ; the calcium chloride was renewed ; finally a good seal was effected by heating the upper portion and the window holder in an air oven and pouring "SIRA" (Scientific Instrument Research Association) wax between the two pieces. These were then screwed together and the wax which extruded was pared away. The photometer has not recently been used at sea, but has been, since December, 1929, upon the roof of the Laboratory attached to a Cambridge Inst. Co. "thread recorder" (1930, 1). No leakage into the cell has occurred.

(*b*) The Neon Lamp Method.

This has been described by J. H. J. Poole (1928), who first devised it, and is figured by J. H. J. and H. H. Poole (1930).

We are indebted to Dr. J. H. J. Poole and to the Physical and Optical Societies for permission to reproduce the figure (Fig. 2). The wooden box containing the condensers, neon tube and safety resistance R (about 20,000 ohms) is indicated in section. Its shape has been modified to

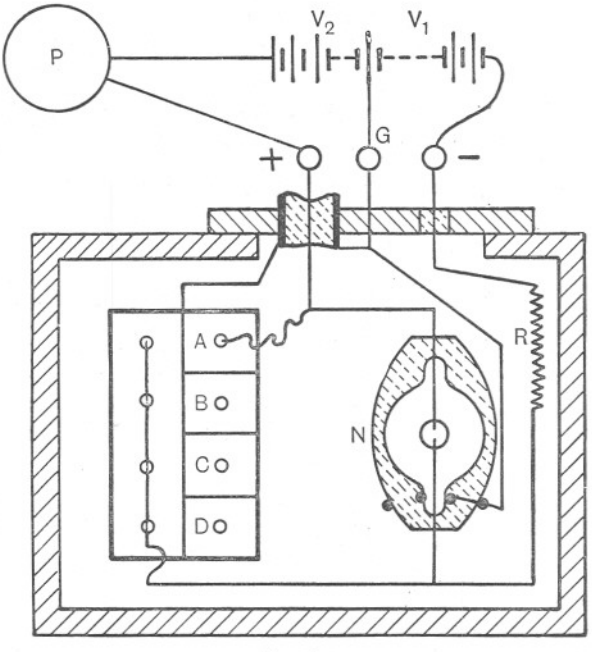

Fig 2.

show the electrical connexions more clearly. For a detailed description the original paper should be consulted.

The ordinary photo-electric circuit is used to charge a condenser, or, in practice, one of a set of four, of capacities as shown, A $=0{\cdot}5\ \mu$F, B $=0{\cdot}05\mu$F, C $=0{\cdot}005\mu$F and D $=0{\cdot}0005\mu$F, any one of which can be used by making connexion with a wander plug. A neon lamp, N, is connected in parallel with the condenser. Provided the voltage across the terminals of the lamp exceeds about 130 a flash will appear from time to time in it, the condenser being partially discharged thereby. It has been shown that the rate of flashing is proportional to the charging current, namely to the mean value of the illumination over the period. The voltage must be high enough not only to ensure flashing but also so that the effective

potential across the photo-electric cell, P, is always in a region in which small changes are without great effect upon the sensitivity, if absolute measurements of illumination are to be made. A sufficient potential, V_1, should be connected to a guard ring, G, attached to the neon lamp, to overcome the effect of small leaks, otherwise a current due to a certain number of metre candles would be required merely to balance the leakage. If the guard-ring potential be too high, flashing will occur in the dark. With a small rate of " dark " flashing, for which allowance can be made, the apparatus is in its most sensitive condition. Usually the total potential, V_1+V_2, should be 230–240 volts, and that across the guard-ring 170 volts.

In the measurements here described the ideal conditions were not satisfied, for though flashing began at about 132 volts, with photometer M, it was not possible to go much above 150 volts without obtaining " dark current " flashes, though at 60 volts M had previously showed no signs of leakage, internal or external. It had accordingly been fitted up without connecting its own guard-ring. For uniformity therefore a nominal, and closely an actual, voltage of 150 was selected and was employed with the deck photometer H (potassium vacuum) and the submarine photometers M (sodium vacuum), L (potassium vacuum) and J (potassium gas-filled).

These preliminary measurements with the neon lamp method were obviously unsuited for the accurate measurement of illumination, especially for low intensities, since the absence of a guard-ring potential introduced the error mentioned above, namely, that a certain minimum illumination was required to overcome the effects of leakage in the neon lamp and condensers. On the other hand, an error of the opposite sign was introduced by the leakage in photometer M. This error was much the larger of the two, and to keep the net dark-current down to a reasonable magnitude, which could be corrected for, the potential was reduced, as above. Hence the anode potential across the photo-electric cell was small, and its variation during the cycle of charge and partial discharge of the condenser must have considerably affected the sensitivity of the cell.

The interest lies rather in determinations of a comparative nature near the surface or at a small number of metres below it. These were, where possible, checked against determinations made by the potentiometer,

It must be pointed out that the effective capacity may differ considerably from the nominal capacity in parallel with the neon lamp, for the leads themselves have a certain capacity which may be quite considerable in the case of the submarine cable. This lessens the sensitivity of the method for work in the sea, but does not impair its usefulness for the lesser depths. This compounded capacity may be denoted thus : A M, capacity A ($0{\cdot}5\mu$F) with that of photometer M, including its leads. In

practice the time taken for a convenient number of complete flashes is measured; from this we can at once find either the time (t) of a single flash, which is inversely proportional to the current, or the number of flashes per minute (n) which is directly proportional to the current.

Inspection of Table I will make the method of standardization clear. This work took one hour under conditions of steady illumination and would have taken longer with variable light or at sea.

TABLE I.

September 29th, 1929. Standardization of neon lamp apparatus on roof of Laboratory, Plymouth, with photometers H and M side by side on parapet. H was used with potentiometer to determine V, shown in thousands of metre candles, k.m.c. When H was attached to the neon lamp apparatus, M, previously standardized against H, was used with the potentiometer. Number of flashes per minute=n. The window of M was wet as used at sea. Voltage was 150 on neon lamp apparatus, usual 60 v. with potentiometer. The series given are the means of five, four, five, and six highly concordant determinations respectively.

G.M.T.	V., k.m.c.	nAM	V., k.m.c., per flash. per min.	Ratios of sensitivities. $\frac{AM}{AH}$
3.10–3.24	40·58	17·6	2·31	11·0
		nAH		$\frac{BH}{AH}$
3.25–3.46	35·18	1·38	25·50	12·4
		nBH		$\frac{BM}{BH}$
3.47–3.59	32·20	15·7	2·06	8·2
		nBM		$\frac{BM}{AM}$
4.0–4.10	27·35	108·9	0·251	9·2

Next day, September 30th, the apparatus was taken to sea on the *Salpa*, but the weather was so bad that preliminary trials only could be carried out, inside the Breakwater. It was necessary to ascertain whether the capacity of the cables attached to M was altered by immersion. The coil had never been in salt water before. The wind was from S.W., strong and freshening, waves breaking, uniformly grey sky.

The ratio of the rates of flashing were determined with photometers side by side : (*a*) coil in air, (*b*) half in water, (*c*) almost all in water ; results were obtained respectively for this ratio :—BM/BH, (*a*) 7·53, (*b*) 5·75, (*c*) 7·09, and 7·47. Under the adverse weather conditions these may be taken to indicate no change. A small alteration would not seriously affect comparative results. Taking the mean of the ratios, omitting the second, we see that BM/BH=7·35, as against 8·22 on the roof the previous day, using the same method and voltage. Comparing M and H, each with 60 volts anode potential, by means of the potentiometer, the ratio M/H=8·89 was obtained as against 8·75 under good weather conditions on the Laboratory roof on September 27th. This ratio 8·89 gives 4·75 metre candles per 10^{-9} amp. for M, for diffuse light, the corresponding value for H being taken as 42·3 m.c. It may be pointed out that the MH

ratios determined by the potentiometer and neon lamp methods are not comparable, both on account of the different voltages—the effective voltage in the latter being low—and of the capacity effect.

TABLE II.

V_a and V denote the illuminations, in k.m.c., as shown by the air and submarine photometers; ss denotes photometers side by side on deckhouse roof, *a* denotes submarine photometer swinging just clear of the water and *b* just below the water surface. The percentages p and p' refer to the roof and sub-surface positions respectively, p_n and $p_{n'}$ being the corresponding values found with the neon lamp apparatus. The values for the vertical absorption coefficients μ_v‡ and μ_{vn} (the latter with the lamp), are entered opposite the lower depth of the range taken, viz. 5 m. value is 4 to 5 m.

Time of flash, with 0·05μF condenser = 2·70 sec., for photometer H and 0·394 sec., for photometer M, ratio M/H = 7·71, at 2·11 G.M.T.

Date, Remarks, etc.	G.M.T.	V_a k.m.c.	d m.	V k.m.c.	p	p'	μ_v	p_n	$p_{n'}$	μ_{vn}
SERIES 47 and SERIES N2 2.10.'29.	2.4	40·2	ss	40·2	100	121	—	100	138	—
Off Pier Cellars, Cawsand Bay, depth 8 m.	2·34	40·4	b	33·3	82·5	100	—	72·7 71·8	100	—
	2.42	35·8	1	13·0	36·3	44·1	0·821	—	—	—
Wind strong N.W., waves	2.51	60·4	1	21·1	35·0	42·5	0·858	—	—	—
breaking at times, long	2.58	56·9	2	10·6	18·6	22·6	0·630	19·0	26·3	0·867†
swell. Sun weak through	3.25	19·5	3	1·62	8·29	10·1	0·809	10·7	14·8	0·568
broken clouds, some blue	3.46	25·9	4	1·04	4·01	4·87	0·725	4·74	6·56	0·821
sky.	3.50	20·2	5	0·385	1·91	2·32	0·744*	1·79	2·48	0·969
	4.4	18·7	6	0·236	1·26	1·52	0·420	0·49	0·68	1·31

* Mean 0–5 m., 0·746 for μ_v and 0·818 for μ_{vn}.

† 0 – 2 m.

‡ In previous papers we used μ for the absorption coefficient calculated on the supposed mean length of the path of the beam reaching the photometer and λ for the vertical absorption coefficient. μ_v is now used for the vertical absorption coefficient as when dealing with the colour of the light we require the usual symbol λ to denote wave-length.

Date, Remarks, etc.	G.M.T.	$\alpha°$	Light.	β	d m.	V_a k.m.c.	V k.m.c.	p %	p' %	μ_v
SERIES 48. 14.10.'29.	1.25		Sun clear, sky	2·32	—	52·0	52·0	100	134	—
M Photometer. At E1.	1.36		clear blue, few		a	51·1	45·2	88·5	116	—
Wind S.W., very light,	1.45		clouds low on		b	51·9	38·8	74·8	100	—
water smooth, almost	1·50	31	horizon. Visi-		1	51·9	32·2	62·0	82·9	0·188
glassy, only slight swell.	1·56		bility good.		2	45·9	20·4	44·5	59·5	0·332
Depth 73 m.	2.0				5	45·7	9·91	21·6	28·9	0·238
	2.4	30			10	44·2	2·70	6·11	8·18	0·253
	2·7				15	44·0	1·02	2·32	3·10	0·194
	2.9				20	43·6	0·396	0·91	1·22	0·187
	2·12	29			25	43·6	0·163	0·375	0·502	0·177
	2·16				30	43·1	0·068	0·157	0·210	0·174
	2·19	28			35	43·1	0·029	0·066	0·088	0·172
	2·25	27			40	37·9	0·010	0·026	0·035	0·186
	2·39				35	38·4	0·017	0·045	0·060	0·168
	2·42	25			30	38·4	0·052	0·131	0·175	0·219
	*									
SERIES 49. 14.10.'29.	4.6	12		1·21	—	14·4	14·4	100	—	
M Photometer. At E1.	4·12	11			5	13·9	2·94	21·1	28·2‡	0·252‡
	4·16				10	13·5	0·878	6·50	8·7	0·236
	4·21	10			15	11·9	0·258	3·07	4·1	0·150
SERIES 50. 14.10.'29.	4·33	8	Sun clear, but		5	9·54	1·410	14·80	37·2	0·198
L Photometer. At E1.	4·36		low, sky clear,		10	8·90	0·444	4·99	12·5	0·217
Surface glassy, a flat	4.40	7	visibility good.		15	8·52	0·134	1·56	3·9	0·232
calm. Secchi disc 8½ m.	4·42			1·11	—	7·74	—	—	—	—
in sun on W., at 4.45 and	4·44	6		1 08	—	7·36	—	—	—	—
9 m. in shade on E.	4·57	4			b	5·17	2·055	39·8	100	—
	5·1	3			a	4·45	2·120	47·7	123	—

* The neon lamp method series N3 came in between.

‡ Calculated on the sub-surface value 74·8 per cent of Series 48, or allowing the usual 15 per cent loss only 0·278.

Date, Remarks, etc.	G.M.T.	$\alpha°$	Light.	d m.	V_a k.m.c.	V k.m.c.	$\frac{p}{\%}$	μ_v
Series 51. 15.10.'29.	12·6	31	Sun hazy but	5	43·1	8·56	19·8	0·291
M Photometer. Near	12.11		clearing, sky	10	44·3	2·36	5·32	0·263
E1. Wind E., light.	12·19		blue with much	10	64·8	3·23	4·97	0·276
Secchi disc 10 m. in	12·29		haze.	15	58·1	1·02	1·77	0·207
shadow of ship to W.,	12·34			20	57·0	0·386	0·678	0·191
9 m. in sun on E. of ship.	12.39			25	56·2	0·161	0·286	0·172
	12·44			30	56·2	0·060	0·107	0·197
	12·48			35	57·9	0·025	0·043	0·181
	12·52			5	59·2	9·05	15·2	0·330*
	1·0	30		ss	56·2	56·2	100·0	—

Date, Remarks, etc.	G.M.T.	$\alpha°$	Light.	d m.	V_a k.m.c.	H k.m.c.	$\frac{p_h}{\%}$‡	$\frac{p_h}{p_v}$	μ_h
Series 52. 15.10.'29.	1.21	29	Sun clear, visi-	5	51·4	2·700	5·26	0·266	—
M Photometer. Slung	1.25		bility good, no	10	51·7	0·995	1·93	0·375	0·201
horizontally. Near E1.	1.28		clouds.	15	50·9	0·248	0·487	0·276	0·275
Moderate swell, waves	1·31	28		20	50·4	0·121	0·241	0·356	0·140
breaking, wind S.E., light	1.33			25	48·7	0·045	0·093	0·323	0·191
to moderate.	1.36			30	48·7	0·034	0·069	0·650	0·058
	1·40	27		5	48·5	1·770	3·66	0·184	— †

* 5–35 m., $\mu_v = 0{\cdot}195$.
‡ Relative to the vertical light in air, p_v is p of Series 51.
† 5–30 m., $\mu_h = 0{\cdot}158$.

Date, Remarks, etc.	G.M.T.	$\alpha°$	Light.	d m.	V_a k.m.c.	V k.m.c.	$\frac{p}{\%}$	μ_v
Series 53. 15.10.'29.	2.42	22	Sun clear, low	ss	38·4	38·4	100·0	—
Photometer J. Near	2.45		clouds only,	ss	36·7	36·7	100·0	—
E1. Wind S.E., light to	2.57		visibility good.	5	32·2	6·57	20·4	0·285*
moderate, swell moderate	3.5	20	$\beta = 1{\cdot}59$.	10	31·2	2·02	6·50	0·228
and decreasing.	3.10	19		—	28·9	—	—	—
	3.15	18		15	26·7	0·644	2·41	0·198
	3.19			20	26·8	0·330	3·12	0·134
	3.22	17		25	26·3	0·187	0·712	0·110
	3.32	16		30	23·6	0·110	0·467	0·084
	3.35			35	23·6	0·073	0·310	0·082
	3·44	14		40	20·0	0·047	0·236	0·056
	3.55	13		35	15·1	0·048	0·317	0·078
	3.59			45	14·9	0·022	0·149	0·091
	4·5	12		50	14·3	0·011	0·075	0·075†
	4.12	11		55	10·8	0·008	0·072	0·114‡
	4.19	10		5	8·88	1·90	21·4	0·275*
	4.26	9		5	7·53	1·63	21·7	0·272*
	4.34	8		ss	6·51	6·51	100·0	—

* Assuming 15% loss at surface, including shading due to ship.
† For 45–55 m. ‡ For 5–55 m.

Date, Remarks, etc.	G.M.T.	$\alpha°$	Light.	β	d m.	V_a k.m.c.	V k.m.c.	$\frac{p}{\%}$	μ_v
Series 54. 21.10.'29.	12.10	29	Sun and blue	2·23	—	48·4			
Photometer J. About	1.12	28	sky with mov-			42·8			
one mile W. of Rame Hd.,	1.26		ing clouds.			21·4			
depth 33 m. Wind S.W.,	1·30					23·9			
light to fresh, some waves	1.42				ss	45·3			
breaking.	1.48				ss	47·6			
	1.54				ss	21·6			
	1.59	24			ss	18·9			
	2.7				ss	40·4			
	2.25	22		1·82	5	33·1	5·78	17·5	0·315
	2.33	21			10	33·6	1·46	4·35	0·278
	2·45	20			15‡	27·4	0·406	1·48	0·216
	2.57				15§	27·9	0·397	1·42	0·223
	2.59				15	25·5	0·376	1·48	0·216
	3.4	18			20	25·1	0·099	0·39	0·263
	3·8				25	24·6	0·036	0·15	0·199
	3.14				30	24·1	0·008	0·03	0·287*
	3·16	16		1·36	—	23·9	—	—	—
	3·30	14			5	18·9	2·89	15·3	0·342
	3.40	13			5†	15·1	2·16	14·3	0·356

‡ J at 12 volts up to this.
§ J at 60 volts. $J_{60}/J_{12} = 2{\cdot}34$.
† J at 12 volts again.
* 5–30 m., 0·244.
ss Photometers side by side for calibration.

Date, Remarks, etc.	G.M.T.	Light.	d	p	p'	μ_v
SERIES N1. 30.9.'29.	11.40	Sky overcast.	ss	100	168	—
Photometer M. Just inside Plymouth Breakwater, depth 13 m. Wind S.W., strong and freshening, waves breaking.		Thickening for rain, occasional drops in afternoon. At 12.30 V=18·6 k.m.c., and at 2.45 V=6·1.	a	70·5	118	—
			b	59·5	100	—
			b^1	55·5	93·5	—
			1	39·6	66·6	0·404
			2	25·6	43·1	0·435
			3	16·0	26·9	0·495
			4	10·0	16·8	0·469
	1.40		5	6·67	11·2	0·401
	2.0		6*	5·12	8·61	0·266
			7	3·43	5·77	0·399
			0–7	—	—	0·410

* Changed over from condenser B (0·05μF) to C (0·005μF) for each photometer, viz. H on deck-house roof and M in water.

SERIES N2. 2.10.'29.	Blue sky and broken clouds; sun weak through clouds.	ss	100	138	
Photometer M. Off Pier Cellars, Cawsand Bay, depth 8 m. Wind strong, N.W., long swell, waves breaking.		b	72·7	100	
		b^1	71·8	98·7	
		2	19·0	26·1	0·867
		2	19·1	26·2	—
		3	10·9	14·7	0·568
		3	10·5	14·3	—
		4	4·75	6·52	0·821
		4	4·74	6·51	—
		5	1·79	2·47	0·969
		6	0·49	0·67	1·31
		6	0·48	0·66	—
		0–6			0·831

Date, Remarks, etc.	G.M.T.	$\alpha°$	Light.	d	p	p'	μ_v
SERIES N3. 14.10.'29.	3.24	17	Sun clear, sky clear blue, few clouds low on horizon. Visibility good.	5	33·7	36·4	0·216
Photometer M. At E1, depth 72 m. Wind S.W., very light, water almost glassy, only slight swell.	3.29			4	41·8	45·2	0·144
	3.33	16		3	48·3	52·2	0·304
	3.39	15		2	65·5	70·8	0·138
	3.44	14		1	75·2	81·3	0·207
	3.51	13		b	92·5	100	—
	3.57			a	100	108	—
				0–5	—	—	0·202
SERIES N4. 21.10.'29.	3.52	11	Sun and blue sky with clouds, light fairly steady.	5	14·3	18·7	0·407
Photometer J. About one mile W. of Rame Hd., depth 33 m. Wind light to fresh, some waves breaking.	3.58	10		4	21·5	28·4	0·228
	4.6			3	27·1	35·7	0·356
	4.10	9		2	38·7	51·0	0·179
	4.16	8		1	46·3	61·0	0·392
	4.21	7		b	68·5	90·3	—
	4·29	6		a	77·0	—	—
	4.39	5		a	76·0	100	—
	4.50	3		ss	100·0	132	—
				0–5			0·312

DISCUSSION OF RESULTS.

Table II records the results obtained in Series 47–54, in which measurements were made as usual by the potentiometer method, and in Series N1–N4, in which the neon lamp method was used.

The lettered sections which follow relate in general to those similarly lettered in the introduction.

(*a*) It was never found possible to use the new vacuum sodium photometer (M) down to the bottom, 70 m.; the greatest depth was 40 m. (Series 48), at which the illumination was 10 m.c. Photometer L had previously been used to 40 m. (Series 19), the illumination being 150 m.c. The inadequate cable length prevented its use at a greater depth. Were the aperture to be increased somewhat and the cable lengthened it

appears that a potassium cell could be used to greater depths than a sodium cell. Thus at Station E1 on 14/10/'29 the sodium cell gave, for the vertical absorption coefficient, μ_v, between 5 and 35 metres, the value 0·193 (Series 48), whereas next day the gas-filled potassium cell J gave 0·139 over the same range (Series 53). Obviously the shorter mean wave-length registered by the sodium cell is more heavily absorbed than is the rather longer radiation to which the potassium cell is sensitive ; for the wave-length sensitivity data see Figure 2, page 466, Vol. 15, this journal. Such a result is in keeping with the findings of Shelford (1928) for the upper 15 m. in the Puget Sound, below which the transmission of the light affecting the sodium cell was the greater. A comparison of photometers M (sodium) and L (potassium vacuum) on 14/10/'29 at E1 gave, from 0–15 m., μ 0·228 and 0·213 for M and 0·216 for L. This is close agreement, but it may be seen in the figure that this particular potassium cell showed greater response to shorter wave-lengths than did other potassium cells ; in any case the gas-filled cells show a sensitivity shift towards longer wave-lengths. The three values of μ_v for 14/10/'29 were obtained at 2 P.M., 4.15 P.M. and 4.35 P.M., mean times, of each series, and serve to show that there was no appreciable alteration in absorption due to phototropic movements of zooplankton, as had been suspected previously on other occasions ; at this season, however, no considerable amounts of zooplankton would be found.

As regards the state of the water from year to year it is of interest to consider the mean values of μ_v from 5–35 m., at E1. The determinations in 1925, 1927 and 1929 were made with potassium gas-filled cells K and J, that for 1928 with a vacuum cell, L ; μ_v=0·146 (1/10/'25), 0·104 (3/10/'27), 0·124 (2/10/'28) and 0·139 (15/10/'29). At this time of year the vertical circulation, brought about by surface cooling, has just taken place, so that the water column is isothermal and homogeneous. There are, however, considerable differences in μ_v from year to year. These are probably to be sought in the amount of suspended matter, in which inshore water is richer than that further out to sea. Examples illustrating this may be found by comparing Series 47, Cawsand Bay, μ_v=0·78, Series N1, Breakwater, μ_v=0·41, Series 54, near Rame Head, μ_v=0·24, Series 51, near E1, but closer to shore, μ_v=0·19. These measurements were with the sodium photo-electric cell, save Series 54, in which a gas-filled potassium cell was used, giving a value rather lower than with a sodium cell. Since it was not possible, as shown in our 1929 paper, to correlate the changes in μ_v with seasonal changes it would appear desirable to study it on a line across the English Channel, or further out into the Atlantic, for it might give indications of the origin of the water similar to those given by salinity determinations, and perhaps more delicate, even though of lesser percentage accuracy.

(*b*) As previously pointed out the shadow error, due to taking the deck-house roof reading as being a measure of the illumination just above the water surface, is both large and variable. Thus in Series N1, with no sun, the shadow loss was 29·5 per cent of the total illumination as measured on the roof; in Series N4, with a clear sky and low sun it was 23·5 per cent; in Series 48, with a clear sun and sky and $\beta=2{\cdot}3$, the loss was only 11·5 per cent. In Series 50, with a clear sun and sky, but late in the afternoon with $\beta=1{\cdot}04$, the loss was 52·3 per cent; in this case the shading must have been abnormally great, the deck-house photometer perhaps sloped towards the sun with the ship's roll and the photometer above the sea was entirely shaded from the sun; but whatever the explanation such measurements were obtained.

In obtaining illuminations below the surface the readings must be multiplied by the factor 0·935, which is the ratio for the light in air to the light just below a smooth water surface for diffuse daylight (see p. 184, 1926 paper).

The submarine photometers were standardized in air, with opal glass in position and window wet, bubbles being excluded. The light in air was measured by the roof photometer, H, so that in the water over the window may be taken as 0·935 of this. Accordingly the "air" reading of the submarine photometer corresponds to an illumination in the layer of water just outside its window only 0·935 times what one assumes for the purpose of standardisation. The factor is an approximate one for an assumed uniformly bright sky. This correction has been made in obtaining the figures given in the table.

The light lost upon entering the water was measured directly in five series, being obtained from the illumination just above the surface "*a*" in the tables, and that just below the surface "*b*." Values for $a-b$ were as follows: Series N1, 15·5 per cent; N3, 7·5; N4, 10·5; 48, 15·5; 50, 16·5; mean, 13·1.

Formerly, in calculating μ_v, 0—5 m., we took the deck-house roof illumination and deducted 15 per cent to obtain the sub-surface illumination, *b*. This would have been approximately correct for the surface loss, but is quite inadequate for the shadow loss.

It would therefore appear that it is essential to obtain *a* directly if *b* cannot be obtained on account of the roughness of the sea. If neither can be obtained values for the percentage submarine illumination may be got by assuming a surface loss of 15 per cent for choppy water or 8 per cent for calm water, and making an approximate allowance for the shading due to the ship according to the lighting conditions prevailing at the time.

It follows from this that the neon lamp method is of value, for only under really good weather conditions can *a* and *b* be obtained by the

potentiometer method. The latter, however, has the advantage for work down to the greater depths.

(*c*) As regards measurement of the "horizontal light," namely, that falling on a vertical surface, only one series (No. 52) has been obtained in addition to those previously reported, Series 15 (12/9/'27), Series 25 (6/3/'28). The latter series, with an efficient opal diffusing disc, gave 0·61—0·47, mean 0·54 as the ratio of horizontal to vertical light from 0—25 m. Series 52, within the same limits, gives 0·37—0·22, mean 0·31, as determined with sodium photometer, instead of potassium in Series 25. Further measurements are desirable.

SUMMARY.

1. J. H. J. Poole's neon lamp method (1928) of integrating the photo-electric current is serviceable for work at sea down to moderate depths, which further experience may extend considerably. It is specially valuable for determining the light just above the water, and at such depths down to 5 m., at which the variability of the light renders the potentiometer method (1925) very difficult or quite impossible in rough water. For greater depths, down to 70 m. (bottom in the English Channel around our normal range) we have so far been able to use the latter only.

2. The loss due to the shadow of the ship, obtained by subtracting the illumination just above water from that on the deck-house roof, was found to vary from an extreme case of 52 per cent, and a normal loss of 30 per cent, with an overcast sky, down to 11 per cent with a clear sun at 31° altitude.

3. The loss of light due to its entering the water was found to vary from 7·5 to 16·5 per cent, mean 13·1 per cent.

4. It is desirable that the illumination just above and just below the water surface should be determined by the neon lamp method as a routine.

5. It was found that, under the isothermal and homogenous water conditions obtaining during the first half of October, the vertical absorption coefficient, μ_v varied at Station E1 (about twenty miles outside Plymouth Sound) from μ_v=0·146 in 1925 to μ_v=0·104 in 1927, 1928 and 1929 being intermediate with μ_v=0·124 and 0·139 respectively, over the range 5–35 m. These potassium cell values are less than similar determinations with a sodium cell, for which the value μ_v=0·193 corresponds to the 0·139 value for potassium.

6. A modified form of submarine photometer case has been described, so constructed that its opal receiving surface can be altered from the

horizontal to the vertical or inverted positions merely by altering one or two bolts and shackles. It has two shackles instead of four. The one series of measurements made with it and its sodium cell, gave a mean value 0·31 for the ratio of the horizontal to the vertical submarine illumination between 0 and 25 metres.

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The Effect of Light of Different Intensities, Reduced Selectively and Non-selectively, upon the Rate of Growth of *Nitzschia closterium.*

By

F. A. Stanbury, M.Sc.

With 7 Figures in the Text.

Introduction.

The effect of light upon plant growth is a problem which has attracted many workers since the discovery of Priestly, in 1771, that a plant could purify fixed air, carbon dioxide, which was followed by the supplementary work of Ingen-Housz and Senebier, who showed that the phenomenon was associated with the nourishment of the plant, and took place only in sunlight and through the agency of the green portions of the plant.

Senebier, 1782, was perhaps the first to attempt to show the effect of the different parts of the spectrum on the process, and found that red light was almost as active as ordinary light in the process of photosynthesis whilst the blue was almost inactive. Draper and Daubeny, 1844, concluded that after white light, the red-yellow portion possessed the highest efficiency, and this was supported by Sachs in 1868. Englemann, Timiriazeff and Wolkaff, however, found that whilst the activity in the red was high, there was an important secondary maximum of efficiency in the blue, and these results have been subject to great controversy amongst later workers.

It must be borne in mind that the physics of the light used by the early investigators was not thoroughly understood, and one of the greatest criticisms brought against these workers is that the blue light used by them contained parasitic rays of long wave lengths, viz. in the red region. Dangeard (1927) asserts that in light of feeble intensity, these parasitic rays are practically inactive, but in light of greater intensity they play a highly important role, and are the cause of the secondary maximum observed by many workers. Richter (1902) using coloured screens, concluded that the rate of photosynthesis was proportional to the amount of energy absorbed, independent of the part of the spectrum and the wave length of the ray, and Kniep and Minder (1909) determined that the

action of the red and the blue was almost similar when the energy in those regions was the same.

Klugh (1925) sought to determine whether photosynthesis was a wave length phenomenon, or dependent upon the total light intensity. To do this he grew unicellular algæ, in light which he regarded to be of the same intensity but of different wave lengths, and took the rate of reproduction as criteria for efficiency of the wave lengths concerned in photosynthesis, for although the method was indirect it was assumed that, fundamentally, the rate of reproduction in chlorophyllous organisms is dependent on the ability to manufacture food. From a single series of experiments lasting from August 16th–September 10th he concluded that photosynthesis is a wave length phenomenon, red light being highly efficient, blue much less so, and green inefficient, but Klugh himself in his concluding remarks says "that it is dangerous to draw conclusions from a single series of experiments."

Using somewhat similar methods to those of Klugh, results are now presented in this paper, which would show that photosynthesis, as indicated by the rate of growth of marine diatoms, is a function of the amount of energy transmitted independent of the wave length between which the energy so transmitted lies.

Plant material used.

Persistent cultures of the marine diatom *Nitzschia closterium*, grown in "Miquel sea water," were used for the plant growths to be studied, a persistent culture, as defined by Allen and Nelson (1910), being one in which only one species of diatom was present, although there might be bacteria.

It is of interest to mention here, that marine diatoms exhibit well-marked periodicity in the sea, the diatom outburst being at its height between early March and late April. The cause of these outbursts is not fully understood.

Marshall and Orr (1928) concluded that the length of day was a factor of the greatest importance, whilst Atkins, Herdman, Scott and Dakin correlated the early spring sunshine with the diatom outburst. Atkins (1928) also found that "a study of the phosphate change affords a measure, in an inverse ratio, of the production of the algal crop, and indicates from year to year the variations that occur in its seasonal waxing and waning."

From results obtained using the marine diatom *Nitzschia closterium* it would appear that the total light intensity is a factor which has a profound effect upon growth.

Method.

It was desired to determine the effect of light of selected wave lengths and of daylight reduced in intensity non-selectively, upon the rate of growth of *Nitzschia closterium*, and this was done by growing cultures of Nitzschia under a series of selective and non-selective filters.

Equal volumes of "Miquel sea water," contained in sterilized crucibles of white porcelain of 10 cubic centimetres capacity and 3·5 centimetres

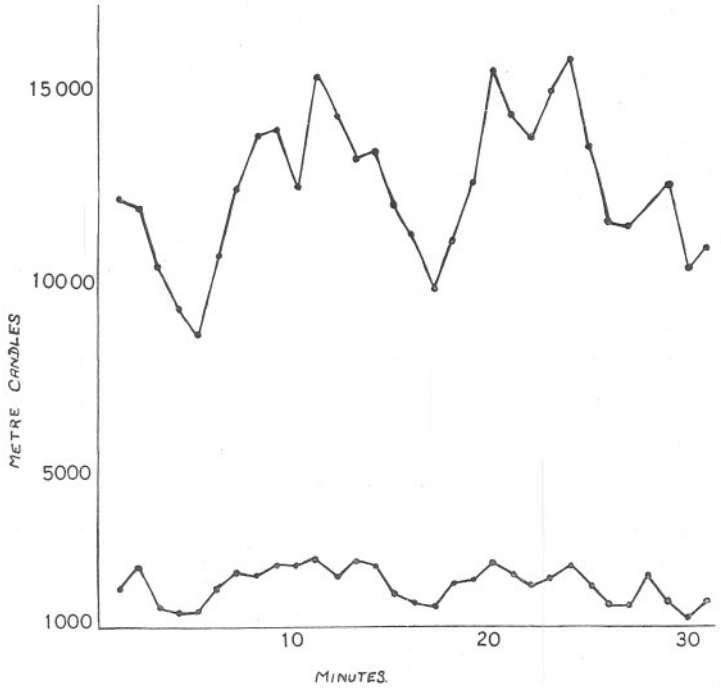

Fig. 1.—Curves showing the variations in illumination for the north window, lower curve, where the cultures were set, and for an open site on the laboratory wall, upper curve, determined simultaneously for a period of 30 minutes. The numbers along the ordinates represent the illumination in metre candles. Those along the abscissæ the time in minutes.

diameter, were inoculated with similar drops of a persistent culture solution, which contained known numbers of diatoms per unit of volume.

The number of diatoms in any culture was determined with the aid of a hœmacytometer, the millimetre square being ruled in Thoma pattern. The culture to be examined was first thoroughly mixed by means of a fine sterilized pipette, this process also serving to aërate the culture. A drop of the mixture was then placed upon the hœmacytometer, and the number of diatom cells per unit of volume, 0·1 cubic millimetre, was then

found by counting. For each reading an average of four counts was made, a difference of ten diatoms being allowed for any accepted count.

Examination of the tables of results as a whole, will show that it would have been better to have used larger initial number of diatom cells since their minute size renders them very difficult to count when present in small numbers. This explains the irregularities in the early counts for the cultures of each series.

The sub-cultures were covered with the selected filters and then placed side by side in the window of a north room. The distance between the two end cultures was 80 centimetres. Opposite the window and 4·2 metres away from it, is a high grey wall of limestone, which receives direct sunshine only for a short time as the sun sets.

On 27.2.30, simultaneous measurements were made of the illumination of the window in the north room (V_s) and of a perfectly open site on the laboratory roof (V_o) by means of photometers furnished with vacuum photo-electric cells. (For method see Atkins and Poole, 1929.) It has been shown that on a dull day, the illumination at a point inside a building bears a very nearly constant ratio to the illumination at a point outside, and this ratio, expressed as a percentage, has been termed the daylight factor δ. Table I shows these values over a period of half an hour.

TABLE I.

February 27, 1930. Grey sky, completely overcast, wind N.E. 12.14–12.43 p.m. G.M.T.

Indoor site is the window-sill of a north room, where the photometer is moved over a range of 80 cm. The outdoor site is a fixed position on a parapet of the Laboratory roof.

Indoor sites (in window sill).		G.M.T.	Illumination in meter candles. In open on Roof Vo.	Illumination in meter candles. In window sill Vs.	Daylight Factor. $\frac{Vs.}{Vo.} = \delta$	Average δ
Site 1.	1.	12.14	12,000	1,950	16·2	
Right extremity	2.	12·16	10,200	1,490	14·6	
occupied by	3.	12·17	9,150	1,389	15·2	
cultures.	4.	12·18	8,500	1,392	16·4	
						15·6
Site 2.	1.	12·19	10,500	1,930	18·5	
To right of centre.	2.	12·20	12,200	2,360	19·3	
	3.	12·21	13,600	2,340	17·2	
	4.	12·22	13,800	2,520	18·3	
						18·3

Indoor sites (in window sill).		G.M.T.	Illumination in meter candles. In open on Roof Vo.	In window sill Vs.	Daylight Factor. $\frac{Vs.}{Vo.}=\delta$	Average δ
Site 3.	1.	12·23	12,200	2,520	20·7	
Centre of window.	2.	12·24	15,200	2,680	17·6	
	3.	12·25	14,100	2,290	16·2	
	4.	12·26	13,000	2,680	20·6	
	5.	12·27	13,200	2,560	19·7	
	6.	12·28	11,800	1,880	15·9	
						18·45
Site 4.	1.	12·29	11,100	1,610	14·5	
To left of centre.	2.	12·30	9,690	1,410	14·7	
	3.	12·31	10,900	2,110	19·3	
	4.	12·32	12,400	2,170	17·5	
	5.	12·33	15,400	2,660	17·4	
	6.	12·34	14,200	2,310	16·3	
						16·6
Site 5.	1.	12·35	13,600	2,060	15·2	
Extreme left of	2.	12·36	14,800	2,260	15·3	
centre.	3.	12·37	15,600	2,660	17·1	
	4.	12·38	13,300	2,000	15·1	
	5.	12·39	11,400	1,610	14·2	
	6.	12·40	11,300	1,550	13·8	
	7.	12·41	14,900	2,310	15·6	
	8.	12·42	12,400	1,670	13·5	
	9.	12·44	10,800	1,680	15·6	
						15·6

Total average for the four sites is 16·6 for δ.

The Filters used.

The filters selected were twelve in number, and Table II gives the details concerning their transmissions of energy and wave length. The non-selective screens were Wratten filters of certain known reduced intensities. The transmissions (T) for these were :—T=50%, 25%, 12·5%, 6·25% and 3·1% respectively, but unhappily the gelatine films were damaged at the outset of the experiments, and their actual transmissions determined photo-electrically, using a sodium vacuum sensitive cell, were T=41·8%, 19·2%, 9·24%, 3·26% and 1·66% respectively.

For convenience these filters will be referred to as Wratten filters $T=\frac{1}{2}$, $T=\frac{1}{4}$, $T=\frac{1}{8}$, $T=\frac{1}{16}$ and $T=\frac{1}{32}$ respectively. The makers' figures refer, however, to light incident normally whereas the photo-electric

measurements refer to light received from the sky as a whole. The latter are necessarily lower than the former on account of the oblique incidence.

Six selective filters were used. Four were of Corning glass of red, orange, green and blue shades, and the actual percentage transmissions for these were determined by Dr. H. H. Poole (Dublin) by means of a Moll thermopile. Figure 2 shows the curves obtained from his data together with the transmission curves of the other coloured filters used.

TABLE II.

To show the wave lengths, light transmissions and relative energy values for the screens and filters used for the culture experiments.

Screen or filter used.	Thickness of screen used. mm.	Wave length in mμ.	Actual percentage light transmitted T.	Average relative energy in arbitrary units (from Dr. Abbot's data).	Total percentage relative energy transmitted E.
Solar spectrum			100	2,880	100
Wratten neutral					
1. Wratten T=$\frac{1}{2}$		400–720	41·8	1,240	41·8
2. ,, T=$\frac{1}{4}$		,,	19·2	570	19·2
3. ,, T=$\frac{1}{8}$		,,	9·5	274	9·5
4. ,, T=$\frac{1}{16}$		,,	3·3	95	3·3
5. ,, T=$\frac{1}{32}$		,,	1·7	49	1·7
6. Ordinary glass		,,	71·0	2,040	71·0
7. Corning red	2.96	620–720	67·1	602	20·9
8. ,, orange	2·96	570–720	73·0	990	34·5
9. ,, green	3·47	490–570	13·4	96	3·3
10. ,, blue	2·96	400–490	60·4	490	17·0
11. Schott and Gen blue	2·21	400–490	50·3	406	14·0
12. Chance blue		400–490	36·2	293	10·2
13. Heat absorbing screen		400–720	27·7	795	27·7
14. Heat absorbing + Corning blue		400–490	16·7	135	4·7

One of these was a blue glass prepared by Schott and Gen of Germany, and the transmission curve was obtained from data supplied by them. The other blue filter was prepared by Chance of Birmingham and the curve for it was obtained by resolving values read from a photograph of the density curve supplied by them. $(\text{Density} = \log \frac{1}{\text{transmission}})$. It may be observed from Figure 2, that the Corning blue transmits a certain low percentage of parasitic red rays. These were eliminated in some experiments, by placing a heat absorbing screen of a green shade over the Corning blue, which effectively cuts off these red rays, but lowers the intensity considerably. A suitable correction has been applied for this, in interpreting the results with the combination of screens. The

other blue screens furnish a blue light of a high degree of purity, the Chance blue shows no inclusion of red at all.

Lastly, a filter of ordinary glass was used as a control, and since it was of a greenish tinge the amount of blue light passing through was lowered, and the total intensity of the light received reduced.

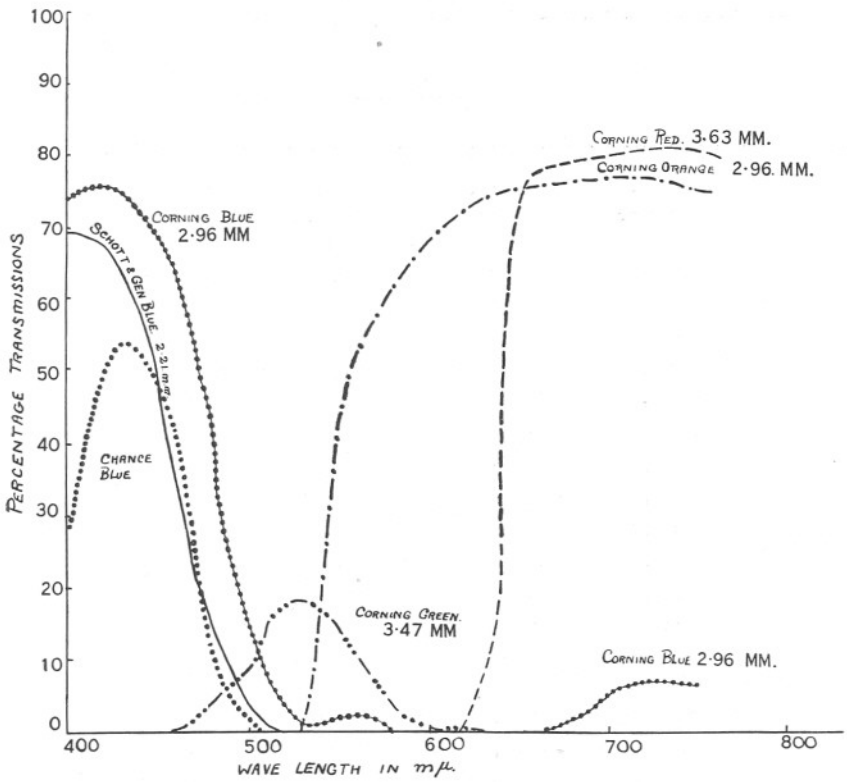

FIG. 2.—The ordinates are percentage transmissions for the selective screens used as determined, using a Moll thermopile. The abscissæ are wave length in mμ. The curves for the Chance blue, Schott and Gen blue glasses were obtained from data supplied by those firms as corrected for reflection losses for light incident normally.

THE RELATIVE ENERGY OF THE FILTERS USED.

Owing to lack of apparatus it was impossible to determine the relative energy transmitted through the screens directly, but it is hoped that this will be done shortly. The energy value is one which is undergoing constant change throughout the day, since it varies considerably in the different portions of the spectrum, and the proportion of the red, yellow, green and blue light changes from hour to hour according to the time of day and the condition of the sky light. An attempt to obtain approximate

values of the relative energy in arbitrary units was made in the following manner.

At the Seventh International Congress of Photography, 1929, it was recommended that the following energy values derived from data of Dr. C. G. Abbot (Smithsonian Institute, U.S.A.) should be adopted as defining the spectral composition of mean noon sunlight. Table III shows these values for the visible part of the spectrum.

TABLE III.

RELATIVE ENERGY VALUES FROM DATA OF DR. C. G. ABBOT.

Wave Length.	Relative Energy.	Wave Length.	Relative Energy.
360	16·0	550	101·7
370	20·5	560	100·0
380	25·1	570	98·4
390	30·1	580	97·2
400	45·2	590	95·6
410	57·2	600	95·2
420	65·8	610	94·3
430	69·2	620	93·2
440	77·2	630	92·2
450	86·8	640	91·0
460	92·2	650	89·7
470	96·9	660	88·5
480	99·0	670	86·4
490	100·6	680	84·7
500	101·8	690	82·7
510	101·2	700	80·5
520	101·2	710	78·1
530	101·1	720	76·1
540	100·9		

Using these figures it was calculated that the average value for the relative energy transmitted from 720mμ—400 mμ. was 89·9 units per sq. cm. per minute, and the light transmitted over this region was taken as 100%. The total energy transmitted, E, for the visible spectrum was thus proportional to $89{\cdot}9 \times (720-400) = 2880$ arbitrary units. Since this is the maximum value for E, it may be taken as 100, and the values of E for the light filters then found by substitution, e.g. considering the Corning red filter $\frac{89{\cdot}9 \times (72-62)}{2880} = 31{\cdot}2\%$, and this is the proportion of

red as defined in the spectral curve. Of this the filter transmits 67·1%, so that the total relative energy transmitted is only 21·0%. Column 5, Table II, shows the values of E for all the filters used.

RESULTS OF OBSERVATIONS

Attempts were first made to conduct the experiments in the open, but the temperature was too high for the growth of the diatoms, and the light intensity also, for all but the more heavily screened.

Three series of observations were made indoors :—a preliminary series in May, 1929, followed by a second series June 13th–July 28th, 1929, which is referred to as the " summer " series. In both cases filters 1–10, Table II, were used. During the interval between the second and third series (January–March, 1930), the actual transmissions of the filters had been determined by Dr. H. H. Poole, revealing the presence of parasitic red rays in the Corning blue. In the third set of observations, therefore, precautions were taken to exclude the red rays of the blue filter by placing a heat-absorbing screen over it, as previously described. The light intensity T was then reduced to 15·0 and the relative energy E to 4·7%. The Schott and Gen and Chance blue filters were used in January in addition to the other filters.

Preliminary Series, May 6th–28th, 1929.

Average hours of sunshine 9 hours daily.

Tables IV, V, and VI are the results of observations made upon the rate of growth of the marine diatom *Nitzschia closterium*, when grown in " Miquel sea-water," under selective or non-selective screens as described in the preceding pages. The following list of screens used indicates the order of the cultures in the window, starting from the right-hand side :—

Corning blue		(400 mμ–490 mμ)
,, green		(490 mμ–570 mμ)
,, orange		(570 mμ–720 mμ)
,, red		(620 mμ–720 mμ)
Ordinary glass		(400 mμ–720 mμ)
Wratten filter	T.=$\frac{1}{2}$ 41·8%	(400 mμ–720 mμ)
,, ,,	T.=$\frac{1}{4}$ 19·2%	,,
,, ,,	T.=$\frac{1}{8}$ 9·5%	,,
,, ,,	T.=$\frac{1}{16}$ 3·3%	,,
,, ,,	T.=$\frac{1}{32}$ 1·7%	,,

TABLE IV

SUB-CULTURES OF *Nitzschia closterium* GROWN IN CRUCIBLES UNDER ORDINARY GLASS, FROM 6TH–28TH MAY, 1929.

Date.	No. of days.	No. of diatoms per unit of volume.
9.5.29	3	18
13.5.29	7	85
16.5.29	10	123
21.5.29	15	270
23.5.29	17	432
28.5.29	22	546

TABLE V.

SUB-CULTURES OF *Nitzschia closterium* GROWN IN CRUCIBLES UNDER NEUTRAL WRATTEN FILTERS FROM 9TH–28TH MAY, 1929.

Date.	No. of days.	No. of diatoms per unit of volume. T=$\frac{1}{3\frac{1}{2}}$	T=$\frac{1}{1\frac{1}{0}}$	T=$\frac{1}{8}$	T=$\frac{1}{4}$	T=$\frac{1}{2}$
13.5.29	4					
16.5.29	7	6	1	42	13	32
21.5.29	12	6	3	60	315	340
23.5.29	14	14	18	218	475	485
28.5.29	19	30	42	590	1400	1206

TABLE VI.

SUB-CULTURES OF *Nitzschia closterium* GROWN IN CRUCIBLES UNDER SELECTIVE FILTERS OF CORNING GLASS FROM 13TH–23RD MAY, 1929.

Date.	No. of days.	No. of diatoms per unit of volume. Red.	Orange.	Green.	Blue.
16.5.29	3	2	3	0	2
21.5.29	8	120	69	152	56
23.5.29	10	285	241	270	106

The figures in the tables represent the number of diatoms per unit of volume (0·1 mm.^{3}) as counted with the aid of a hæmacytometer. From these results it would appear during the period of observation for May 1929 :—

1. That the diatoms can utilise light of all wave lengths.

2. That light of reduced intensities is much more favourable than full illumination at this time of year. Light reduced to about 6%–3·3% being the most suitable of the series.

Second Series, June 13th–July 29th, 1929.

Table VII gives the results of observations from a new series of sub-cultures grown under the same conditions as in the preliminary experiments and occupying the same sites as formerly. During this period,

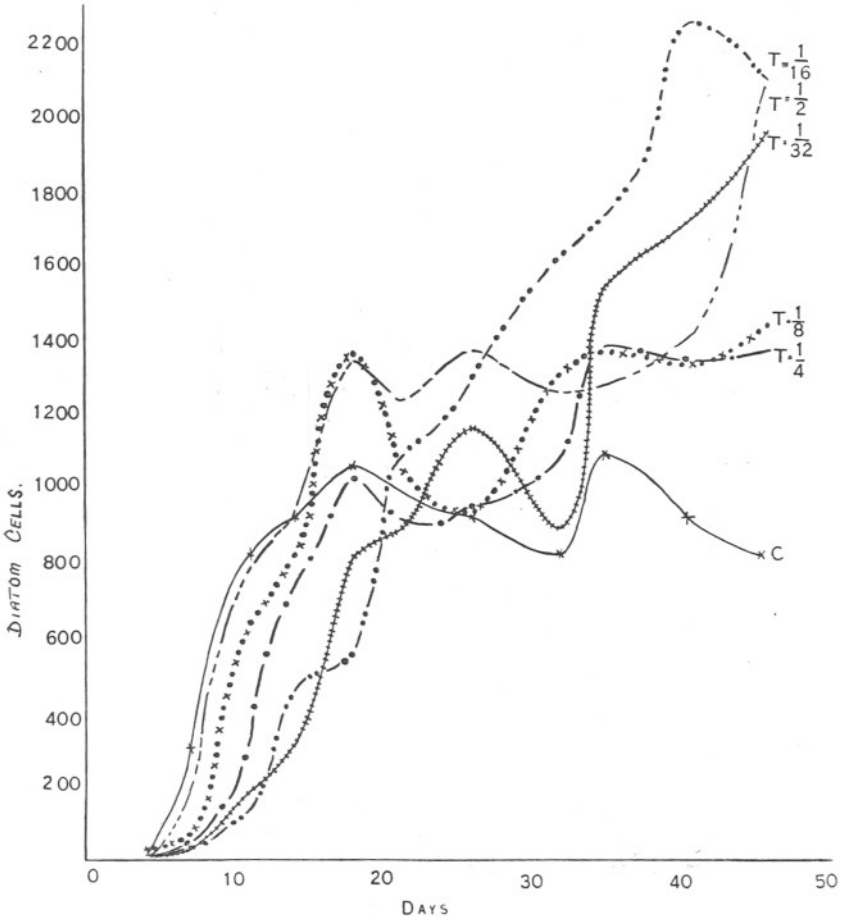

FIG. 3.—The ordinates are numbers of diatom cells in 0·1 cubic millimetre. The abscissæ are days. The curves show the rates of growth of the cultures of *Nitzschia closterium*, when grown under screens reducing the light intensity non-selectively, for a period of 46 days during the months of June and July, 1929.

however, the average number of hours of sunshine was 8 hours 11 minutes for June and 8 hours 49 minutes for July. Many days had 14 hours sunlight. Figures 3 and 4 give the curves obtained from the data.

When grown in ordinary flasks, cultures of *Nitzschia closterium* appear yellowish brown. Distinct colour changes of the cultures grown under

the selective filters were observed during this second series, and also throughout the January–March growths. Under the heading of the concluding remarks for the last series, the subject is dealt with more fully. Reference to Figure 6 will show at a glance that a curious drop in the

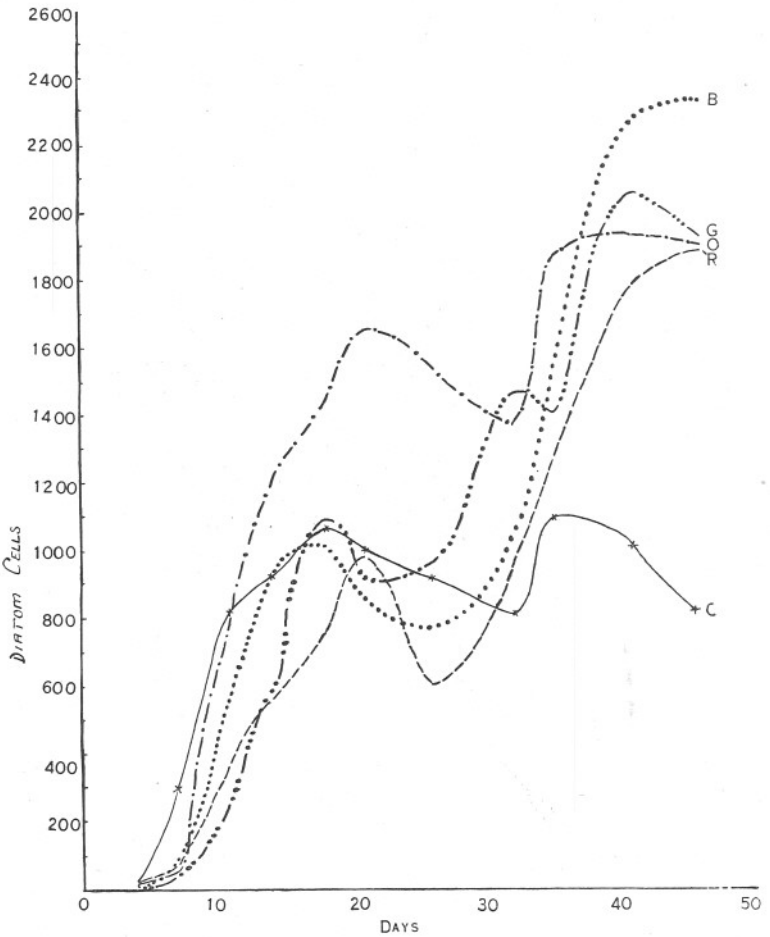

Fig. 4.—The ordinates are numbers of diatom cells in 0·1 cubic millimetre. The abscissæ are days. The curves show the rates of growth of the cultures of *Nitzschia closterium*, when grown under screens reducing the light selectively, for a period of 46 intensity days during June and July, 1929.

number of diatoms is shown by all the growths. Allen and Nelson (1910) state that the siliceous shell of marine diatoms generally, is markedly thinner than in the great majority of other forms, and that this is even more emphasised in cultural forms. Dr. Allen has also stated that it is a common experience for cultures to show periodic decrease in numbers.

TABLE VII.

To Show the Growth of the sub-cultures of *Nitzschia closterium* Grown under Selective and Non-selective Filters, from June 13th–July 29th, 1929.

	No. of diatoms per unit of volume.									
	Wratten filters.							Corning filters.		
No. of days.	T=$\frac{1}{32}$	T=$\frac{1}{16}$	T=$\frac{1}{8}$	T=$\frac{1}{4}$	T=$\frac{1}{2}$	Ordinary Glass.	Red.	Yellow.	Green.	Blue.
4 . .	4	4	24	8	2	15	19	20	9	8
7 . .	22	36	64	147	196	299	68	54	51	92
11 . .	184	132	620	336	792	816	384	786	276	576
14 . .	304	468	816	732	924	920	552	1184	584	920
18 . .	812	544	1360	1024	1344	1060	728	1444	1092	1016
21 . .	884	1072	1060	912	1234	996	976	1652	920	860
26 . .	1160	1296	932	940	1372	920	604	1548	968	772
32 . .	886	1624	1304	1088	1256	816	980	1372	1468	1060
35 . .	1544	1860	1368	1376	1720	1092	1276	1864	1404	1540
41 . .	1728	2256	1330	1340	1412	1012	1788	1928	2064	2272
46 . .	1868	2092	1432	1336	2080	812	1884	1900	1920	2328

Accordingly, a special watch was made for empty frustules, and these were very seldom seen. The problem of the fate of the diatoms, which causes these well-marked falls in the curves, is further discussed in the third series. It may be mentioned here, however, that this decrease can hardly be due to lack of food material. Under the ordinary course of the experiments the volume of the culture solutions was made up to 10 c.c. from time to time by the addition of distilled water, to compensate for the small losses in volume due to evaporation and the minute drops extracted for counting purposes. After the 29th July, 1929, however, the observations were abandoned for about two months. During this time the cultures remained untouched. Yet counts made for all the cultures on September 29th, 1929, showed such dense growths that it was almost impossible to see the ruling on the hæmacytometer when drops were examined in the usual way after the culture solutions had been restored to their original volume of 10 c.c. with distilled water.

Conclusions from Second Series.

Thus it appears that diatoms can utilise light of all wave lengths even in the green region of the spectrum. It is true that the Corning green transmits parasitic rays of yellow and blue, but the percentage is so small as to be scarcely responsible for the astonishing growth under a screen which has a total transmission of light of only 13·5%. Miquel (1892) found that orange light was best suited to the growth of freshwater diatoms. A study of Table VII will show that orange light is highly favourable for growth of the marine diatom Nitzschia, being slightly better than red, which it includes. During the last few days of the experiments the numbers under the blue and green filters exceeded those of the diatoms under both the red and orange. It must be remembered that the Corning blue filter was transmitting a small percentage of parasitic red rays, but results obtained in the third series indicate that they alone are not responsible for the prolific growth under this screen.

The light intensity and energy transmitted by the control (T and E =71%) were too high for good growth, the amounts transmitted by all the reducing non-selective filters being much more favourable. Under the selective filters the cultures grew well, for although the light intensity was in some cases high, e.g. orange and red, the relative energy in these regions is considerably less than for white light (Table II).

Third Series. Winter and Early Spring. January 2nd–April 14th, 1930.

The cultures were set up in the same manner as before, the only difference being in the use of additional filters, viz. the heat-absorbing

screen which was placed over the Corning blue, and the extra filters of Schott blue, and Chance blue (Nos. 11, 12, and 13, Table II).

Attention is here drawn to the fact that the transmission curves for 11

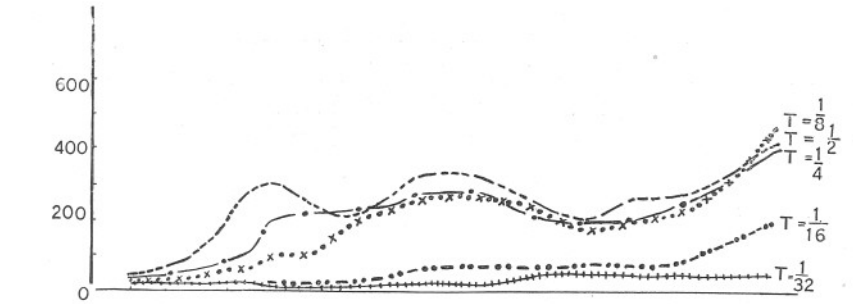

FIG. 5.

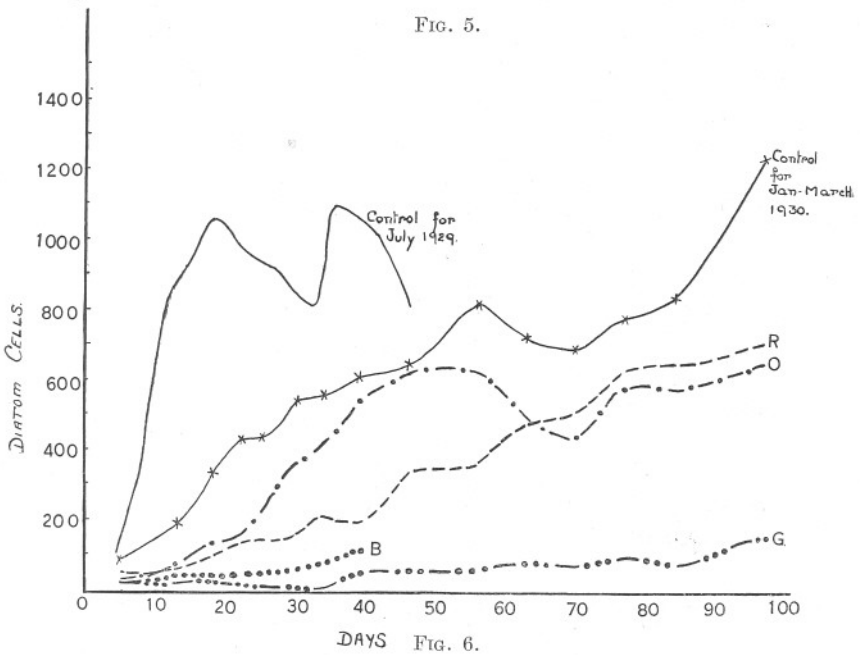

FIG. 6.

FIGS. 5 & 6.—The ordinates are numbers of diatom cells in 0·1 cubic millimetre. The abscissæ are days. The curves show the rates of growth of the cultures of *Nitzschia closterium* when grown under screens reducing the light intensity selectively, Fig. 6, lower portion, and non-selectively Fig. 5, upper portion, for a period of 97 days during January-March, 1930. The curve showing growth under the control screen during June and July, 1929, is also shown.

and 12 were obtained from data supplied by the makers in January, 1930, and it has not been possible as yet to verify these figures, but the absence of any appreciable amount of red has been verified by visual spectroscopic examination.

The average number of hours daily sunshine in January was 1 hour 10 minutes, in February 3 hours 18 minutes, and in March 3 hours 50 minutes. Table VIII and Figures 5, 6, and 7 are records of growth for this period.

Conclusions from Third Series.

1. The results suggest that the total light intensity received is a factor of great importance. Excepting the Schott blue filter, the diatoms under the ordinary glass screen show the best growth, whilst the cultures under

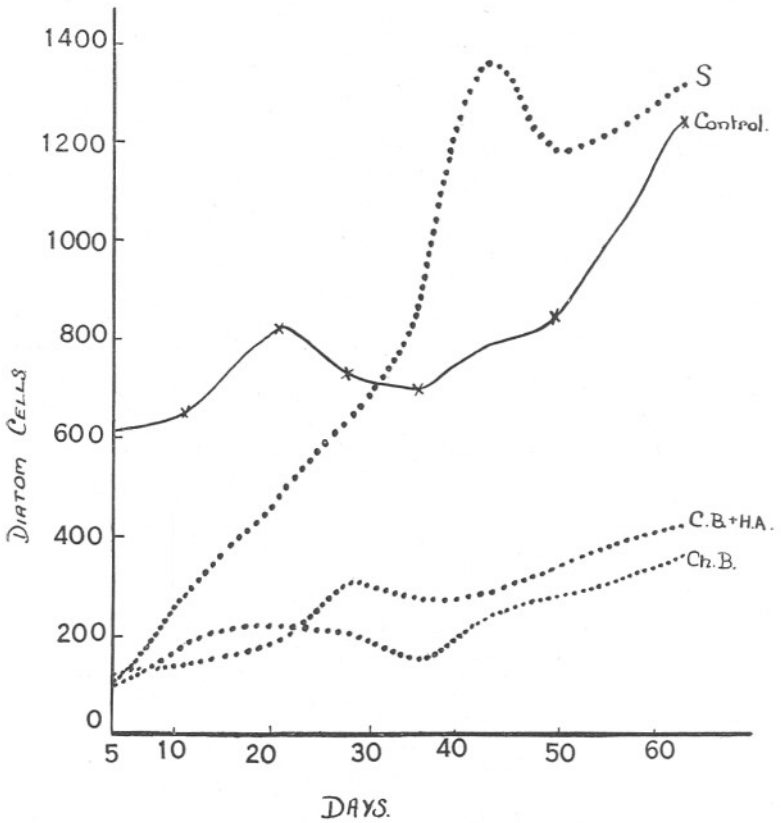

Fig. 7.—The ordinates are numbers of diatom cells in 0·1 cubic millimetre. The abscissæ are days. The curves show the rates of growth of the cultures of *Nitzschia closterium* when grown under the influence of blue light for a period of 63 days during February and March, 1930. The curve showing growth under the control screen during the same period is also given.

the Wratten filters show poor growth where the intensity is heavily reduced. The figures shown in Table IX would suggest that the relative energy is a limiting factor, the ratio $\frac{\text{Relative Energy}}{\text{No. of diatoms}}$ being a constant in the experiments and having a value of 24·5.

TABLE VIII.

To Show the Growth of the sub-cultures of *Nitzschia closterium* grown under Selective and Non-selective Filters from January 2nd–April 9th, 1930, and from February 5th–April 9th, 1930.

Number for diatoms per unit of volume.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
No. of days.	°C.	T=$\frac{1}{2}$	T=$\frac{1}{4}$	T=$\frac{1}{8}$	T=$\frac{1}{16}$	T=$\frac{1}{32}$	Control Glass.	Corning Red.	Corning Orange.	Corning Green.	Corning Blue.	Corning Blue + Heat Ab.	Schott and Gen Blue.	Chance Blue.	No. of days.
—	—	—		—	—	—	—	—	—	—	—				
5	13·1	48	36	32	28	28	88	48	48	32	20				
13	13·2	88	52	32	20	17	188	60	72	20	45				
18	13·1	172	84	56	20	20	332	96	136	26	40				
22	11·8	280	108	64	20	20	432	136	160	16	44				
25	10·6	300	200	96	20	8	432	144	224	9	50				
30	10·1	256	220	98	16	8	544	168	368	8	60				
34	12·6	220	224	152	20	12	560	212	428	8	88				
39	9·9	232	236	216	28	12	616	200	544	57	116	116*	108*	104*	5*
46	10·6	320	272	256	60	40	650	340	624	60	—	140	281	184	12
56	13·3	318	272	260	62	40	825	368	630	60	—	192	484	216	22
63	13·2	250	212	240	64	45	728	488	500	88	—	302	640	200	29
70	14·2	200	200	170	66	40	696	516	436	82	—	276	860	150	36
77	11·2	259	200	200	70	43	788	632	576	100	—	280	1360	232	43
84	12·9	266	240	232	76	40	944	652	584	88	—	332	1180	280	50
97	14·1	408	396	456	156	40	1244	716	656	168	—	420	1316	360	63

* Columns 13–16 give the figures for the cultures started February 4th, 1930.

TABLE IX

To Show that the Ratio of the Relative Energy to the Number of Diatoms tends to be a Constant when the Relative Energy transmitted is Low.

Screen Used.	T=$\frac{1}{3\cdot2}$	T=$\frac{1}{1\cdot6}$	Corning Green.	T=$\frac{1}{8}$
Percentage Light Transmitted . . .	1·7	3·3	13·5	9·5
Percentage Relative Energy	1·7	3·3	3·3	9·5
No. of Diatoms at the end of 84 days . .	40	76	88	233
$\frac{\text{Relative Energy}}{\text{No. of Diatoms}}$ . .	23·5	23·1	26·3	25·2
Average Ratio . .	24·5			

2. The large growth under the Schott blue filter (T=50·3 and E=14·0) is difficult to account for unless the screen transmits almost the optimum light intensity and energy. This view would explain the relatively poor growths under the Chance blue, and combined Corning and heat-absorbing screens where T=36 and E=10 for the Chance and T=16·7 and E=4·7 for the combination. Under the red filter (T=67, E=30), and the orange (T=73, E=34), the rates of growth were very similar to each other, that under the orange being slightly better than that under the red for the greater part of the third series. Unlike the summer results, the growths under these two filters were poorer than that under the ordinary glass screen. Under the green filter (T=13·5, E=3·3) growth was poor, and suggested the importance of the relative energy transmitted when the light intensity was low (Table IX).

3. The difference in colour exhibited by some of the cultures has already been referred to. When grown in ordinary culture flasks the growths are yellowish brown. Under the coloured screens they vary from a rich dark brown shade to decided greenish tints. Under the reduced light of the non-selective Wratten filters the cultures remained yellowish brown as under the control. These colours are not due to differences in the numbers of diatoms present, for counts made on April 9th gave 1244 per unit of volume under the glass filter and 1316 under the Schott blue, yet the culture under the latter was the rich brown colour, whilst under the ordinary glass the culture was yellowish brown. Under the red and yellow filters the cultures always assumed a decided yellow-green shade, whilst under the blue and green they were decidedly dark brown, i.e. the cultures tended to assume colours complementary to those in which they were grown. The dark brown colour of the cultures under the blue and

green filters is probably an adaptation which helps to compensate the deficiency of red and yellow rays by furnishing an added power to absorb the rays available. This is of interest when it is considered that marine diatoms are frequently abundant between depths of 5–15 metres in the sea, being seldom found very near the surface because of the harmful effect of high light intensity. It is known that at a depth of 5 metres most of the red rays are absorbed, whilst at 15 metres the light that penetrates is reduced to about 10–20% of the total intensity and is deprived of all the red, practically all the yellow, and consists of green and blue light only.

4. The cultures showed the same periodic decrease in numbers of diatoms similar to those of the summer series. Drops of solution from the cultures gave pH values from pH 8·8–9·2, showing that the solutions in which the diatoms grew were strongly alkaline. Whilst silica is highly resistant to acids it yields to alkalines, and it is suggested that the falling off in numbers is due to the fact that the thin shells of the dead frustules are dissolved in the culture solutions. This view is upheld by the results of the following experiments. A certain volume of culture solution containing a known number of diatoms per mm.^{3} was gently heated and kept just below boiling point for some time. The solution was then made up to the original volume with water and counts made for the number of individuals present in the usual way. Nearly all the diatoms had disappeared, suggesting that all but the most resistant frustules had dissolved, the boiling being a quick method of showing what would be a slow process in the culture solutions.

GENERAL CONCLUSIONS.

Three series of cultures of the marine diatom *Nitzschia closterium* were grown under selective and non-selective filters, the transmissions of which were known between definite limits of wave length.

From results of observations on the growth of the cultures it would appear :—

1. That the amount of energy transmitted is of greater importance than the precise wave lengths between which the energy so transmitted lies. When the amount of radiation is small then growth tends to be proportional to the relative energy, but when the energy received is too intense then the effect is harmful to the cultures.

2. At all times the cultures tend to show chromatic adaptation when grown under selective filters, assuming colours which are complementary to those in which they are growing, e.g. a dark rich brown shade under the green and blue screens and a decided green colour under the red and yellow.

Since these experiments were completed, Klugh (1930) has published a further report on the effects of light of different wave lengths, but of equal intensities, on the photosynthetic rates for certain green and red algæ. His results would appear to confirm the conception of the complementary nature of the brown colour.

3. The cultures are subject to periodic decrease in numbers, which is probably due to the thin siliceous shells of the diatoms being dissolved in the culture solutions which have become highly alkaline.

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Studies on *Ligia oceanica.* I. A. Habitat and Effect of Change of Environment on Respiration. B. Observations on Moulting and Breeding.

By

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With 2 Figures in the Text.

CONTENTS.

INTRODUCTION.

THIS paper is the outcome of work done at the Laboratory of the Marine Biological Association at Plymouth during the period October, 1929, to January, 1931, while holding a studentship under the Council for Scientific and Industrial Research of Australia.

It gives me pleasure at the outset to express my thanks to the Director and members of the staff at Plymouth for their interest and help in my work, also to the many visitors to the Laboratory who have given much assistance. In particular would I like to thank Dr. C. M. Yonge, without whose help part of this work would never have been attempted.

During the course of sixteen months at Plymouth several aspects of the biology of Ligia were touched on and it is my intention to deal with the subject under three headings. The first, "Habitat and Effect of Change of Environment on Respiration," will include a general description of the nature of the habitat of this animal with reference to its food, reaction to light, animals which prey upon it, and an account of some experiments upon its respiration. These latter were performed during the course of a short visit to the Marine Station at Millport, Scotland, and much of the

success of the results is due to the interest displayed and assistance given by Miss S. M. Marshall and Mr. A. P. Orr. I have also to thank Mr. Elmhirst, the Superintendent, for permitting me to occupy a table at the Station during that period.

The second heading, "Observations on Moulting and Breeding," will cover work which occupied sixteen months during which the animals were watched in the Laboratory and notes taken on their moulting and breeding, with reference to temperature, etc. It will also include experiments to discover the viability of the unfertilised ova. In Part II will be described the structure of the foregut, and the paper will be concluded with a description of the processes of feeding, digestion, and absorption.

A. HABITAT AND EFFECT OF CHANGE OF ENVIRONMENT ON RESPIRATION.

Historical.

Though many workers, particularly in the last decade of the nineteenth century, have been interested in the lower Crustacea, attention was mainly devoted to the Amphipods or, where Isopods were investigated, the terrestrial members of that group received most attention. On the whole Ligia has come in for very little notice, though occupying a very interesting position amongst the Crustacea by virtue of its structure and habitat. Among the more recent workers, Tait (1917) has carried out experiments on immersion, moulting, limb-flexure, and colour change in Ligia; Stewart (1913) has also published the results of experiments on immersion in salt and fresh water. An excellent description of the general morphology of Ligia is provided by Hewitt (1907).

Habitat.

The distribution of Ligia is very wide, covering practically the whole of the north coast of Europe; it has also been recorded from Morocco and America. The natural habitat consists of crevices in rocks just above high-water mark, or where the beach is sandy they will be found under stones and rocks at a similar level. When occupying such an area very large specimens are rare, though females with brood pouches have been found frequently. The largest animals occur on rocky areas, and a particularly favourable spot is to be found along the quays at Plymouth where the mortar has been washed out from between the rocks composing the walls, forming ideal crevices in which to hide.

Ligia is a nocturnal animal, never appearing during the day unless disturbed, and for that reason always difficult to obtain in any quantity by daylight. At night, during low tide, they emerge in large numbers and descend to the lower levels of the walls on which is growing a thick layer

of *Fucus vesiculosus* and other algæ. Here they feed, making the most of the time while the tide is out, and while the seaweed forms the main article of diet, nothing edible comes amiss, particularly if it be of the nature of animal offal. One specimen collected from the region above that affected by the sea-water and apparently feeding on moss was killed and the contents of the gut examined under a microscope. Amongst the material therein contained, moss capsules and part of a syncytium of Vaucheria were easily identified. Evidently this animal is not confined to marine vegetation.

When feeding in this manner, with the aid of a torch specimens can be collected in large numbers by simply walking along the base of the wall and picking the animals off the seaweed. They are quickly disturbed by the light and will retreat to the crevices if not captured quickly. The light of a bright moon is sufficient to prevent them from emerging. How they manage to feed on bright moonlight nights I am at a loss to explain, but experience proved time and again that it was useless to expect to obtain more than a dozen specimens from a wall which on dark nights provided 1000 specimens in just over two hours. Doubtless if they emerged during the day they would be preyed upon by sea-gulls and other birds, and as it is, when feeding at night, they are liable to fall a prey to the common shore crab, *Carcinus mœnas*. I have observed on several occasions an unfortunate Ligia caught, by a sudden movement of these usually slow moving animals, in the chelæ of a crab.

Only very young individuals are found in the open during the daytime and then not very abundantly. The young seem to have much less aversion to light than the mature animals, this being noticed in those bred in the laboratory as well as in nature.

Immersion Experiments.

Though preferring a moist locality above high water, Ligia can withstand immersion for a considerable time in salt water. Stewart (1913) immersed a number of Ligia in fresh pond water and others in sea-water, but apparently took no measures to aerate the water with the natural result that all died within 48 hours, those in fresh water living longer than those in salt. These experiments were repeated, the water being changed continually with the result that they survived nine days, death being ascribed rather to lack of food than to the ill-effects of immersion. Tait (1917a) showed that specimens immersed in sea-water survived for more than 83 days (2 specimens) ; those immersed in half sea-water lived for, at the most, 42 days ; those in quarter sea-water only 15 days, while others immersed in distilled water lived only a matter of hours. Care was taken in every case to aerate the water. He showed, moreover, that during that period of immersion those living in clean sea-water fasted, and moulted normally.

During the course of my investigations I carried out similar experiments with animals of varying ages, employing the method in use by Sexton and Clark of gradually changing the salinity of the water by adding a constant amount of fresh water daily, having first removed a similar quantity. The volume was kept constant by the addition of distilled water to counteract evaporation. The water was aerated by passing a fine stream of air through it and a small piece of Fucus was placed in each jar for food and as an object of attachment for the Ligia. This, though not important, is useful, as otherwise the animals will wander round and round the bottom of the jar, periodically swimming vigorously about in an apparent attempt to escape. If only a stone or shell be placed at the bottom Ligia will soon settle down upon it.

Two jars, K1, E1, were employed containing each about 300 c.c. sea-water, and four, K2, E2, E3, E4, containing each 250 c.c. Into each jar were placed three small Ligia on 2nd December, 1929. In the two jars, K1, K2, used as controls, the level of the water was maintained by the addition of distilled water as required, and of the remaining four 5 c.c. of water from E1, 10 c.c. from E2 and E3, and 25 c.c. from E4 were removed daily, a similar quantity of fresh (tap) water being substituted. Moulting was observed to occur in these young specimens.

Those undergoing the quickest dilution died first, surviving only five days, while those in E2 and E3 were dead by 14th December, having survived less than 12 days. There were animals still alive in K2 and E1 at the end of the month.

An interesting record was that of an adult animal which at some time had fallen into a large jar of sea-water and become quite at home. This jar was taken as a whole and placed under the system of aeration and dilution (E5), 25 c.c. being removed daily from a total volume of about 2 litres. This started on 10th December.

It was noticed that the rate of beating of the pleopods appeared to be considerably faster than when placed in sea-water, accordingly the time for 100 beats was measured with a stop-watch, as follows :—

On 24th	December	time for 100 beats	60·8	secs.
25th	,,	,,	60·0	,,
29th	,,	,,	56·9	,,
5th	January	,,	53·5	,,
13th	,,	,,	50·0	,,

showing a steady increase in rate of beating with further dilution of the sea-water. This was compared with the rate of beating of another specimen which had been in sea-water for some time and it was found that this animal beat its pleopods very rarely and then only for a short time and very slowly unless disturbed, when it would beat at the rate of 50 beats

in 65·7 secs. On January 13th this specimen, E5—a female—was due to moult but succumbed in the attempt, probably due to asphyxiation during the process of liberating its pleopods.

While at Millport specimens had been collected from beneath stones and small rocks that were moistened by a stream of fresh water running into the sea, and when the tide rose were actually covered by water which would have a very reduced salinity. Water from this pool was kindly tested by Mr. Elmhirst and was shown to have a salinity only slightly above that of normal fresh water.

Effect of Change of Temperature on Respiration.

The following series of experiments carried out at Millport gives some idea of the effect of change of temperature on the animal as a whole, though most strikingly demonstrated by the change in rate of beat of the pleopods. The first shows the effect of sudden change in temperature.

Three specimens were placed in sea-water at ordinary room temperature, and thermos flasks were prepared containing water at definite temperatures. Into the neck of each flask was fitted a test-tube containing sea-water at the same temperature as that in the flask; the tubes were corked to prevent loss of heat, and provided with thermometers. The animals for experiment were then transferred to these tubes with the following results :—

TABLE I.

Effect of Sudden Change in Temperature on Ligia Immersed in Sea-water.

At 4.35 p.m.	Specimen A was	placed in sea-water at 25° C.
5.03 p.m.		apparently unharmed.
6.00 p.m.		changed to flask at 35° C.
7.35 p.m.		temperature down to 30° C., animal almost dead, transferred to water at 15° C.
8.35 p.m.		quite recovered.
At 4.35 p.m.	Specimen B was	transferred to sea-water at 30° C.
5.03 p.m.		still living, temperature 29° C.
5.53 p.m.		apparently dead, temperature 29° C., transferred to water at 15° C.
7.35 p.m.		had not recovered.
At 4.35 p.m.	Specimen C was	transferred to sea-water at 35° C.
4.43 p.m.		unable to flap pleopods, tending to curl up, to all appearances dead, replaced in cold sea-water.
5.23 p.m.		completely recovered.

Thus it will be seen that the greater the rise in temperature the shorter the period of survival and yet though apparently dead, that is when all movement of the pleopods has ceased, if transferred to more normal conditions the animal may recover. Specimen C withstood a temperature of 35° C. for 8 minutes and then recovered, though apparently dead. Specimen B having been subjected to 30° C. for half an hour was unaffected, though a further 50 minutes was sufficient to kill it.

This experiment led naturally to an attempt to discover the lethal temperature for this animal when subjected to a gradual increase in temperature, and a comparison of its survival in air under those conditions with its survival in water.

A large tank was set up filled with water which was stirred mechanically and the temperature controlled by a thermostat. Into this tank was placed a number of small bottles each containing one Ligia, 30 specimens being used in all. Half of these bottles were filled with sea-water and the other half contained only the animals, five adult males, five adult females, and five young specimens being used in each experiment. In order that those immersed in water should not suffer from lack of oxygen the water was changed at regular intervals, care being taken to ensure that the added water was at the appropriate temperature. Each bottle was numbered and those filled with air were fixed into a wire basket and weighted to keep them properly submerged.

The water in the thermostat was raised 1·0° C. every hour and kept constant for that period. The sea-water inside the bottles was changed once every three hours. The time of death of each animal was noted along with the temperature. This information will be found summarised in Table II.

TABLE II.

SHOWING TEMPERATURE AT WHICH DEATH OCCURRED FOR INDIVIDUALS IN AIR AND IN WATER.

Temp. °C.	28	30	31	32	33	34	35
			IN AIR.				
Males	–	–	–	–	–	2	3
Females	–	–	–	–	1	2	2
Young	–	–	–	–	–	5	–
			IN WATER.				
Males	1	2	–	2	–	–	–
Females	–	–	–	1	2	1	1
Young	–	1	–	1	1	2	–

TABLE III.

Showing Number of Beats per minute with increased Temperature in Males, Females, and Young.

No.	Temperature in degrees Centigrade. 12	15	16	17	19	21	23	25	27	29	31	33	35
							Males.						
1.	93·8	114	121	131	146	164	174	173	204	231	Dead		
2.	90·9	108	115	122	136	159	177	171	200	200	Dead		
3.	90·9	112	121	123	160	174	171	180	213	216	113	Dead	
4.	107	118	121	133	152	170	177	172	201	222	217	Dead	
5.	95·3	116	118	121	155	155	189	172	183	201	Dead		
Mean	95·6	114	119	126	150	164	178	174	200	214	—		
							Females.						
1.	88·2	107	115	131	155	174	197	179	211	224	217	Dead	
2.	79·5	113	119	132	155	173	184	184	227	227	211	Dead	
Mean	83·9	110	117	132	155	174	191	182	219	226	214	—	
							Young.						
1.	109	—	135	154	186	195	200	189	224	240	294	309	Dead
2.	112	—	160	181	206	216	203	217	246	259	300	316	Dead
3.	113	—	156	163	188	201	210	221	250	259	300	306	Dead
Mean	111	—	150	166	193	204	204	209	240	253	298	310	—

The lethal temperature in air lies at about 34° C., though a certain proportion survived that temperature for one hour and withstood for a short time a further rise to 35° C., though none for more than 10 minutes. When immersed in water the adult males seem to be much less able to withstand any increase in temperature above 30° C., while the majority of adult females and young of both sexes succumbed between 32° and 34° C.

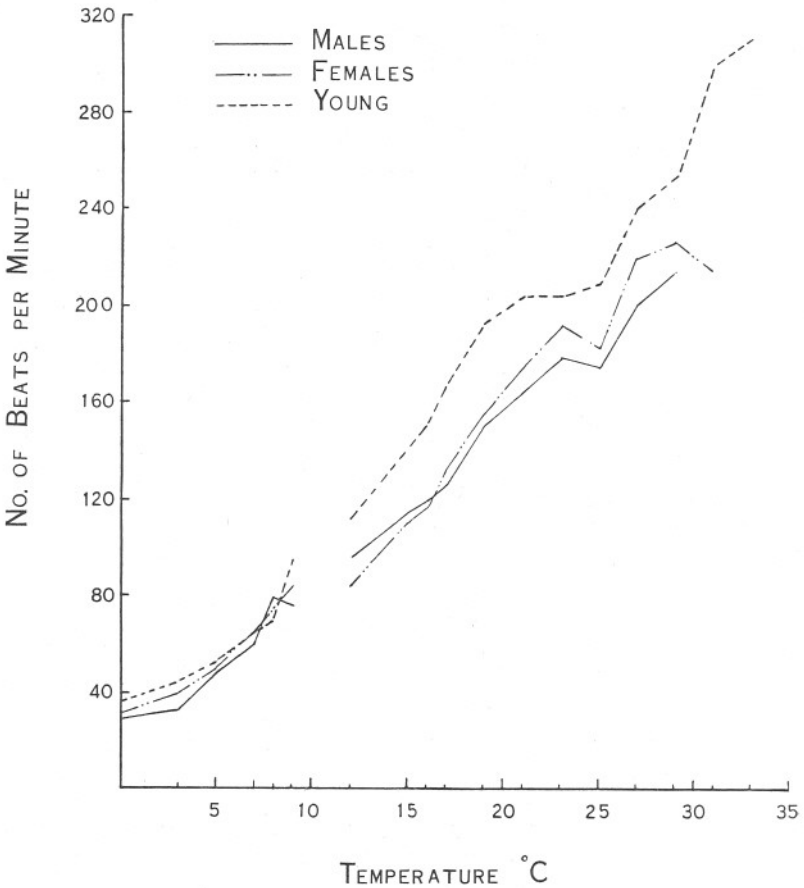

FIG. 1.—Graph showing the change in rate of beating of the pleopods with change in temperature; drawn from the averages of the males, females, and young in Tables III and IV.

Respiration seems to be the limiting factor for immersed animals; the continued beating of the pleopods to obtain sufficient oxygenation of the blood while immersed, and the consequent drain on the energy of the animal would account for the earlier death of immersed animals compared with those in air. It was apparent that as the temperature was increased

the rate of beat of the pleopods also increased. With a view to obtaining data on the increase in rate of beat the above experiment was repeated on a number of animals immersed in water, the time taken for 100 beats being measured with a stop-watch at the end of each hour. In addition to starting at room temperature and gradually increasing it another experiment was run simultaneously in which, by adding ice, the temperature was lowered finally to zero. The results of these experiments, expressed as the number of beats per minute, will be found in Tables III and IV and depicted graphically in Figure 1.

TABLE IV.

SHOWING NUMBER OF BEATS PER MINUTE WITH DECREASED TEMPERATURE IN MALES, FEMALES, AND YOUNG.

	Temperature in degrees Centigrade.					
No.	9	8	7	5	3	0
			MALES.			
1 . . .	75·8	75·8	64·4	56·0	35·3	29·9
2 . . .	76·5	82·0	56·2	39·9	30·7	28·7
Mean . .	76·2	78·9	60·3	48·0	33·0	29·3
			FEMALES.			
1 . . .	92·5	82·4	72·1	59·3	42·0	34·3
2 . . .	75·8	67·6	59·1	40·2	37·7	28·7
Mean . .	84·2	75·0	65·6	49·8	39·9	31·5
			YOUNG.			
1 . . .	96·8	74·3	69·9	56·8	48·9	36·1
2 . . .	92·6	65·2	60·0	49·5	41·6	36·9
Mean . .	94·7	69·8	65·0	53·2	45·3	36·5

On reference to Figure 1 it will be seen that in effect it is a straight line graph, indicating a constant change in rate of beat as the temperature rises or falls between 5° and 35° C. Between 5° and 0° C., however, there is a tendency for the rate to become constant.

B. OBSERVATIONS ON MOULTING AND BREEDING.

HISTORICAL.

In October, 1929, a number of Ligia were brought into the laboratory and kept under observation to watch the process of moulting and in the hope of inducing them to breed. Since they were found under natural conditions feeding on Fucus it was thought that they might survive for some time if placed on moist Fucus in a bowl and covered to prevent evaporation. To this end a number of finger bowls were employed, in each were placed a piece of *Fucus vesiculosus* and a pair of animals to be

observed and they were then covered with glass squares. Each bowl bore a numbered label.

It was found by experience sufficient to wash the bowls and weed in sea-water two or three times a week and to change the weed about once a fortnight during the winter. In summer more frequent changing of the weed was required, with washing on alternate days. Under these conditions the animals lived, fed, moulted, grew, and bred apparently quite normally for several months, some surviving 15 months before being killed, while one is still alive at the time of going to press.

The cast cuticles of each animal, when not eaten, were preserved (70% alc.) and the animals measured as soon as the new cuticle had hardened after the process of moulting. Notes were taken of any changes in colour of the skin or eyes, condition of brood plates and other points of interest. From the information obtained it has been possible to reconstruct a fairly complete history of the life of the animal subsequent to emergence from the brood pouch.

As stated by Hewitt, the body is broadest across the fourth (free) thoracic segment, gradually decreasing in size posteriorly. This statement applies to all normal individuals with the exception of females which have developed mature brood plates, in which case the greatest breadth is in the third free thoracic segment, and by means of this distinction in shape animals with brood pouches can be picked out at a glance quite easily.

The colour of the eyes is normally black, but in a certain proportion, particularly females, a chocolate brown occurs which is most noticeable after each moult, gradually darkening as the new " skin " grows older. In one young specimen found towards the end of 1929 the colour of the eyes was noticed to be very bright red, while the general body colour was very pale, almost white, probably due to lack of development of chromatophores.

The process of moulting has been described by Tait (1917b) and it will suffice here merely to add the results of a few of my observations. With reference to the " chalky whiteness " which appears some time before moulting on the ventral side of the first four free thoracic segments, rough tests of its composition made by me support the statement of Herold (1913) that it is a deposition of calcium carbonate. A gas that will not support combustion is evolved when treated with acid, and the flame test indicates calcium. This deposit appears a number of days before moulting, the period varying with the time of year and the age of the animal, as does also the interval between the posterior moult and the anterior. The longest times are shown in adult males during winter (average laboratory temperature about 14° C.), when the first appearance of the deposit may precede the moult of the posterior portion by six days and there are four full days between the moulting of the posterior and anterior portions ; while the shortest times occur in young specimens in summer, when the

first appearance of the deposit, the posterior moult and the anterior moult follow one another on successive days. The average laboratory temperature in summer was about 18° C. Further it may be worth noting that, though there was little or no tendency for Ligia to eat their cast "skins" during the earlier part of their captivity, towards the end of the period this tendency became more and more marked until it was seldom that one could rescue a complete moult for preservation.

Rate of Growth and Breeding.

In Table V will be found figures showing the total increase in size for a number of animals over different periods. It was noticed that members of both sexes grew until a certain size was attained, after which further moulting showed no increase.

TABLE V.

Showing Total Growth over a Given Period for a number of Animals.

No.	Date of first Measurement.	Size in mm.	Date of last Measurement.	Size in mm.	Total Growth mm.	Time in Months.
			Females.			
1.	25/10/29	20·5 × 9·0	27/5/30	22·5 × 10·0	2·0 × 1·0	7
4.	25/10/29	23·0 × 10·0	4/5/30	24·5 × 11·0	1·5 × 1·0	6¼
5.	12/11/29	24·5 × 10·5	11/8/30	27·5 × 12·0	3·0 × 1·5	9
7.	31/10/29	22·5 × 10·5	4/7/30	25·5 × 11·0	3·0 × 0·5	8¼
8.	31/10/29	23·2 × 11·0	1/7/30	26·5 × 11·5	3·3 × 0·5	8
9.	12/11/29	22·8 × 10·0	3/7/30	27·0 × 12·0	4·2 × 2·0	7¾
10.	22/10/29	22·0 × 10·0	18/2/30	23·8 × 11·0	1·8 × 1·0	4
15.	12/11/29	23·7 × 10·3	4/5/30	26·0 × 11·5	2·3 × 1·2	5¾
18.	12/11/29	22·0 × 10·0	8/5/30	23·8 × 11·5	3·8 × 1·5	6
19.	12/11/29	21·0 × 9·5	23/12/30	25·8 × 11·0	4·8 × 1·5	13½
20.	12/11/29	24·5 × 10·2	9/1/30	26·0 × 11·5	1·5 × 1·3	2
21.	12/11/29	20·0 × 9·0	4/8/30	23·0 × 10·0	3·0 × 1·0	8¾
22.	12/11/29	22·3 × 9·5	18/2/30	24·0 × 10·5	1·7 × 1·0	3¼
23.	12/11/29	22·0 × 9·5	18/6/30	25·0 × 11·0	3·0 × 1·5	7¼
24.	12/11/29	20·0 × 9·0	5/2/30	23·2 × 10·0	3·2 × 1·0	2¾
25.	12/11/29	25·8 × 11·5	11/12/29	27·5 × 12·3	1·7 × 0·8	1
			Males.			
2.	28/10/29	30·0 × 14·5	25/4/30	31·8 × 15·5	1·8 × 1·0	6
6.	28/10/29	29·2 × 13·8	20/12/29	30·3 × 14·0	1·1 × 0·2	1¾
15.	5/11/29	27·0 × 11·5	19/6/30	29·5 × 14·0	1·5 × 2·5	7½
19.	12/11/29	26·7 × 12·4	8/9/30	30·0 × 15·5	3·3 × 3·1	10
20.	12/11/29	25·0 × 13·0	24/3/30	27·4 × 13·8	2·4 × 0·8	3½
21.	12/11/29	23·0 × 10·2	6/6/30	29·0 × 14·5	6·0 × 4·3	6¾
22.	12/11/29	23·0 × 10·5	4/4/30	28·6 × 14·8	5·6 × 4·3	4¾
23.	12/11/29	25·0 × 11·0	8/11/30	30·0 × 14·0	5·0 × 3·0	12
24.	12/11/29	22·7 × 10·3	26/12/29	24·0 × 12·0	1·3 × 1·7	1½
27.	21/11/29	30·0 × 14·7	30/3/30	31·5 × 16·5	1·5 × 1·8	4¼
37.	23/12/29	31·0 × 15·7	24/4/30	32·2 × 17·0	1·2 × 1·3	4
			Young.			
12.	22/10/29	3·0 × 1·3	18/3/30	7·5 × 3·3	4·5 × 2·0	5
14.	22/10/29	3·0 × 1·3	23/12/30	20·5 × 8·5	17·5 × 7·2	14
26.	21/11/29	6·1 × 2·6	23/12/30	20·0 × 8·75	13·9 × 6·15	13

Two young (3·0×1·3) liberated from the brood pouch on 22nd October, 1929, were kept alive in the laboratory. These both moulted within a fortnight and again at the end of a second fortnight, this being continued with gradually increasing intervals until April, 1930, by which time the interval between moults was just over a month. Growth was not the same in both cases, No. 12 moulting a few days before No. 14 and showing a greater increase with each moult. By the end of January, 1930, moreover, after the sixth moult the larger specimen was discovered to be a male, the appendages appearing in the " skin " of the 7th moult. No. 14 at this time showed no signs of secondary sexual characters and was assumed, therefore, to be a female, the brood plates being expected to appear at a later stage. At this time, March 16th–18th, their respective sizes were, male : 9·2×4·0 mm. and female : 7·5×3·3 mm., and from now until the beginning of September the interval between the moults decreased, averaging about $2\frac{1}{2}$ weeks.

The size attained by April was such that it was found impracticable to measure the animals accurately. They were still too small to be held in the fingers as larger animals were treated and were too strong to be held on the measuring slide with a brush, the method employed on them up to date. Thus no measurements were taken through April, May, June, and July. During the latter month No. 14 escaped, a most unfortunate loss. It was not until the moult of July 2nd that the brood plates appeared in this animal and it was noticeable that after this moult it was larger than the male, having also decreased the interval between moults relative to the male, so that now No. 14 was moulting a week before No. 12, a complete reversal of the previous state of affairs. It was at this most interesting point that the specimen was lost.

The male, No. 12, continued to grow, and by the end of July had attained to 15·0×6·5 mm. Five successive moults brought it to 20·5× 8·5 mm. at the end of December and after moulting again in January, 1931,was fixed at the beginning of February, having survived $14\frac{1}{2}$ months. There is apparently only a very slight variation in the rate of growth in summer and winter, the specimen holding very closely to an increase of 1·3×0·5 mm. at each moult, which was the average for the whole period. The summarised histories of these two will be found in Table VI.

To return to the female. Had not the specimen been lost it is safe to assume that it would have been at least as large as the male in December (in view of its sudden increase in size relative to the male in July), by which time it would have reached maturity and would have been able to produce a brood ; in support of this we have the evidence of three females (No. 43) who all produced broods on attaining a size of 22·0×9·5 or 10·0 mm. and also the record of one female measuring only 19·0×8·5 mm. which was found in the natural state with a brood. Thus we see that within 16

months of birth, probably earlier, a female may produce her first brood of young. Further, we see that by June, when the second brood might be expected, the animal has attained a size of 24·5 × 10·0 mm. (No. 21) and from the history of No. 16 we see that this animal after having a period of rest through the autumn might start breeding again in January with a fourth brood in May and a fifth in August, most probably dying after liberating that brood in November.

TABLE VI.

	Number 12.			Number 14.		
	Date.	Size.	Int. bet. Moults days.	Date.	Size.	Int. bet. Moults days.
Birth	22/10/29	3·0 × 1·3	—	22/10/29	3·0 × 1·3	—
1st Moult	—	—	(15)	—	—	(15)
2nd ,,	22/11/29	4·3 × 1·7	(16)	22/11/29	3·8 × 1·7	(16)
3rd ,,	8/12/29	4·6 × 2·0	16	7/12/29	4·5 × 1·9	15
4th ,,	24/12/29	5·3 × 2·5	16	24/12/29	5·0 × 2·1	17
5th ,,	10/1/30	5·9 × 2·5	17	11/1/30	5·6 × 2·5	18
6th ,,	*27/1/30	7·0 × 3·2	17	29/1/30	6·0 × 2·5	18
7th ,,	21/2/30	8·0 × 3·5	25	23/2/30	6·5 × 3·1	25
8th ,,	16/3/30	9·2 × 4·0	23	18/3/30	7·5 × 3·3	23
9th ,,	10/4/30	—	25	11/4/30	—	24
10th ,,	11/5/30	—	31	12/5/30	—	31
11th ,,	6/6/30	—	26	4/6/30	—	23
12th ,,	23/6/30	—	17	17/6/30	—	13
13th ,,	9/7/30	—	16	*2/7/30	—	15
14th ,,	26/7/30	15·0 × 6·5	17		Lost.	
15th ,,	15/8/30	16·5 × 6·8	20	*N.B.* Female at this stage larger than male.		
16th ,,	2/9/30	18·4 × 7·0	18			
17th ,,	28/9/30	—	26			
18th ,,	30/10/30	—	32			
19th ,,	9/12/30	20·5 × 8·5	40			
20th ,,	30/1/31 Fixed.	—	52			

* Indicates appearance of secondary sexual characters.

This hypothetical case has been constructed from data obtained from the records of actual specimens, only the results from animals of comparable size being taken into consideration. The records of these animals referred to in the text will be found in Table VII.

TABLE VII.

Extracts from Histories of Nos. 21, 24, and 16.

No.	Date of Moult.	Size.	Date of Moult.	Size.	Date of Moult.	Size.
21.	25/12/29	23·0 × 9·1	†7/2/30	23·0 × 10·1	3/5/30	24·0 × 10·2
	†4/6/30	24·5 × 10·0				
24.	25/12/29	23·5 × 9·6	†5/2/30	23·2 × 10·0		
16.	†22/5/30	25·0 × 11·0	22/7/30	26·0 × 11·0	†19/8/30	

† Indicates mature moult with brood.

Thus it will be seen that the expected life of a female is just over three years, the first being one of active growth, maturity being reached early in the second with the production of perhaps two broods, while the third year might see the release of three broods, culminating in the natural death of the animal in winter. The average number of young produced in each brood is about 80, a few cases of over 100 having been found, and sometimes as few as 40, varying with the age of the animal.

In Table VIII will be found the dates of spawning of the animals kept in the laboratory. Through the winter the average period taken by the eggs to develop and be liberated from the date of spawning was about 90 days, the young embryos becoming pigmented at about 40 days ; as the summer approached this period was gradually reduced until a period of 40 days only was required for the whole process during mid-summer, No. 21 spawning on 5th June, pigmentation starting 27 days later, and the brood being liberated on 15th July.

TABLE VIII.

SHOWING DATES OF SPAWNING AND MONTHS OF YEAR IN WHICH FEMALES WERE FOUND WITH BROOD POUCHES.

No.	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.
1.	27/30	—	—	—	30/30	—	—					
2.		18/30	—	—								
4.	—	—	—	—	6/30	—	—					24/29
5.	—	—	—	—	10/30	—	—					31/29
6.		28/30	—	—	—							
7.	30/30	—	—	—								
8.			21/30	—	—			←	←	←		
9.			26/30	—	—							
10.		20/30	—					←	←	←		
15.	—	—	—		6/30							29/29
								←	←	←		
16.	20/30	—	—		25/30	—	—	21/30	—	—		
17.	—	—		10/30	—	—						5/29
18.		14/30	—	—								
19.	14/30	3/31	—	—		19/30	—	—				
20.	10/30	—	—									
21.		9/30	—	—		5/30	—					
22.		20/30	—	—								
23.			7/30	—	—	19/30	—					
24.		7/30	—	—								
25.	—	—										13/29
27.	—	—	—	15/30	—	—						15/29
29.	13/30	—	—									
30.	—	—	—	30/30	—	—						27/29
31.	—	—										10/29
32.	15/30	—	—									
33.	9/30	—	—									
34.	7/30	—	—									
35.	6/30	—	—			(7)/30	—					
36.	4/30	—	—		6/30	—	—					
37.	12/30	—	—									
39.	13/30	—	—									
40.	12/30	—	—		17/30	—	—					
41.	3/30	—	—		6/30	—	—					

In Table VIII the figures refer to the day and year, being placed in the appropriate month column, the date being that of spawning. The dashes following each date indicate the months during which the brood was developed and liberated. The arrows (reversed) show that the specimen when collected possessed mature brood plates but that the brood had been liberated, e.g. No. 8 collected in October, found to have mature brood plates but young liberated, must have spawned in August and have had young in pouch through September into October.

From this table it will be seen that Ligia may be found with a brood during any month of the year, though the spring appears to be the main

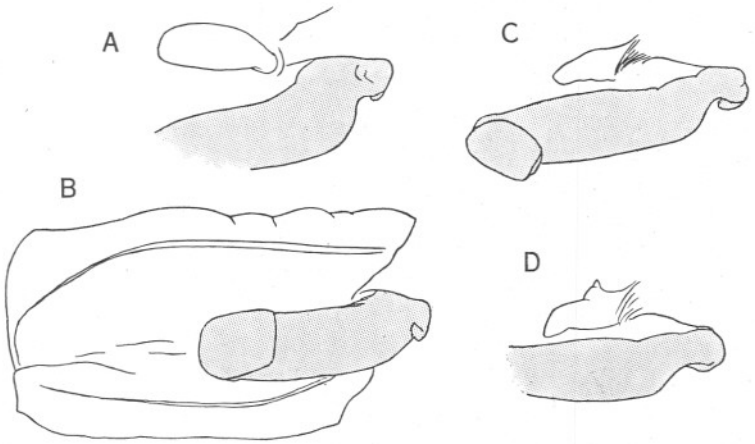

FIG. 2.—A, B, and C illustrate the form of the brood plates in three successive moults (drawn from No. 19). A. Normal condition. B. Mature condition. C. Reduced condition, always followed by a return to the normal. D. Reduced, with anterior projection; a modified form of C which occurs occasionally (drawn from No. 41). All drawn to the same scale.

breeding season, if that term can be applied to any part of the year in particular.

In the normal course of events about 10 days after the brood has been liberated the female moults, the mature brood plates (Fig. 2, B) being replaced with small ones, even smaller than those of the "normal" state (Fig. 2, A) in which they are rounded projections from the ventral sternites of the first five free thoracic segments of the body. Instead of being rounded, these "reduced" plates are pointed (Fig. 2, C). This condition is invariably followed by a return to the normal condition at the next moult. On a few occasions, without any relationship to temperature, season or any other factor apparently, a variant of the reduced condition appeared, the plates being pointed but each bearing a small projection on the anterior edge of the plate (Fig. 2, D). This state was followed by a return to the normal.

Viability of Unfertilised Ova.

The following is an abstract from the history of the pair of animals, No. 23.

March	1st.	Male carrying female ; latter about to moult. Male removed, female left to spawn alone.
	2nd.	Female moulted posterior.
	4th.	Female moulted anterior.
	7th.	Spawned.
(About May	14th.	Young should have been liberated.)
	24th.	Female moulted posterior.
	26th.	Female moulted anterior.
	29th.	Male replaced.

Assuming that during the period in which the male was carrying the female spermatozoa were transferred to her, then it is obvious that these must have been cast off with the moult of 2nd–4th March, since the eggs did not develop, and thus, in order that the ova should be fertilised, copulation must occur subsequent to the moulting of the posterior portion at least. When the moult of the male coincides with that of the female, as happened in several instances, the male would be unable to effect the transference of sperm at the times of moulting each portion and thus it would be advantageous that the ova should remain fertilisable until the male had completed the moult. (In a state of nature it is not likely that the animals pair or that any one female is restricted to any one male and, therefore, the state of affairs described above would be purely due to laboratory conditions.) Nevertheless, it may be seen from the following extracts from the histories of two pairs of animals that the ova were fertilised despite the overlap of the moulting of male and spawning of female.

No. 32.	Jan. 13th.	Female moulted anterior.
	14th.	Male moulted posterior.
	15th.	Female spawned.
	17th.	Male moulted anterior.
	Eggs fertile.	
No. 36.	Jan. 2nd.	Female moulted anterior.
	3rd.	Male moulted posterior.
	4th.	Female spawned.
	6th.	Male moulted anterior.
	Eggs fertile.	

In both these cases the interval between the posterior and anterior moult of the male, during which the female spawned, was sufficient for

the male to recover from the posterior moult and to fertilise the ova before proceeding to slough the anterior portion, but if for any reason copulation could not occur until the male had completed the moulting of the anterior, then a period of three days must elapse subsequent to the appearance of the eggs in the brood pouch before they could be fertilised. That they can survive this period is demonstrated by the following cases where the animals were separated for varying periods, the period of separation being the interval between the appearance of the eggs in the brood pouch and the reuniting of the male and female in the same bowl.

No. 16.	24 hours	separation.	Eggs infertile.
21.	40 hours	,,	Eggs fertile.
19.	3 days	,,	Eggs fertile.
6.	14 days	,,	Eggs infertile.
41.	35 days	,,	Eggs infertile.
23.	83 days	,,	Eggs infertile.

No explanation for the infertility of No. 16 can be put forward other than the possibility of sterility in the male due to age ; the male was full grown and died an apparently natural death in July, about six weeks after the date of spawning.

It is certain, however, that copulation must occur after the female has moulted the posterior portion and may be delayed until certainly three days after the eggs have appeared in the brood pouch. This indicates that the sperm are liberated into the cavity of the brood pouch rather than being passed into the oviducts. Copulation was observed in one case (No. 5) after the female had moulted the posterior portion and before moulting the anterior, in which case if the sperm were not passed into the oviducts they must have been retained beneath the brood plates of the fifth free thoracic segment. Possibly, of course, copulation was repeated after the completion of the anterior moult, certainly the eggs were fertilised.

SUMMARY.

1. Ligia is a nocturnal animal inhabiting crevices in rocks above high-tide level. It is omnivorous though Fucus spp. form the main article of diet.

2. Immersion experiments were carried out in which the animals were subjected to a gradual transition from salt to fresh water. None survived this treatment for more than one month. It was noticed that the reduction in salinity was accompanied by an increase in the rate of beat of the pleopods.

3. Animals were subjected to sudden and gradual changes in temperature. One specimen survived a change from water at 15° C. to water at

30° C. for 28 minutes, but was dead after 78 minutes ; a second, changed from water at 15° C. to water at 35° C., was to all appearances dead after 8 minutes, but recovered after being replaced in water at the original temperature.

4. The lethal temperature for Ligia, when subjected to gradual rise, was determined for males, females, and young in water and in air. Those in water died first, the males by the time 32° C. was reached, the others succumbing between 32° and 34° C. The lethal temperature in air lies about 34° C., a few surviving 35° for a short time.

5. The change in rate of beating of pleopods with change in temperature was determined for immersed males, females and young. The temperature of the water was raised from room temperature to the lethal temperature and lowered from room temperature to zero, the rate of beating being measured at regular intervals. The change in rate of beating is proportional to the change in temperature between 5° and 35° C. Below 5° C. the rate of beating tends to become constant.

6. A number of Ligia were kept in the laboratory for a long time and moulting and breeding observed. The greatest interval between moults occurs in full grown males in winter, the shortest in young specimens during the summer.

7. The growth rate was observed in a young specimen to average 1·3 mm. increase in length and 0·5 mm. in width per month. The growth of a number of adults is tabulated.

8. A hypothetical reconstruction of the life of a female has been made from the histories of several specimens. It is estimated that the length of life of Ligia is 3 years, with a probable production of at least 5 broods of young. The average number of young per brood is 80.

9. The time taken for the development of the young varies from 40 days in summer to 90 in winter.

10. The greatest number of animals with brood pouches is found in spring, but breeding occurs throughout the whole year.

11. In the moult following the liberation of the young the brood plates assume a shape (the reduced condition) distinct from that at any other time. This is followed by a return to the normal condition at the next moult. The reduced form is subject to variation in individuals.

12. Experiments indicate that copulation must occur subsequent to the appearance of the mature brood plates in the female. The ova are spawned about two days after the completion of the moult and, if unfertilised, remain viable for at least 3 days subsequent to their appearance in the brood pouch.

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Studies on *Ligia oceanica.* Part II. The Processes of Feeding, Digestion and Absorption, with a Description of the Structure of the Foregut.

By

Aubrey G. Nicholls, B.Sc.

With 1 Plate and 12 Figures in the Text.

CONTENTS.

1. FOOD AND FEEDING.

The normal food of Ligia is *Fucus vesiculosus*, though other species of Fucus and even Laminaria are eaten. Fine epiphytic algæ which form furry growths upon the surface of the larger seaweeds when growing in places sheltered from the full force of the waves are also eaten extensively. Ligia is not, however, entirely vegetarian in its diet, having definite tendencies towards scavenging and even cannibalism, as observed by other workers who have kept this animal in captivity for any length of time.

The method of feeding is best described as "browsing." The animal clings to its food and cuts off very small portions with its mandibles, passing them through to the œsophagus, whence they arrive at the foregut.

Owing to the animal's dislike of bright light it feeds at night and, since its food is found on the Fucus zone, half-tide is required before it can feed; thus there is only a limited period during every twenty-four hours during which feeding can occur. It is, therefore, necessary that the food taken in should be dealt with as quickly as possible and the animal can be observed feeding voraciously, passing a continuous stream through its alimentary canal, the fæces containing nearly as much undigested as indigestible food.

2. STRUCTURE OF THE GUT.

(*a*) Introductory.

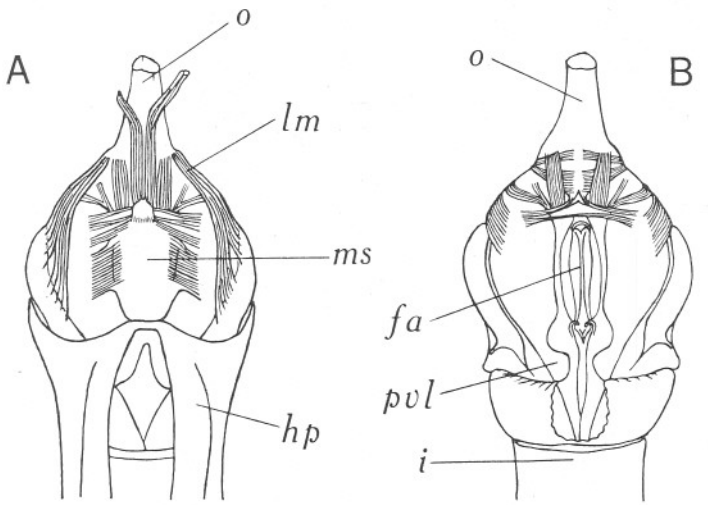
One of the earliest workers on Crustacea to refer to the armature of the foregut, or stomach as it was then called, was Sars (1867). Subsequently Huet (1883), Rosenstadt (1888), Ide (1892), and Schonichen (1898) studied the alimentary canal and its armature in practically every group of Crustacea. Ide concluded that the stomach of the Edriophthalmate orders (Tanaidacea, Isopoda and Amphipoda) was built on the same structural plan as that of the Decapoda, whilst Gelderd (1906) found homologies between the Schizopoda and the Decapoda. Hewitt (1907) described the structure of the gut of Ligia, but ascribed to some parts of the foregut names which are somewhat misleading. Rehorst (1914), in his paper "Der Filtermagen von *Asellus aquaticus*," gives an admirable résumé of the conclusions of previous authors on this subject, as well as giving a detailed description of the foregut of Asellus and assigning functions to its various parts. Barnard (1924) deals with the general shape of the foregut in Isopods, but does not go into detail of structure. Finally, we have detailed accounts of the foregut in Astacus by Jordan (1904), in Homarus by Williams (1907), and in Nephrops by Yonge (1924).

(*b*) The Foregut.

(i) *The External Form and Musculature.*

The main part of the foregut lies in the cephalic and first free thoracic segments, supported by the sternal alæ of the endophragmal skeleton (see Jackson [1926], p. 899, and Lloyd [1908]). Viewed dorsally it is rounded in front, tapering slightly posteriorly, its length being twice its greatest width. The intestine envelops about two-thirds of its posterior portion, only the anterior portion being closed in on all sides, the hinder region consisting of plates which project freely into the intestine.

A general idea of the musculature will be obtained from Text-Figure 1. On the ventral surface are muscles attached to the ventro-lateral walls of the gut and running towards the middle line, where they meet and form a sheath (*m.s.*) to the structure lying immediately above. To the anterior end of the sheath is attached a pair of muscles which can be traced forwards and upwards, separating round the œsophagus and finding their



TEXT-FIG. 1.—A, Foregut and hepato-pancreas from ventral surface showing musculature of foregut. B, same with hepato-pancreas, lateral muscles, muscle sheath, and portion of intestine removed showing some of internal structure of foregut through the ventral wall.

f.a., filter apparatus; *h.p.*, hepato-pancreas; *i.*, intestine; *l.m.*, lateral muscle; *m.s.*, muscle sheath; *o.*, œsophagus; *p.v.l.*, posterior ventral lamella.

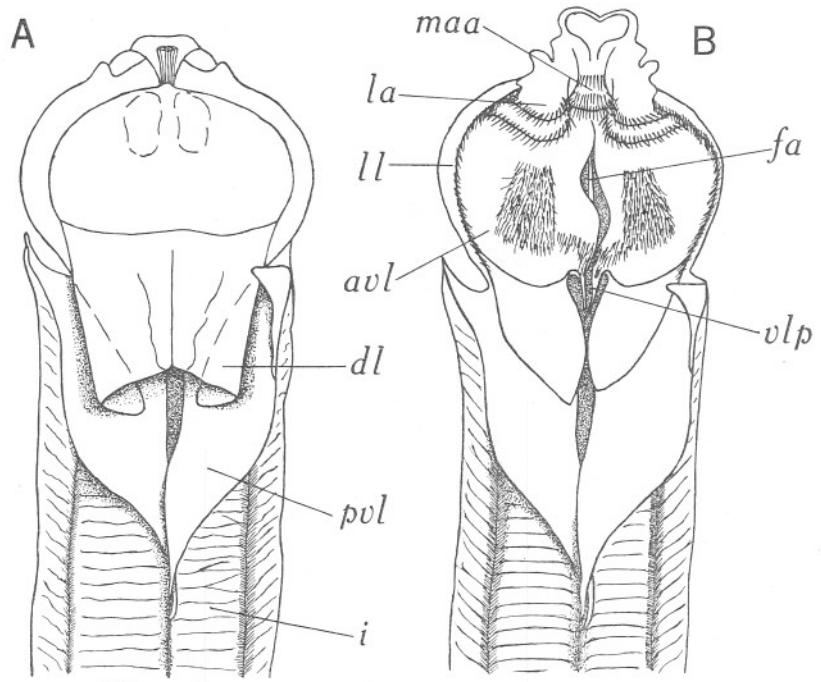
distal attachment dorsal to the antennal fossæ. On removal of these muscles others will be seen attached to the ventral wall of the gut and to the "median tooth" of Hewitt's description.

(ii) *Internal Structure.*

In the description of the foregut that follows the terminology employed by Hewitt has been retained as far as possible, to avoid further confusion. It has been essential to delete the term "tooth," which is very misleading, as are also the terms "cardiac" and "pyloric" when applied to this animal, the use of which suggests a division into two parts comparable with the state of affairs in other Malacostraca. No such division can be observed in the foregut of Ligia. For the term "tooth" the word "ampulla" has been substituted for all cushion-like projections, hollow

and covered with a thin layer of chitin. The term lamella has been retained throughout.

From the anterior regions of the side walls of the foregut arises a pair of large, bilobed projections, the lateral ampullæ (*l.a.*, Text-Figs. 2, 3, 4, 6, and 8), meeting above the opening to the œsophagus. Anterior to these and hidden behind them is a pair of very small antero-lateral ampullæ



TEXT-FIG. 2.—A, Foregut from dorsal surface with intestine cut open along mid-dorsal line. B, same with dorsal lamella removed to show underlying structures.

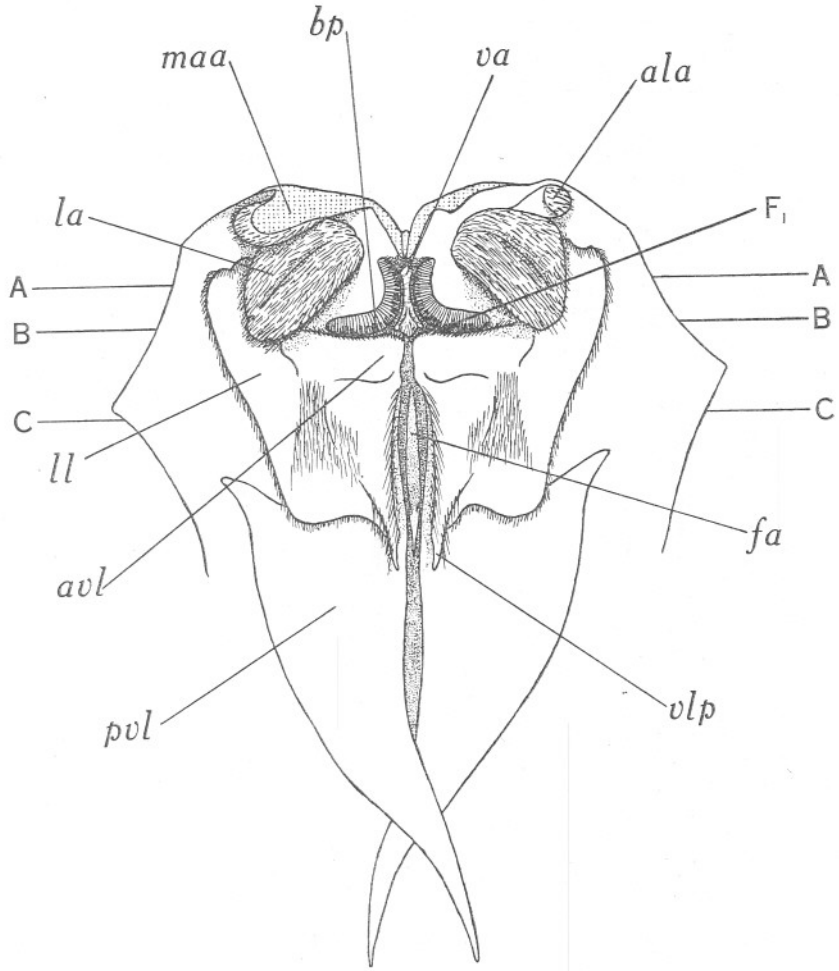
a.v.l., anterior ventral lamella; *d.l.*, dorsal lamella; *f.a.*, filter apparatus; *i.*, intestine; *l.a.*, lateral ampulla; *l.l.*, lateral lamella; *m.a.a.*, median anterior ampulla; *p.v.l.*, posterior ventral lamella; *v.l.p.*, projections from anterior ventral lamellæ.

(*a.l.a.*); in the mid-line of the anterior wall arises a single large median anterior ampulla (*m.a.a.*), while in the floor of the foregut lies a single median projection, the ventral ampulla (*v.a.*). These are all provided with strong, backwardly projecting bristles, and on contraction of the muscles of this region these ampullæ meet and effectively close the entrance to the œsophagus.

From the floor of the foregut and directly behind the ventral ampulla arises a pair of plates, the anterior ventral lamellæ (*a.v.l.*) forming to all appearances the actual floor which here appears to have a median ridge.

This ridge is formed by the approximated inner edges of these plates which rise towards the mid-line, each bearing a pointed projection (*v.l.p.*).

The anterior ventral lamellæ fuse laterally with the lateral lamellæ (*l.l.*), a pair of plates arising from the antero-lateral walls of the chamber,



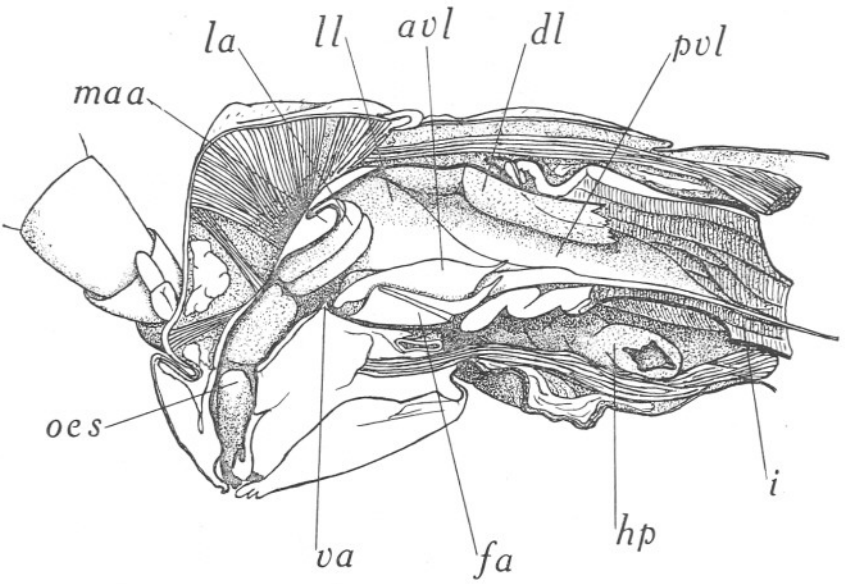
TEXT-FIG. 3.—Foregut opened along mid-line of the dorsal and anterior walls as far as the opening of the œsophagus. The two halves of the dorsal lamella are drawn apart, giving a flattened view of the main structures of the interior. The right half of the median anterior ampulla has been removed to disclose the small antero-lateral ampulla.

AA, BB, and CC indicate the lines through which the sections shown in Fig. 8 are drawn.

a.l.a., antero-lateral ampulla ; *a.v.l.*, anterior ventral lamella ; *b.p.*, bristle plate ; FI., Filter I ; *f.a.*, filter apparatus ; *l.a.*, lateral ampulla ; *l.l.*, lateral lamella ; *m.a.a.*, median anterior ampulla ; *p.v.l.*, posterior ventral lamella ; *v.a.*, ventral ampulla ; *v.l.p.*, projection from anterior ventral lamella.

beneath the lateral ampullæ and proceeding backwards and downwards as a flap attached ventrally. They are provided along the free dorsal edge with strong backwardly projecting bristles. The anterior ventral lamellæ, moreover, fuse posteriorly with a pair of long plates, the posterior ventral lamellæ (*p.v.l.*) which taper gradually to end in the intestine, projecting considerably beyond the apparent limits of the foregut.

If the ventral lamellæ are drawn apart a wedge-shaped projection is seen arising from the true floor of the foregut, widening posteriorly and



TEXT-FIG. 4.—Sagittal section through cephalon and first free thoracic segment, slightly to left of mid-line to include filter apparatus, showing internal structure of the right side. The cut edges of the alimentary canal are heavily outlined in black.

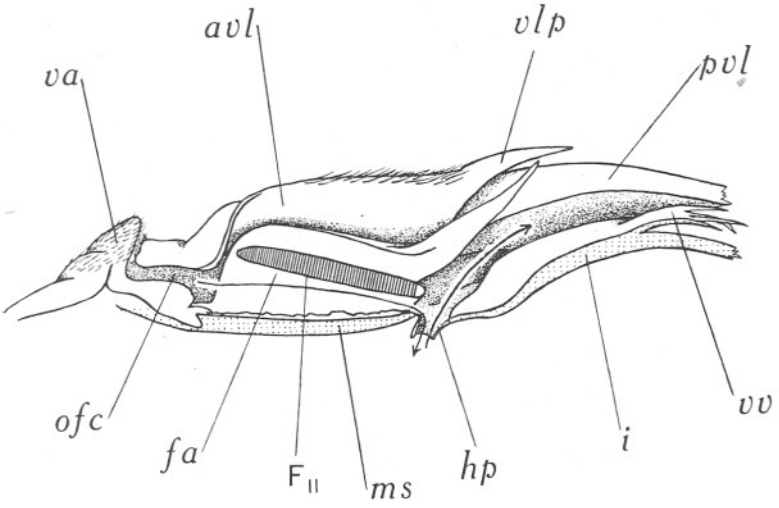
a.v.l., anterior ventral lamella ; *d.l.*, dorsal lamella ; *f.a.*, filter apparatus ; *h.p.*, hepato-pancreas ; *i.*, intestine ; *l.a.*, lateral ampulla ; *l.l.*, lateral lamella ; *m.a.a.*, median anterior ampulla ; *oes.*, œsophagus ; *p.v.l.*, posterior ventral lamella ; *v.a.*, ventral ampulla.

bearing on its postero-dorsal surface a finely pointed projection, similar to those of the ventral lamellæ, between which it is inserted. This structure, for want of a better name, may be called the filter apparatus (*f.a.*). It is, presumably, the "median ventral tooth" of Hewitt. Nothing appears more certain than that it is not a tooth ; a more detailed description of this apparatus appears below.

There remains one more lamellar structure to be mentioned, a simple projection from the dorsal surface of the foregut, arising almost directly over the junction of the anterior and posterior ventral lamellæ and

proceeding backwards to project freely into the lumen of the intestine, the dorsal lamella (*d.l.*). This is, apparently, without setose armature.

On the floor of the foregut and on either side of the elongate ventral ampulla lies a crescentic row of bristles, fused at their bases to form a plate (*b.p.*), but with their distal ends lying against the sides of the ventral ampulla in the mid-line and against the anterior ventral lamellæ behind. Beneath these bristles and on each side of the ventral ampulla is a channel running posteriorly under the anterior ventral lamellæ.



TEXT-FIG. 5.—Section through the foregut, slightly to left of mid-line, showing the filter apparatus and associated structures. The arrows indicate the course of food passing into the hepato-pancreas and the path taken by the secretion when forced out.

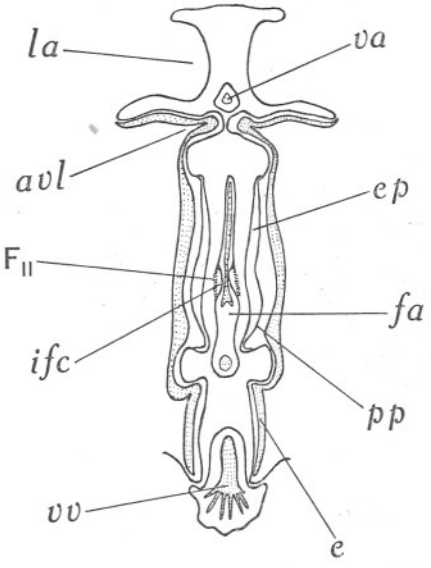
a.v.l., anterior ventral lamella ; *f.a.*, filter apparatus ; FII., Filter II ; *h.p.*, junction of hepato-pancreas with intestine ; *i.*, intestine ; *m.s.*, muscle sheath ; *o.f.c.* outer filter channel ; *p.v.l.*, posterior ventral lamella ; *v.a.*, ventral ampulla, *v.l.p.*, projection from anterior ventral lamella ; *v.v.*, ventral valve.

This will best be seen in Text-Figure 8. It constitutes Filter I. The occlusion of this channel (*o.f.c.*) between the bristle plates and the anterior ventral lamellæ is effected by a row of hairs which project forwards and interlock with those of the bristle plates.

Beneath the anterior ventral lamellæ the channel is divided into two by the filter apparatus (*f.a.*). As shown in Text-Figures 5, 6, and 8, this is wedge-shaped in two directions. It is broader at the base than at its dorsal edge and widens from in front backwards. On either side and parallel with the dorsal edge lies a groove covered with strong bristles attached to the ventral surface and free dorsally. This groove ends blindly anteriorly, opening over the entrance to the hepato-pancreas posteriorly. This is

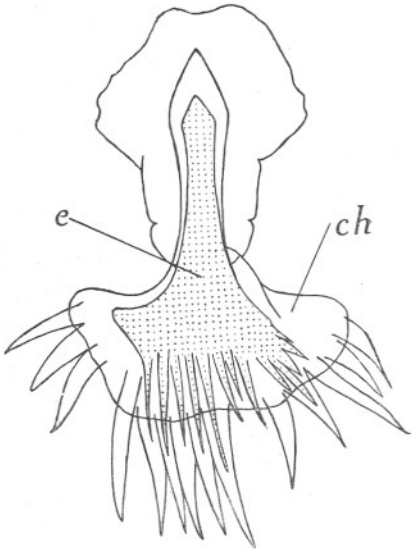
Filter II. Rehorst describes similar structures in the foregut of Asellus and the filters and filter channels of Ligia are directly comparable with those of Asellus, for which reason I have used the names given by him.

Finally, there is a structure, the ventral valve (*v.v.*, Text-Figs. 5, 6, and 7), attached to the ventral wall of the intestine and bearing against the lower surface of the posterior ventral lamellæ. We have now a space stretching from the ventral ampulla anteriorly to the ventral valve



TEXT-FIG. 6.—Semi-diagrammatic horizontal section through the filter apparatus showing its relationship to the surrounding structures.

a.v.l., anterior ventral lamella; *e.*, epithelium; *e.p.*, "elastic pad" of Rehorst; *f.a.*, filter apparatus; FII., Filter II; *i.f.c.*, inner filter channel; *l.a.*, lateral ampulla; *p.p.*, perforated plate; *v.a.*, ventral ampulla; *v.v.*, ventral valve.



TEXT-FIG. 7.—The ventral valve. *e.*, epithelium; *ch.*, chitin.

posteriorly which can be completely closed to any but liquid substances, all the possible entrances being guarded by strong hairs.

The chitinous lining of the anterior ventral lamellæ facing Filter II is composed of a double layer, the outer in contact with the filter being provided with very fine, upwardly projecting hairs, the inner being a plate with many minute holes, the two layers being connected by a network of fine fibres. Behind this inner plate lies the ordinary epithelial tissue, but at a little distance, thus enclosing a second space. This, however, is probably an artifact due to fixation since this space is found throughout

where chitin forms the lining of the foregut. (See Text-Figures 6, 8, and 9.)

Below is a list of the parts of the foregut as named by Hewitt in the first column; the terminology employed in this paper in the second, and that used by Rehorst for Asellus, as far as it is comparable, in the third.

Lateral cardiac tooth.	Lateral ampulla.	Laterale.
Antero-lateral tooth.	Antero-lateral ampulla.	—
Median anterior tooth.	Median anterior ampulla.	—
Ventral cardiac tooth.	Ventral ampulla.	Y-shaped piece.
Ventro-lateral tooth.	Anterior ventral lamella.	Infero-Laterale.
Median ventral tooth.	Filter apparatus.	Infero-Medianum.
Lateral cardiac lamella.	Lateral lamella.	Dorsal branch of the Laterale.
Dorsal lamella.	Dorsal lamella.	Supero-Medianum.
Ventro-lateral pyloric lamella.	Posterior ventral lamella.	Intero-Laterale.

Actually Rehorst includes his Y-shaped piece as part of the Infero-Laterale; he also confines the term "outer filter channel" to that portion of the cavity enclosed between the two ventral lamellæ which lies below Filter II, the whole space being termed the "storeroom."*

(*c*) The Hepato-pancreas.

This consists of three pairs of tubules lying along the alimentary canal which they partially enclose. Their external morphology has been fully described by Hewitt, but a little more must be said about their internal structure. Reference to Plate I, Figures 4 and 5, will show that there are small and large cells, as mentioned by many workers on the histology of this organ in the Isopods. The cell walls are distinct and homogeneous, the contents granular with many small vacuoles, the significance of which cannot be entered into here. Each cell contains a nucleus, and nucleoli are present in most.

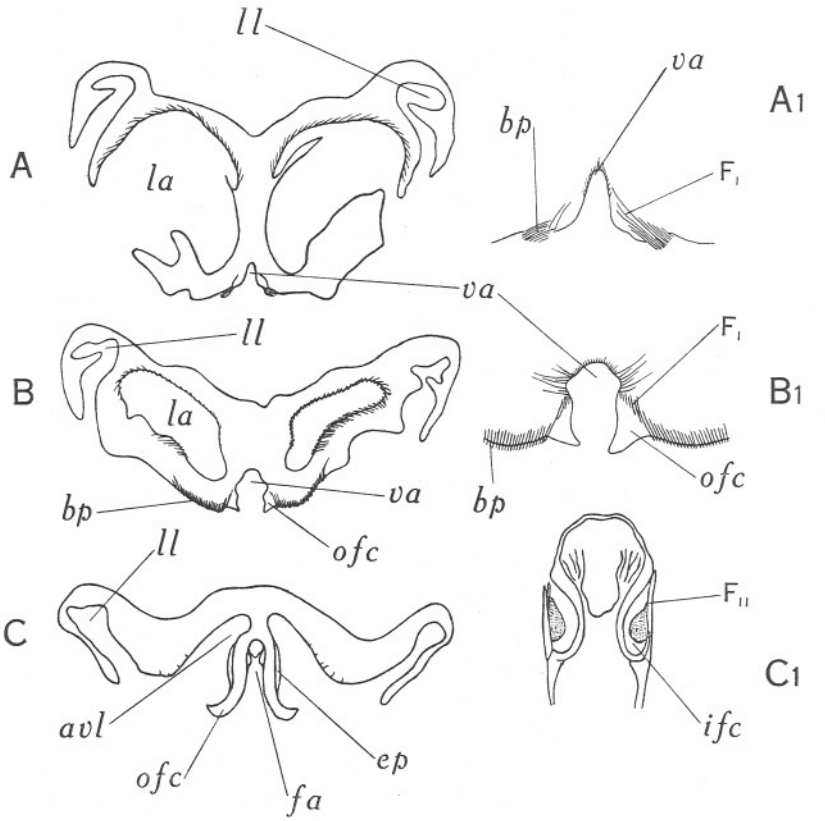
It is the opinion of Nusbaum-Hilarowicz (1920) that the small cells are young stages of the large ones which, as they become mature, break up, liberating their contents into the lumen and thus providing the secretion. In this respect Nusbaum-Hilarowicz supports the view held by Murlin (1902) though Weber (1880) thinks that they are absorbing and secreting cells respectively.

(*d*) The Intestine

As McMurrich (1896) has shown, the portion of the alimentary canal extending from the point of entry of the hepato-pancreatic glands to the

* I wish to thank Dr. H. G. Jackson for details of the technique employed by him in dissecting the head of Ligia.

rectum, usually termed the midgut, is, in Isopods, the anterior portion of the proctodæal invagination and cannot, therefore, be justly termed midgut. This statement is supported by my observations on Ligia in that the whole of this region is lined throughout by chitin. This layer of chitin is, as McMurrich has shown, double, but whereas this author

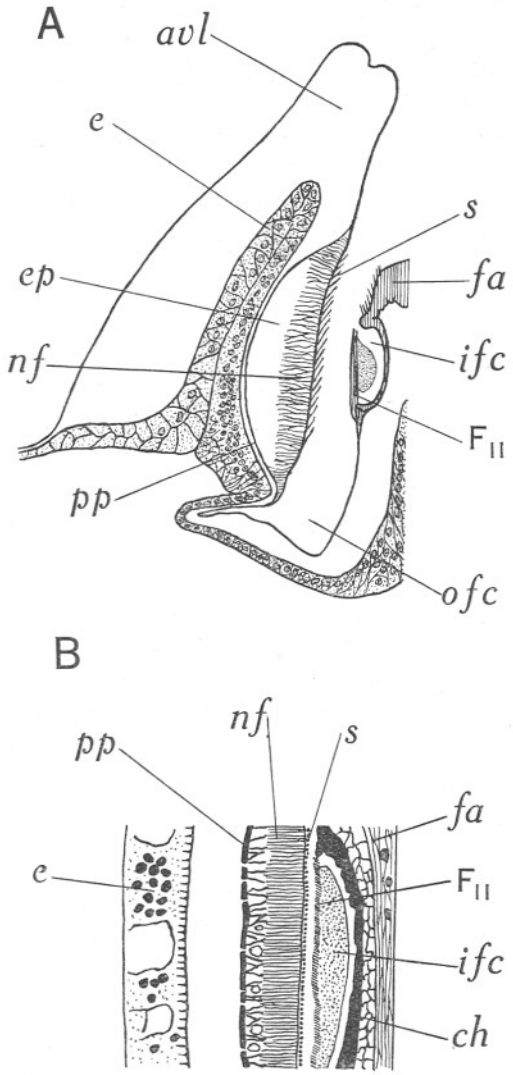


TEXT-FIG. 8.—Semi-diagrammatic transverse section through foregut, A and B passing through bristle plates, ventral ampulla and Filter I ; C, passing through filter apparatus and Filter II, as indicated by AA, BB and CC in Fig. 3. A1, B1 and C1, enlargements of portions of A, B, and C.

a.v.l., anterior ventral lamella ; *b.p.*, bristle plate ; *e.p.*, " elastic pad " of Rehorst ; *f.a.*, filter apparatus ; FI., Filter I ; FII., Filter II ; *i.f.c.*, inner filter channel ; *l.a.*, lateral ampulla ; *l.l.*, lateral lamella ; *o.f.c.*, outer filter channel ; *v.a.*, ventral ampulla.

describes both layers as homogeneous, in Ligia the inner layer appears to be vacuolated (Plate I, Figs. 1, 2, and 3).

Murlin (1902, p. 310) describes the presence of minute pores which perforate the chitinous lining of the lumen of the " midgut " in land Isopods. He does not illustrate these pores though he states that they are easily



TEXT-FIG. 9.—A, semi-diagrammatic representation of transverse section through ventral lamella and filter apparatus, showing relationship between Filter I and "elastic pad" of Rehorst. B, semi-diagrammatic representation of horizontal section through same region, showing network of fibres, perforated plate and space behind plate.

a.v.l., anterior ventral lamella; *ch.*, chitin; *e.*, epithelium; *e.p.*, "elastic pad" of Rehorst; *f.a.*, filter apparatus; FII., Filter II; *i.f.c.*, inner filter channel; *n.f.*, network of fibres; *o.f.c.*, outer filter channel; *p.p.*, perforated plate; *s.*, setæ of "elastic pad."

demonstrated in the fresh intima found in a moulted posterior portion of the animal. Schonichen (1898) also found such pores in the Oniscidæ and Asellidæ. Examination of similar material and also of sections has failed to establish the presence of such pores in Ligia, but as will be seen from Plate I, Figures 2 and 3, the chitin lining the epithelium of the intestine is of a complicated nature.

It is composed of two layers of unequal thickness making up a total of surprising thickness for such a region. The inner layer, comprising about three-quarters of the total thickness, is of a loose spongy texture containing cavities, many of which are permeated by cytoplasm. The outer layer is very thin but apparently homogeneous and quite imperforate.

In the absence of any pores in these layers Ligia is in perfect agreement with McMurrich's description for Armadillidium, Porcellio, Oniscus, and *Idothea robusta*.

The epithelium underlying the chitinous layer is devoid of cell boundaries and forms a syncytium. "Supportive fibres" arise from both this layer and the basement membrane and run towards the opposite sides, representing all that is present of cell walls.

The infoldings of the intima, which project into the syncytial layer, are very regular and viewed from the surface under low magnification give the impression of an epithelium composed of large, very regularly arranged cells, each containing a large nucleus. This impression is heightened by the arrangement of the muscle fibres on the outside which form a network, each strand lying in a groove on the surface. No trace of a typhlosole can be seen in Ligia.

(*e*) The Rectum.

The terminal portion of the alimentary canal is a short region with very much folded walls, well supplied with muscles. It is separated from the intestine by a sphincter. The epithelium in this region is a syncytium continuous with that of the intestine, but much thinner.

3. PHYSIOLOGY OF THE GUT.

The structure and function of what we now term the hepato-pancreas has been investigated in Isopods and other Crustacea by Weber (1880), his work being done largely on Asellus. Murlin (1902) and Nusbaum-Hilarowicz (1920) have dealt similarly with the land Isopods, the latter going into much histological detail, while Patrick (1926) alone has investigated the cells of the hepato-pancreas of Ligia. Gelderd (1906) concluded from his research on the function of the foregut that the "cardiac chamber" primarily masticates the food particles "as an auxiliary to the mouth pieces" and secondarily it "acts as a sieve or filter for the further

retention in the cavity of such particles of food that have not been sufficiently divided." The "pyloric chamber," he says, has the function "of mixing the already masticated food with the ferments of the digestive gland. This is brought about by the action of the spines and hairs upon the pyloric pieces, when the chamber is put into movement by the muscles."

Hewitt (1907), speaking of Ligia, says: "The stomach forms an efficient mill for triturating the miscellaneous substances upon which the animal feeds." Tait (1917), in describing the structure of the foregut of Glyptonotus, says: "The use of the term 'gizzard' (chosen apparently as an improvement on the older and admittedly unsuitable term 'stomach') is in itself misleading, for the name suggests that the function of the organ is to triturate the food. The idea is disposed of by the condition of the ingesta discovered in the midgut of the dissected specimens. When the food had consisted of amphipods these were found, according to size, almost intact or cut into longitudinal blocks of about $\frac{1}{4}$ inch length." He goes on to say: "The cutting had evidently been done by the incisor processes of the mandibles, the length of the blocks corresponded roughly to the reach of these processes from the position of abduction to that of adduction, and the food had evidently been 'bolted' without the occurrence of any further process of comminution in the vestibule." This latter is the term he employs in place of the previous misleading terms. He is further of the opinion that the foregut is "merely a propelling mechanism." While, in my opinion, the above description of the supposed method of feeding of Glyptonotus applies equally well to Ligia, since I have found the contents of the intestine to consist of equal sized particles of algæ, yet it will be shown that the foregut is more than a mechanism for propulsion. I have, moreover, through the kindness of Professor D. M. S. Watson, been able to dissect a specimen of Glyptonotus and find that in main principles the foregut resembles that of Ligia very closely. Hewitt, in using the term "tooth," admits its inadequacy, but still assigns to it a triturating function, which rather nullifies the admission. None of the structures termed by him "teeth" are in any way comparable with the hard chitinous teeth of the Decapods.

Assuming, then, that no further mastication is performed after the food has passed the mouth parts, it will pass up the œsophagus as a "mush" and will enter the foregut between the bristle plates and ventral ampulla below, and the lateral and median anterior ampullæ above. Here, by contraction of the muscles enclosing this part of the vestibule (Text-Fig. 1), to use Tait's term, the liquid portion of the food will be squeezed through Filter I carrying with it only very fine particles. The same motion which compresses the food will tend to force it back into the larger cavity of the foregut, by virtue of the backwardly projecting hairs with which

it will be in contact all round. Imagine now a contraction of the muscles, shown in Text-Figure 1 running forward from the lateral lamellæ, to occur simultaneously with a contraction of the muscle sheath across the ventral, convex surface of the foregut. The result would be the drawing apart of the ventral lamellæ and the pushing up of the filter apparatus. Thus the secretion from the hepato-pancreas would be liberated into the cavity of the vestibule and mixing would also be effected.

Moreover, on the return of the parts to their normal position, a quantity of partly digested food would be caught between each ventral lamella and the filter apparatus, and the liquid portion squeezed through Filter II into the inner filter channel, whence it would pass into the hepato-pancreas along with the liquid forced through Filter I into the outer filter channel.

This process is further aided by the rhythmical contractions of the hepato-pancreatic tubules. These were observed in the living animal, through the transparent ventral surface of a recently moulted specimen, to consist of waves passing forwards along the tubules expelling the contents. On the relaxation of the muscles of the tubules, liquid was observed to return into the lumen. The contraction of the tubules probably coincides with that of the muscle sheath which, as we have seen above, separates the ventral lamellæ and elevates the filter apparatus. Thus is the secretion from the glands passed into the foregut and intestine. With the return of the parts of the foregut to their normal position and the relaxation of the muscles of the tubules, liquid forced through the filters into the filter channels is drawn into the hepato-pancreas. The entrance from the intestine is automatically closed by the action of the ventral valve. Thus the liquid products of digestion may be absorbed in the tubules of the hepato-pancreas. The more solid portions of the food, mixed with the digestive enzymes, will pass into the intestine, where further digestion and absorption will occur.

It will be seen from the above description of the assumed functioning of the foregut that no time is wasted with mastication, the whole principle being one of extracting as quickly as possible the most readily obtainable nourishment. It is suggested that this may be correlated with the limited period during which the animal feeds, as described above, in which case it would be expected also that the enzymes which break down the food would be very powerful, and this will be shown to be the case.

Rehorst, apparently, assumes the filtering action to be quite passive, at least in Filter I, and to the surfaces which come into contact with the filters and are themselves setose, he assigns primarily the function of cleaning the filters and keeping them free from large particles. This may easily be an additional function in Ligia. Further, he assumes that the space enclosed between the double layer of chitin lining the opposing walls of the ventral lamellæ is filled with liquid, forming an elastic pad

which, pressed against Filter II, would separate the outer filter channel from the space above. He makes no mention of perforations in the inner wall of the pad, possibly they are absent in Asellus, but such a function as he suggests for this pad, besides being superfluous, would be rendered difficult in Ligia unless liquid could be forced in at will. The function of this part remains somewhat obscure.

4. COMPARISON OF THE FOREGUT OF LIGIA WITH THAT OF THE DECAPODS.

As may be seen from the work of Jordan (1904), Williams (1907), and Yonge (1924), the foregut in the Decapods is divided into two parts, the cardiac and the pyloric, to each of which are assigned definite functions.

The cardiac portion is a sac serving mainly for the reception of food and contains the masticatory ossicles which triturate the food and assist in the mixing of the food with the secretion from the hepato-pancreas. The food then passes into the pyloric region whence the liquid portion and fine particles pass through the filter into the hepato-pancreas, the larger particles passing above the press into the midgut.

Whereas the Decapods merely tear their food with their mouth parts and pass it into the foregut for complete mastication and digestion, Ligia, as has been seen, not being provided with a triturating mechanism in the foregut, cuts up its food with the mouth parts and then depends on the great power of its digestive enzymes to complete the process in the foregut and intestine. Both are provided with means of limiting the size of the particles entering the hepato-pancreatic tubules, and both the valves and the plates of the Decapods and the ventral valve and lamellæ of Ligia prevent the blockage by food particles of the exit from the tubules. Further, in the action of the ventral lamellæ working in conjunction with the filter apparatus, there is in Ligia a mechanism comparable with the press of the Decapods.

5. DIGESTION.

(*a*) The pH of the Gut.

In Table I will be found the pH of the different regions of the gut of normally feeding animals, of starved animals (48 hrs.), and of those whose pH had been estimated at different periods after feeding following on a period of starvation of 48 hours or more.

From Table I it will be seen that the pH of the gut varies very slightly from one end to the other, whether the animals are starved or feeding. As a result of feeding after starvation the pH of the intestine

was found to be slightly higher than the contents of the hepato-pancreas and slightly lower than that in the same region of a starved animal. This was the same whether estimated $\frac{1}{2}$ hr. or 4 hrs. after feeding.

For the estimation of pH on the small quantities of liquid found in the gut of this animal the method employed was that described by Wigglesworth (1927, p. 792), and used by him in similar work on the cockroach.

TABLE I.

Showing pH of Gut under Different Conditions.

ANIMALS ALL FEEDING.

No.	Intestine.	Rectum.
1.	6·0	6·2
2.	6·2	5·9
3.	6·7	—
4.	6·3	—
Mean.	6·3	6·05

ANIMALS STARVED FOR 48 HOURS.

No.	Foregut.	Intestine.	Rectum.
1.	—	6·05	6·0
2.	6·3	6·55	6·2
3.	6·3	6·45	6·2
4.	6·4	6·4	6·5
5.	6·3	6·55	6·1
6.	6·1	6·25	5·8
7.	6·25	7·2	6·3
Mean.	6·27	6·49	6·16

STARVED ANIMALS BEFORE AND AFTER FEEDING.

No.	Period of Starvation hours.	Intestine.	Hepato-pancreas.
1.	48	6·4	6·0
2.	60	6·3	6·0

No.	Period of Starvation hours.	Time after feeding hours.	pH of Intestine.
1.	60	$\frac{1}{2}$	6·2
2.	60	4	6·2
Mean.	–	–	6·2

(*b*) The Digestive Enzymes.

The enzymes secreted by the cells of the hepato-pancreas are passed into the gut by rhythmical contractions brought about by the network of muscles on the outside, described by Pump (1914).

An extract was made from the hepato-pancreatic tubules of a large number of animals ground up with silver sand and extracted on ice in distilled water for 48 hours.

This was then filtered and made up to a 10% solution based on the weight of tubules and secretion obtained, the whole being kept under toluol continuously. The pH of this extract was 5·9. Table II shows the result of incubation of various substances with this extract.

TABLE II.

5 c.c. substrate ; 5 c.c. extract ; toluol. Controls boiled. Temperature 30° C.

Presence of glucose determined by Fehling's solution, and of disaccharides by Barfoed's solution. Fatty acids produced by digestion of fat titrated against N/100 NaOH.

— indicates no action ; ± indicates a trace ; + indicates positive action ; ++ indicates extensive action.

Substrate.	Experiment after				Control after			
	24 hrs.	48 hrs.	4 days.	10 days.	24 hrs.	48 hrs.	4 days.	10 days.
Starch 1%	++	++	..	..	±	±	..	..
Glycogen (Saturated)	+	+	..	..	±	±	..	..
Sucrose 5%	++	++	..	..	–	–	..	..
Raffinose 1%	++	++	..	..	–	–	..	..
Inulin 1%	–	–	–	..	–	–	–	..
Maltose 2%	+	+	..	..	–	–	..	..
Lactose 2%	–	–	–	..	–	–	–	..
Cellulose	–	–	–	–	–	–	–	–
Amygdalin 1%	+	+	..	..	–	–	..	..
		CN evov.						
Salicin 1%	+	+	..	..	–	–	..	..
Fibrin	Digestion complete 24 hours. Positive reactions with Millon's Reag. and Br. water.				–	–	–	..
Olive Oil	..	2·15 c.c.	2.0 c.c.	..	..	1·9 c.c.	1·88 c.c.	..

From the above Table it will be seen that most carbohydrates are readily split up, the exceptions being Lactose, Inulin, and Cellulose, while the protease is exceptionally strong, digestion of a large piece of fibrin being complete within 24 hours. A lipase is also present.

In order to discover if any secretion was liberated by the intestine a number of these were taken, split open, and washed carefully in water and ground up as were the tubules of the hepato-pancreas, being extracted in 50% glycerin for 48 hours. Table III shows the result of this experiment, from which it will be seen that after 24 hours glycogen and sucrose both showed a trace of reduction and starch after 48 hours.

TABLE III.

5 c.c. substrate with 5 c.c. extract and toluol; incubated at 30° C.
— indicates no action; ± indicates a trace; + indicates positive action. Tests as before.

Substrate.	Experiment after		Control after	
	24 hours.	48 hours.	24 hours.	48 hours.
Starch 1%	±	+	—	—
Glycogen (Sat)	±	±	±	±
Sucrose 5%	+	+	—	—
Raffinose 1%	—	—	—	—
Inulin 1%	—	—	—	—
Maltose 2%	±	±	—	—
Lactose 2%	—	—	—	—
Cellulose	—	—	—	—
Amygdalin 1%	—	—	—	—
Salicin 1%	—	—	—	—
Fibrin	—	—	—	—
Olive Oil	..	0·35 c.c.	..	0·30 c.c.

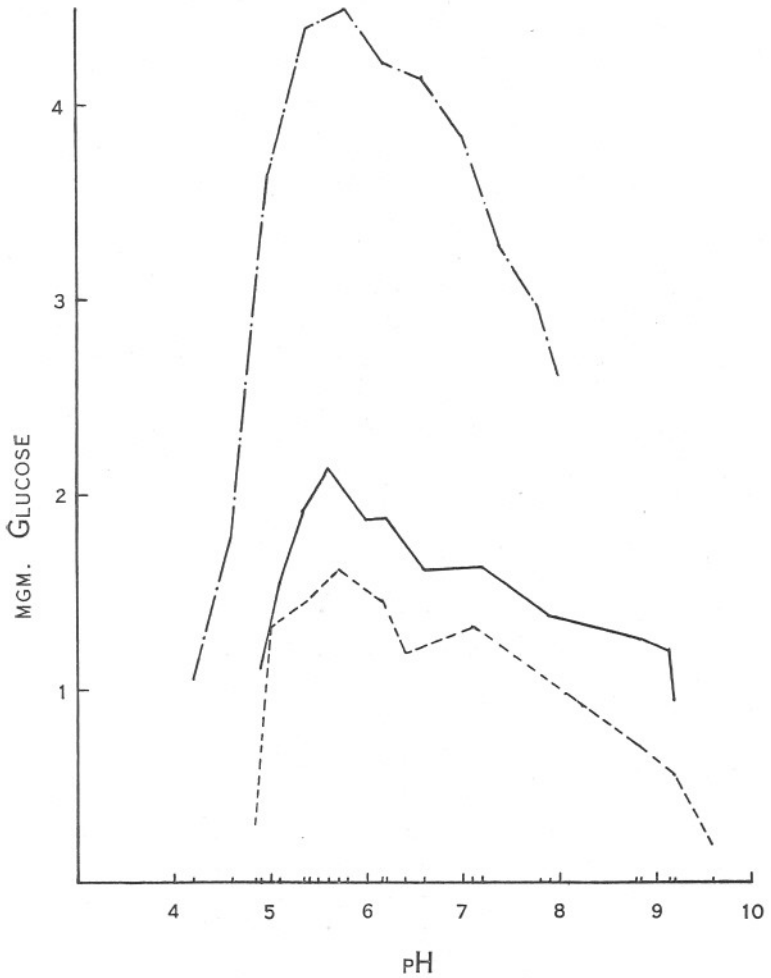
The original sample of glycogen, however, was found to contain a certain amount of reducing sugar, while the trace of reduction in the other two can be explained by the great ease with which they are reduced by the secretion from the hepato-pancreas, combined with the difficulty experienced in washing the intestines completely free from that secretion. It can safely be assumed that there are no enzymes secreted by the epithelium of the intestine which can act on carbohydrates, proteins or fats. Thus the whole of the digestion is performed by the enzymes present in the secretion from the hepato-pancreas.

(*c*) The Sucroclastic enzymes.

Since algæ form the normal food of this animal, it was thought advisable to investigate the possibility of enzymes being present which would reduce pentosans and cellulose. Accordingly tests were made on Gum Arabic, Agar Agar, and Pectin. No reducing substances were found in any case after 24 hours' incubation at 27° C., using 10% extract.

For the detection of a possible cellulase other tests were applied. A small piece of clean Fucus was placed in the extract and incubated for several days. At the end of that time microscopic examination showed that the contents of only those cells whose walls had been cut through were digested. Further, hand sections were cut and mounted on a slide in the actual secretion from the hepato-pancreas, the cover glass being sealed and the whole left in a warm, constant temperature for several

days, being examined from time to time for dissolution of the cell walls. None, however, was observed. In tests on filter paper and cotton wool incubated for some time with the extract, Fehling's solution failed to demonstrate the presence of any reducing sugar. Thus it will be seen



TEXT-FIG. 10.—Graph showing pH optimum and range of activity for amylase ——; invertase ——.——; glycogenase – – – – –.

that this animal, though its main diet consists of Fucus and other vegetable matter, is quite unable to digest either cellulose or the pentosans contained in such food. Yonge (1927) failed to find a cellulase in extracts of the wood-boring Isopod *Limnoria lignorum*.

A series of experiments was carried out to determine the pH optima of

the various sucroclastic enzymes. The effect of the change of pH upon the activity of the amylase, invertase and glycogenase is shown in Tables IV, V, and VI respectively, below and in Text-Figure 10.

In these experiments Clark and Lub's Buffer Solutions were used, at first, for providing a known pH. These, however, were found in some cases to be altered by the addition of the extract and did not give true readings. The method then resorted to was that of adding a certain quantity of acid or alkali and/or water to the extract and finding the pH of the resultant mixture.

MacLean's blood sugar method was used throughout in estimating the amount of glucose. Briefly, this is as follows: The proteins are precipitated from the sample by heating with acid sodium sulphate and adding dialysed iron to the hot liquid. The mixture is cooled and filtered and to the filtrate is added an excess of alkaline copper iodide solution. This is then boiled for a definite length of time, during which an amount of copper is reduced equivalent to the amount of glucose present in the sample. The iodine is liberated from the excess alkaline copper iodide by the addition of acid and titrated with sodium thiosulphate in the usual way. The amount of iodine present in the total amount of copper iodide solution added is also determined directly, the difference giving the amount of copper iodide reduced by the glucose, from which the amount of glucose present can be determined.

TABLE IV.

pH Optimum for Amylase.

1% starch solution, 1 c.c. 10% enzyme extract, 1 c.c. Acid or alkali and/or water to 2 c.c.

Incubated for $2\frac{1}{2}$ hours. Temperature, 28° C.

No.	Acid		Alkali		H_2O	pH.	Thio. ·01 N	Glucose
	c.c.	N.	c.c.	N.	c.c.		c.c.	mgm.
1.	1·0	·01	–	–	1·0	4·9	5·43	1·11
2.	·5	·01	–	–	1·5	5·1	4·37	1·53
3.	·3	·01	–	–	1·7	5·35	3·49	1·91
4.	–	–	–	–	2·0	5·65	2·96	2·13
5.	–	–	·25	·01	1·75	6·0	3·58	1·87
6.	–	–	1·0	·01	1·0	6·2	3·58	1·87
7.	–	–	2·0	·01	–	6·6	4·20	1·61
8.	–	–	·3	·1	1·7	7·2	4·16	1·62
9.	–	–	·45	·1	1·55	7·9	4·78	1·37
10.	–	–	1·0	·1	1·0	8·85	5·11	1·25
11.	–	–	1·5	·1	·5	9·15	5·27	1·18
12.	–	–	2·0	·1	–	9·2	5·83	0·94

TABLE V.

pH Optimum for Invertase.

5% sucrose solution, 2·5 c.c. 10% enzyme extract, 2·5 c.c. Buffer solution, 5 c.c.

Incubated for 2 hours. Temperature, 32° C.

No.	pH.	Thio. ·01 N. c.c.	Glucose mgm.
1.	4·2	7·60	1·05
2.	4·6	6·60	1·79
3.	5·0	4·36	3·63
4.	5·4	3·46	4·39
5.	5·8	3·35	4·48
6.	6·2	3·66	4·22
7.	6·6	3·87	4·13
8.	7·0	4·12	3·83
9.	7·4	4·78	3·27
10.	7·8	5·15	2·96
11.	8·0	5·60	2·60

Note.—In the above table the amount of glucose represented is, in some cases, greater than the amount that can be estimated by the amount and strength of reagents advised by MacLean. In estimating glucose in this experiment half the quantity was taken and the result doubled.

TABLE VI.

pH Optimum for Glycogenase.

Saturated solution of Glycogen, 3 c.c. 10% enzyme extract, 1 c.c. Acid or alkali and/or water to 2 c.c.

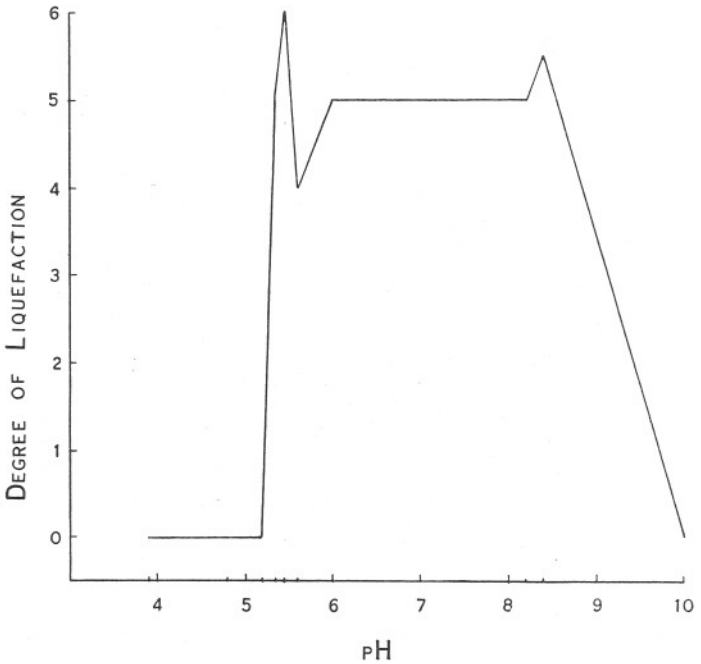
Incubated for 70 minutes. Temperature, 32° C.

No.	Acid		Alkali		H_2O	pH.	Thio. ·01 N. c.c.	Glucose mgm.
	c.c.	N.	c.c.	N.	c.c.			
1.	2·0	·01	–	–	–	4·85	7·16	0·3
2.	1·0	·01	–	–	1·0	5·0	4·97	1·31
3.	·5	·01	–	–	1·5	5·4	4·54	1·46
4.	–	–	–	–	2·0	5·7	4·20	1·61
5.	–	–	1·0	·01	1·0	6·15	4·58	1·45
6.	–	–	2·0	·01	–	6·4	5·25	1·19
7.	–	–	·35	·1	1·65	7·1	5·01	1·32
8.	–	–	·4	·1	1·6	8·8	6·46	0·71
9.	–	–	·6	·1	1·4	9·2	6·86	0·56
10.	–	–	1·0	·1	1·0	9·6+	7·62	0·20

There is a range of activity between pH 5 and pH 7 in the case of all three sucroclastic enzymes, with the optimum lying between pH 5·65 and pH 5·8.

(*d*) The Proteoclastic Enzymes.

These are very powerful, so much so that it was necessary to reduce the proportion of extract to substrate very considerably in order to prevent the digest from acting too quickly. Table VII and Text Figure 11



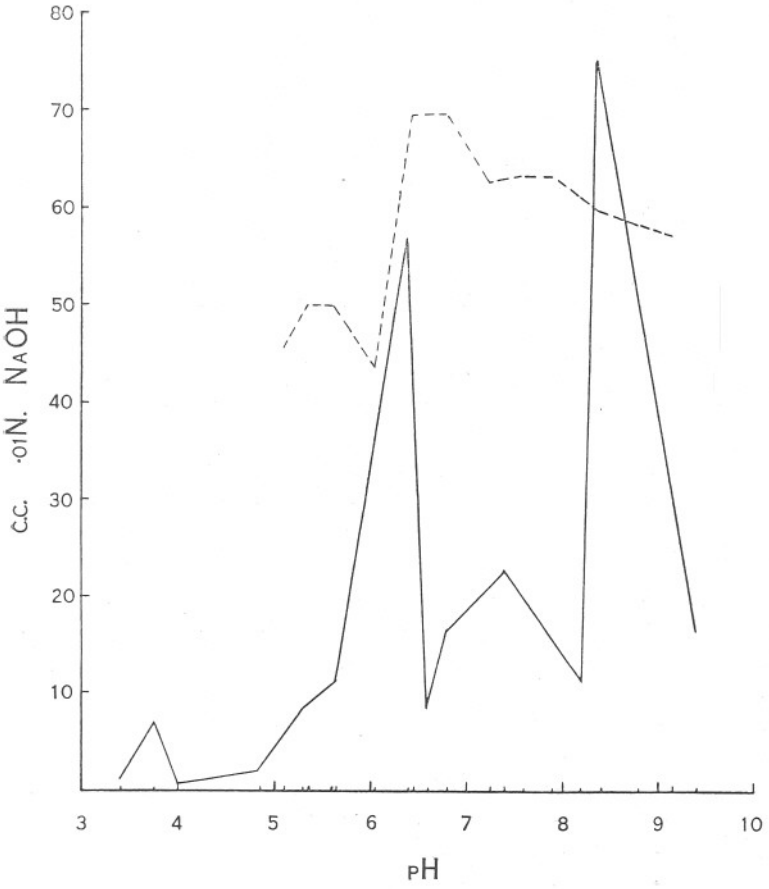
Text-Fig. 11.—Graph showing activity of protease, with change in pH, on the liquefaction of gelatine.

represent the results of an experiment to determine the effect of change in hydrogen ion concentration on the liquefaction of gelatine, i.e. the conversion of proteins to soluble polypeptides.

In this Table the degree of liquefaction is expressed by the figures of an arbitrary scale used by Yonge (1926a) who quotes Dernby, as follows :—

0 Completely solid.
1 Solid, but small pieces may be torn off by strong shaking.
2 Solid, but the surface moves somewhat when the tubes are shaken.
3 Soft.
4 Half liquid.
5 Almost liquid.
6 Entirely liquid.

From these it will be seen that the range of activity extends from pH 5·35 to pH 5·85, with an optimum about pH 5·45 and a second at pH 8·4. To determine the quantities of amino acids produced these were estimated by titration with alkali after treatment of the digest with 90% alcohol. This proved an unsatisfactory method owing to the precipitation of proteins which masked the end point. Sørensen's formaldehyde titration was employed with more success on digests with blood fibrin. The results of this experiment are given in Table VIII and Text-Figure 12. Two optima were again found, the first at pH 6·4 and the second at pH 8·4.



TEXT-FIG. 12.—Graph showing optimum pH and range of activity for protease on blood fibrin ——; and on peptone – – – – – –.

TABLE VII.

pH Optimum for the Protease by the Liquefaction of Gelatine.

10% gelatine solution, 5 c.c. and 1 c.c. of the following mixture: 0·5% enzyme extract in sea-water, 5 c.c., acid or alkali and/or water to 5 c.c. Temperature, 32° C.

No.	Acid		Alkali		H_2O	pH	Degree of liquefaction after given number of hours.							
	c.c.	N.	c.c.	N.	c.c.		1	2	3	4	4½	5	5½	6
1.	5·0	·1	–	–	–	3·9	0	0	0	0	0	0	0	0
2.	2·5	·1	–	–	2·5	4·8	0	0	0	0	0	0	0	0
3.	5·0	·01	–	–	–	5·2	0	0	0	0	0	0	0	0
4.	–	–	–	–	5·0	5·35	0	0	1	1	2	4	4–5	5
5.	–	–	2·5	·01	2·5	5·45	0	1	1–2	2–3	4	5	5–6	6
6.	–	–	1·0	·1	4·0	5·6	0	0	1	1–2	2	3	3	4
7.	–	–	3·0	·1	2·0	6·0	0	1	1	2	3	3	3–4	5
8.	–	–	4·0	·1	1·0	8·2	0	1	1–2	2	3	4	4–5	5
9.	–	–	5·0	·1	–	8·4	0	1	1–2	3	3–4	4	4–5	5–6
10.	–	–	1·0	1·0	4·0	10·0	0	0	0	0	0	0	0	0

TABLE VIII.

pH Optimum for the Protease.

1% enzyme extract in sea-water, 5 c.c. Acid or alkali and/or water to 5 c.c. Blood fibrin, 0·2 gm. Incubated for 5 days. Temperature, 30° C.

No.	Acid		Alkali		H_2O	pH	NaOH ·01N
	c.c.	N.	c.c.	N.	c.c.		c.c.
1.	5·0	·01	–	–	–	3·4	1·25
2.	3·0	·01	–	–	2·0	3·75	6·9
3.	2·0	·01	–	–	3·0	4·0	0·6
4.	1·5	·01	–	–	3·5	4·85	2·05
5.	1·0	·01	–	–	4·0	5·3	8·4
6.	·75	·01	–	–	4·25	5·65	11·3
7.	·5	·01	–	–	4·5	6·0	32·5
8.	–	–	–	–	5·0	6·4	56·6
9.	–	–	·5	·01	4·5	6·6	8·5
10.	–	–	·75	·01	4·25	6·8	16·15
11.	–	–	1·0	·01	4·0	7·4	22·6
12.	–	–	1·25	·01	3·75	8·2	11·25
13.	–	–	1·5	·01	3·5	8·4	75·0
14.	–	–	5·0	·01	–	9·4	16·4

In order to determine whether the two optima were present when a polypeptide was used as a substrate the following experiment was carried out.

A 10% solution of peptone was used as the substrate and the optimum range of activity determined for the production of amino acids. Table IX and Text-Figure 12 show the result of this experiment; it will be noticed that while the range of activity extends from pH 5·6 to pH 8·8 there is now only one optimum point situated at pH 6·8, the higher optimum at pH 8·4 having been eliminated.

TABLE IX.

pH Optimum for the Protease.

1% enzyme extract in sea-water, 5 c.c. Acid or alkali and/or water to 5 c.c. 10% solution of peptone, 3 c.c. Incubated for 22 hours. Temperature, 29°–30° C.

No.	Acid		Alkali		H_2O	pH	NaOH ·01N
	c.c.	N.	c.c.	N.	c.c.		c.c.
1.	5·0	·01	–	–	–	5·1	45·8
2.	–	–	–	–	5·0	5·35	50·0
3.	–	–	5·0	·01	–	5·6	50·0
4.	–	–	1·0	·1	4·0	6·05	43·8
5.	–	–	2·0	·1	3·0	6·45	69·6
6.	–	–	3·0	·1	2·0	6·8	69·7
7.	–	–	4·0	·1	1·0	7·25	62·7
8.	–	–	4·5	·1	·5	7·6	63·3
9.	–	–	5·0	·1	–	7·9	63·2
10.	–	–	·4	1·0	4·6	8·4	59·6
11.	–	–	·5	1·0	4·5	8·8	58·2
12.	–	–	·6	1·0	4·4	9·15	57·1

In view of the fact that the pH of the gut lies between 5·8 and 6·7, the higher optimum cannot be of use to the animal during digestion. It is probable, however, that it may be an autolytic enzyme such as Shinoda (1928) found in Astacus, and this supposition is strengthened by the absence of this optimum when peptone was used as a substrate. Shinoda also found differences between the optimum pH for the working of the protease on different substrates such as have been recorded above.

6. ABSORPTION.

(*a*) Introductory.

This subject has been one of great controversy amongst the workers on the physiology of digestion in Isopods for many years. An excellent résumé of the work of previous authors is provided by Nusbaum-Hilarowicz (1917) in a preliminary summary of his work, and at greater length in the introduction to his paper of 1920.

As mentioned above in the description of the intestine, McMurrich (1896) showed that the so-called midgut is lined throughout by chitin and thus, according to him, cannot absorb, but can serve only for the storage of food, whereas Murlin showed this cuticle to be porous and demonstrated the absorption of fat and certain albuminous substances. This latter author did not discuss the question of absorption in the hepato-pancreas, though he dealt with the structure of its epithelium and with its function of secretion.

(*b*) Methods and Results.

In the investigation of the absorption of food in Ligia, the method used was that frequently employed by workers of recent years. Iron, in the colloidal form of ferrum lacticum or ferrum oxydatum saccharatum, in this case the latter, was fed to the animals under investigation. After a given period the gut and hepato-pancreas were dissected out and fixed, the usual fixative employed being a 5% solution of ammonium sulphide in 95% alcohol. In this case Yonge's modification (1926b, p. 709) of mixing the ammonium sulphide in alcohol with an equal volume of Bouin's fixative, just before use, was employed with satisfactory results. The sections were treated for 10 minutes with a 10% aqueous solution of potassium ferrocyanidè, followed by a few minutes in a dilute solution of HCl, a bright Prussian blue colouration resulting wherever the colloidal iron had been absorbed. The sections were counter-stained with alum carmine.

By means of this treatment it was possible to demonstrate absorption throughout the whole length of the epithelium of the intestine and also in that of the hepato-pancreas, as shown in Plate I, Figures 1–5.

In the latter organ the granules found usually at the bases of the cells, termed zymogen granules by many authors, appear to act as centres round which the absorbed material aggregates.

In the experience of most workers who have employed this technique to demonstrate absorption, the colouration due to the iron tends to be concentrated in localised areas, somewhat as in Figures 4 and 5 which illustrate absorption in the hepato-pancreas. In the intestine the absorbed material was distributed much more diffusely, dense in patches as shown in Figures 1–3, but the greater mass of absorbed material (not illustrated) appeared a much paler blue with denser centres, gradually fading away towards the periphery of each region of absorption.

This effect was met with by Steudel (1912) when investigating absorption in the insects and is well illustrated by him. He describes the appearance in the following words: "Unterhalb des Kernes erscheint vielfach das Plasma selbst (ob nur scheinbar oder in Wirklichkeit, ist zweifelhaft) diffus blau gefärbt. Im diffusen Plasma liegen die Eisenkörnchen in allen

Grössen, teils deutliche Flecken, teils Punkte, teils kaum als solche zu unterscheidende feinste Pünktchen, die einen allmählichen Ubergang zu der erwähnten diffus bläulichen Grundfärbung bilden."

It is interesting to note that, though the chitinous lining of the intestine in Ligia is not perforated, yet absorption occurs very largely in this region of the alimentary canal. This can best be seen in Figures 2 and 3, Plate I, in which the absorbed iron is shown in actual transit through the chitinous layer.

One is struck by the resemblance between the relationship of this layer to the underlying epithelium and that of the peritrophic membrane to the absorptive epithelium in insects.

Steudel considers that the peritrophic membrane should be regarded as an organ of protection and compares it thus with the filter of Astacus. He states, moreover, that it allows only dissolved food to come into contact with the epithelium. The chitinous membrane in Ligia appears to function in an exactly similar way and to be analogous to the peritrophic membrane of the insects.

One further point of interest might be noted. McMurrich (1896, p. 93) remarks on the vacuoles "appearing as more or less extensive blisters of the epithelium" which he noticed on the inner surface of the epithelium of the "midgut" in the Isopods he examined. This peculiar condition was met with to a very great extent in Ligia after feeding, suggesting that it is associated with the absorptive processes. Its true significance is yet to be discovered.

7. SUMMARY.

1. Ligia is an omnivore, though normally feeding on Fucus. Portions of food are cut off by the mandibles and passed into the œsophagus. Its feeding period is limited.

2. The foregut is provided with a number of ampullæ and lamellæ which are furnished with spines and bristles and are so arranged as to form a filter for the separation of the liquid portion of the food from the solid particles.

3. A second filter is found in the floor of the foregut protecting the entrance to the hepato-pancreas.

4. A ventral valve is present preventing the entry into the hepato-pancreas of solid food from the intestine.

5. The hepato-pancreas consists of three pairs of tubules provided with a muscular network for producing contractions. The epithelium possesses discrete cells.

6. The intestine extends from the point of entry of the hepato-pancreas

into the foregut, to the rectum. Its epithelium is a syncytium lined throughout by a homogeneous layer of chitin. No typhlosole is present.

7. The rectal epithelium is syncytial, chitin lined and muscular.

8. Food entering the foregut is subjected to pressure which forces liquid through a filter, whence it passes into the hepato-pancreas.

9. The solid food is passed back, mixed with secretion from the hepato-pancreas and further pressed to expel liquid which passes through a second filter into the hepato-pancreas.

10. This is further aided by the tubules of the hepato-pancreas which force the secretion into the lumen of the gut and withdraw liquid by rhythmical contraction and relaxation.

11. The functioning of the foregut and associated organs appears to be designed for quick extraction of nutriment from the food.

12. The pH of the foregut averages 6·3 ; that of the hepato-pancreas, 6·0 ; of the intestine, 6·5 ; and of the rectum, 6·2.

13. The digestive enzymes are secreted by the hepato-pancreas ; none is secreted by the intestine.

14. The enzymes act readily on most carbohydrates, proteins and fats.

15. No cellulase is present, nor any enzyme which will act on pentosans.

16. The range of activity of the sucroclastic enzymes lies between pH 5 and pH 7 ; the optimum occurs between pH 5·65 and pH 5·8.

17. The proteoclastic enzymes are more powerful than the sucroclastic.

18. The range of activity for the liquefaction of gelatine lies between pH 5·35 and pH 8·5, with optima about pH 5·45 and pH 8·4.

19. Digestion of blood fibrin proceeds most rapidly at pH 6·4 and pH 8·4.

20. The range of activity for the digestion of peptone lies between pH 5·6 and pH 8·8 ; the optimum condition of pH being at 6·4. No second optimum was found.

21. The existence of an optimum at pH 8·4 probably indicates the presence of an autolytic enzyme.

22. Absorption was demonstrated by feeding with ferrum oxydatum saccharatum, and occurs in the epithelium of both the hepato-pancreas and intestine.

23. The appearance of the absorbed iron in the intestine was diffuse and resembled that described by Steudel in insects.

24. An analogy is suggested to exist between the chitinous membrane lining the epithelium of the intestine of Ligia and the peritrophic membrane lining the same region in the insects.

I wish to thank Dr. C. M. Yonge for his help throughout the course of this investigation and for reading the manuscript before publication.

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EXPLANATION OF PLATE.

FIG. 1.—Portion of syncytial epithelium of anterior region of intestine in longitudinal section, showing region of absorption demonstrated by iron saccharate. 24 hours after feeding. × 400.

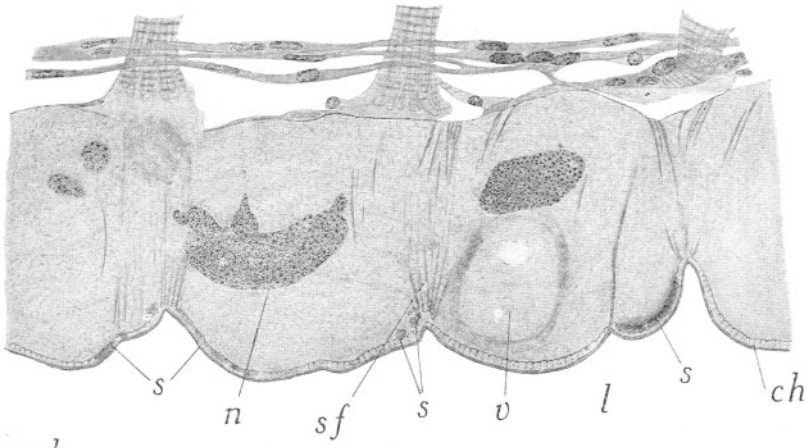
FIGS. 2 AND 3.—Portions of Fig. 1 enlarged to show absorption of the saccharate through the chitin. × 815.

FIG. 4.—T.S. through hepato-pancreatic tubule, showing absorption of iron saccharate. × 100.

FIG. 5.—Cell from epithelium of hepato-pancreas, demonstrating absorption of saccharate. × 425.

ABBREVIATIONS USED IN PLATE.

ch., chitin ; *l.*, lumen ; *n.*, nucleus ; *nl.*, nucleolus ; *s.*, iron saccharate ; *s.f.*, "supportive fibres" ; *v.*, vacuole.



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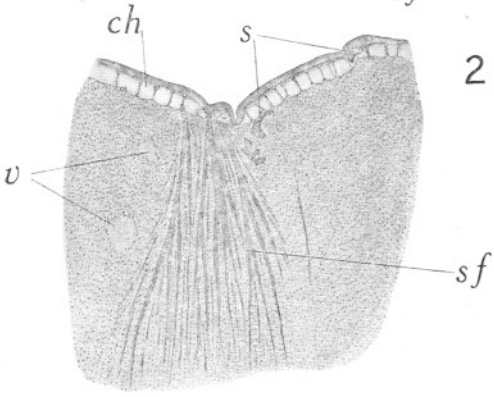

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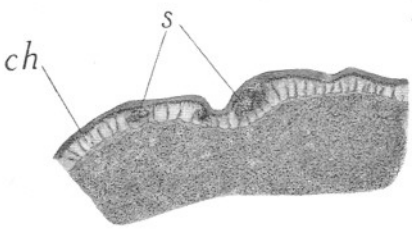

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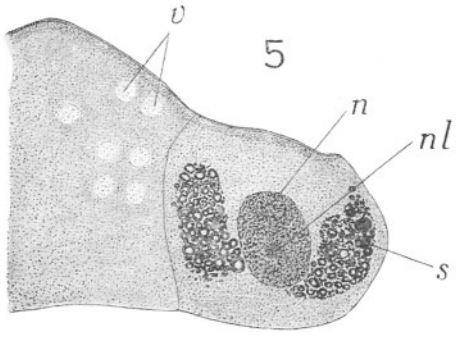

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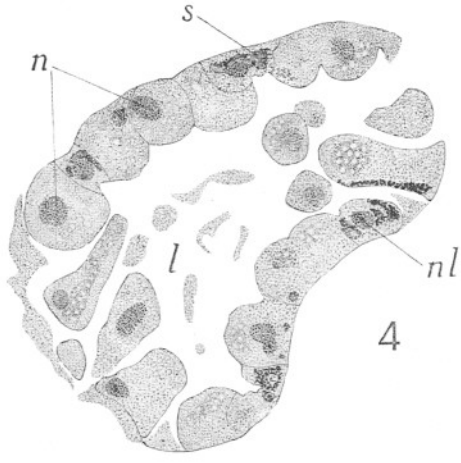

4

A Study of the Respiration and of the Function of Hæmoglobin in *Planorbis corneus* and *Arenicola marina*.

By

Mabel A. Borden, M.A.

This work was carried out while holding an 1851 Exhibition Scholarship.

With 15 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE presence of hæmoglobin in the invertebrates has generally been found to be correlated with a habitat at times deficient in oxygen; the function assigned to the hæmoglobin being either that of storing oxygen, or of transporting it at low pressures. Thus Leitch (1916) has shown that in Planorbis the hæmoglobin is used only when the oxygen pressure is so low that the necessary amount cannot be supplied by diffusion. Barcroft and Barcroft (1924) suggested that in Arenicola it acts "as a reserve store which the organism can use up when it has not access to sea-water." This

indicates that in Planorbis and Arenicola, both of which have hæmoglobin dissolved in the plasma and are adapted to environments in which the oxygen concentration must at times be considerably reduced, the function of the hæmoglobin is different.

Hill (1913–24), Meyerhof (1920) and others have shown that the fundamental mechanism of muscular contraction is an anaerobic one, by which nearly the whole of the energy is liberated in the breakdown of carbohydrate, as glycogen, to lactic acid ; while the recovery process, consisting of the restoration of a portion of the lactic acid to glycogen, is aerobic. It has also been proved that when an isolated muscle is stimulated in an oxygen-free atmosphere lactic acid accumulates, and the tissue goes into debt for oxygen, the magnitude of the debt being proportional to the quantity of the acid formed.

Slater and Davis (1926–28) have demonstrated that this phenomenon occurs also in the whole animal. They found that the common cockroach and the earthworm, when subjected to oxygen lack, went into debt and by this means were able to survive short periods of anaerobiosis.

It appears, therefore, that there are two mechanisms by which an animal can obtain the oxygen necessary for its life. Firstly, the circulatory system functioning under normal conditions ; secondly, the initial phase of muscular metabolism providing an emergency mechanism by which the animal is tided over short critical periods of oxygen deficiency.

In view of these facts it seemed of interest to study the respiration of, and the function of hæmoglobin in, Planorbis and Arenicola, and to find more exactly the significance of the hæmoglobin. Is it for the latter a storer of oxygen and for the former a transporter at low pressures, or are the animals able to go into oxygen debt and, therefore, not dependent on their blood for a supply of oxygen during anaerobiosis ?

EXPERIMENTAL METHODS AND RESULTS.

A. *PLANORBIS CORNEUS.*

1. Normal Rate of Respiration.

The respiratory rate was measured by observing the oxygen intake in Barcroft's differential blood gas apparatus (1914). Small snails weighing about 0·5 gm. were used, one animal being used for each experiment. The snail, having been first lightly dried to remove moisture and organic matter from the shell, was weighed and placed in the right-hand flask of the apparatus. About 2 c.c. of water were added to each flask, a slight additional amount being put in the left-hand flask to compensate for the volume of the snail. In the reservoir of each was placed a small piece of caustic soda to absorb carbon dioxide. The flasks were then attached to the U-shaped manometer and the apparatus set shaking in a water-bath,

the temperature of which closely approximated that of the room and was constant to within 0·5° of 15° C. The oxygen intake was recorded every 15 minutes for several hours, ample time having been first allowed for conditions of equilibrium to be established within the apparatus.

The average oxygen intake for a number of animals was 0·026 c.c. per gm. per hour. The results from which this figure was obtained are expressed in Table I.

TABLE I.

No. of Animal.	Weight gm.	Oxygen consumption in c.c. per hour. 1	2	3	4	5	6	Average in c.c. per gm. per hr.
1.	0·49	0·022	0·015	0·021	0·017	0·024	0·019	0·040
2.	0·62	0·016	0·014	0·014	0·012	0·018	—	0·024
	0·65	0·017	0·021	0·014	0·017	0·013	0·016	0·025
	0·66	0·017	0·017	0·010	0·018	0·015	0·017	0·024
3.	0·68	0·020	0·015	0·020	0·022	0·020	0·020	0·029
	0·69	0·028	0·024	0·027	0·027	0·020	0·022	0·036
	0·71	0·013	0·011	0·016	0·012	0·020	0·014	0·020
4.	0·68	0·017	0·013	0·014	0·015	0·013	0·012	0·021
5.	0·70	0·012	0·011	0·013	0·013	—	—	0·018

It may be seen from the above Table that the oxygen consumption of a snail weighing 0·49 gm. was 0·040 c.c. per gm. per hour, while that of snails weighing on the average 0·67 gm. was 0·024 c.c. per gm. per hour, or 0·016 c.c. less than that of the smaller animal. It is thought that, as in the case of the cockroach (Davis and Slater, 1926), the apparent relationship between the body weight and oxygen consumption is in reality a correlation between age and oxygen intake, the younger animals having a quicker metabolic rate. The oxygen consumption of two snails, Nos. 2 and 3 respectively, was measured for each on three different occasions. The results for each are fairly uniform.

Figure 1 represents the oxygen intake measured at 15° C. over a period of six hours, for a snail weighing 0·64 gm.

2. The Blood Volume.

Estimations of the blood volume were made in a Duboscq colorimeter. The snail was bled as thoroughly as possible, the blood being collected from the pulmonary cavity into which it had been driven by an artificially stimulated contraction of the foot. About 0·5 c.c. was thus obtained.

A known volume of blood was diluted to 10 c.c. with distilled water and used as the standard solution in the colorimeter. The rest of the snail was chopped up under a known volume of water to extract the blood from its tissues, and the wash-water was then filtered from the macerated

tissue by suction through a Buchner filter. Ten cubic centimetres of the diluted blood were then matched against the standard solution in the colorimeter, and the concentration of hæmoglobin in the sample of wash-water estimated according to the formula $C_1 = \frac{R_2}{R_1} \times C_2$, where R_1 and R_2 are the readings on the colorimeter of the unknown and standard solutions; C_1 and C_2 their respective concentrations. Care was taken always

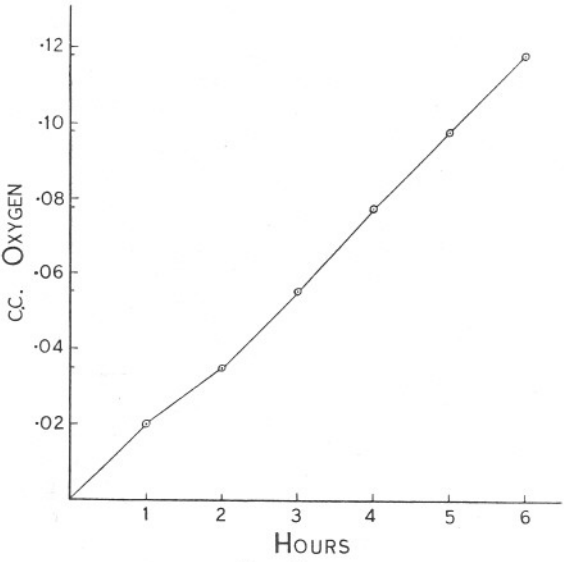

Fig. 1.

to use the same calibrated pipettes for measuring the solutions. The data of one estimation are tabulated as follows :—

TABLE II.

Showing Estimation of Total Blood in One Snail.

Weight of snail 1·61 gm.
Undiluted blood 0·42 c.c. made up to 4·2% aqueous solution.
Wash-water 18·65 c.c.

Colorimetric Readings.

No.	R_2	R_1	C_2	C_1
1.	1·27	1·65	4·2	3·23
2.	1·13	1·48	4·2	3·21
3.	1·08	1·37	4·2	3·31
4.	1·22	1·60	4·2	3·20
5.	1·23	1·54	4·2	3·35

Mean Value for C_1, 3·26%, therefore in 18·65 c.c. wash-water there is 0·61 c.c. blood, and the total volume of blood in the snail is 1·03 c.c.

The results of the experiments in Table III show the average blood volume to be 0·58 c.c. per gm.

TABLE III.

No.	Weight of Snail in grams.	Volume of Blood in c.c.	Volume of Blood per gm. of Snail.
1.	0·75	0·47	0·63
2.	1·10	0·74	0·67
3.	1·14	0·86	0·75
4.	1·44	1·00	0·69
5.	1·54	0·79	0·40
6.	1·56	0·98	0·63
7.	1·58	0·68	0·43
8.	1·61	1·03	0·65
9.	1·83	0·83	0·45
10.	1·90	0·98	0·51

3. The Oxygen Capacity of the Blood.

The oxygen capacity of the hæmoglobin was estimated by the ferricyanide method in Barcroft's apparatus and at a later date additional experiments were made in Van Slyke's manometric gas apparatus.

The experimental procedure was similar to that employed by Barcroft (1914), and Van Slyke and Neill (1924) respectively. A slight modification of the Barcroft apparatus was, however, introduced by using a small glass tube, as suggested by Keilin (1928, p. 217), to hold the ferricyanide solution in place of the reservoir in each flask more generally used for that purpose. The tube was hooked on to the reservoir in such a manner that the contents, and if desirable the tube itself, could be upset into the flask. This proved a more convenient method of bringing the ferricyanide in contact with the blood as, owing to the small amount of reagent used, great difficulty was formerly experienced in overcoming the effect of surface tension in the narrow reservoir.

The snails were bled as described above, undiluted blood from several individuals being mixed and well shaken to saturate the blood with oxygen. One cubic centimetre of the mixture was used for each measurement of the oxygen capacity.

The experiments showed that in 1 c.c. of blood the amount of oxygen held by the hæmoglobin was approximately 0·013 c.c., the total oxygen content of the blood 0·014 c.c. The results from which these values were obtained are given in Table IV.

TABLE IV.

ESTIMATIONS MADE ON 1 C.C. OF BLOOD.

	Combined Oxygen by Barcroft's Apparatus in c.c.	Total Oxygen Capacity of Blood by Van Slyke's Apparatus in c.c.
	0·011	0·015
	0·010	0·014
	0·013	0·014
	0·011	—
	0·015	—
	0·016	—
Mean	0·013	0·014

The length of time that the total oxygen content of the blood will last the animal was calculated as follows :—

Blood volume per gm. of snail	0·581 c.c.
Oxygen content per c.c. blood	0·014 c.c.
Oxygen capacity of blood per gm. of snail	0·0081 c.c.
Oxygen consumption per gm. per hour	0·026 c.c.

Hence oxygen content of blood will last the animal 18 minutes.

4. SPECTROSCOPIC EXAMINATION OF THE HÆMOGLOBIN.

(*a*) *Under Anaerobiosis*

Although the oxygen reserve of the blood and the extent to which it serves as a store of oxygen had been estimated, it seemed desirable to make a direct observation of the blood pigment during anaerobiosis. Stated briefly, the method of obtaining the information consisted of placing a number of animals in an inert gas ; obtaining and examining a sample of blood at frequent intervals ; noting at what time the bands of oxyhæmoglobin were replaced by that of reduced hæmoglobin. The examination of the blood was in every instance made under anaerobic conditions.

The apparatus for examining the blood was comprised of a micro-spectroscope fitted to a compound microscope. This, with the animals, was housed in a large box into which a steady flow of nitrogen could be maintained. Figure 2 illustrates the general structure of the box, the more particular features of which, however, require a brief description.

The back and upper half of the front were of glass, the rest of the box being made of wood, one inch in thickness. The top was removable to allow for the entrance of the microscope which, when once in place, was not withdrawn until the conclusion of the investigation. The top could be screwed down firmly and the junction between it and the rest of the box

was made air-tight by means of putty. To allow for focussing the microscope, the draw-tube projected through an opening in the top, the opening being lined with baize, so that the tube fitted snugly and yet could be moved up or down. At the bottom right-hand side was situated an inlet tube for nitrogen, the outlet being located on the opposite side near the top. Near the inlet tube a small door was cut, and by means of this opening the animals were admitted to and withdrawn from the box. The aperture into which the door fitted was lined with baize, and during the experiments when the door was shut the outside was covered with adhesive tape to prevent the leakage of nitrogen through the cracks, the pressure of nitrogen inside the box tending to be greater than atmospheric. In the lower half of the front two fairly large holes were made and over each the wrist part of a rubber glove was stretched and held in place by being firmly nailed, between two strips of elastic, to the wood. Seccotine was then run round the outside edge of the join which proved to be air-tight. By means of the gloves it was possible, without letting in any air, to put one's hands inside the box and thus manipulate the animals. Both the inner and the outer surfaces of the box were painted, the inside also being coated with paraffin wax.*

The nitrogen used for producing an oxygen-free atmosphere was filtered on its way to the box through alkaline hydrosulphite and alkaline solutions of pyrogallol to remove the traces of oxygen usually present in the commercially prepared gas. At the commencement of each experiment the air inside the box was swept out with nitrogen for half an hour or longer, the outlet tube was then closed, the door opened and the animals quickly placed inside. A constant flow of nitrogen was maintained throughout the experiment, the excess escaping around the draw-tube of the microscope. The atmosphere in the box was frequently tested for oxygen by Haldane's gas analysis apparatus. A connection between the latter and the outlet tube had been established with pressure tubing. Tests showed that the atmosphere in the box was never entirely anaerobic, the partial pressure of oxygen being approximately 0·5 mm.

At frequent intervals separate snails were bled directly on to a clean glass slide, and the blood examined for the presence of reduced hæmoglobin. The whole operation of bleeding the snail and noting the condition of the hæmoglobin took only a few seconds.

On account of the ability of Planorbis to hold a quantity of air in its lung it was necessary, before placing the snails in the nitrogen-box, to expose them for a few minutes to a vacuum. The investigation of the time taken for the blood to be reduced was also performed on snails in

* I am indebted to the Department of Botany, University College, London, for the use of the microspectroscope and to Mr. A. G. Nicholls for the construction of the nitrogen-box.

which the air had not been removed from the lung. Comparison of the results of these two types of experiments revealed the extent to which the lung supplemented the blood as a store for oxygen.

The results are given in Figure 3.

A survey of the investigation shows that for the experiments in which the snails were without air in their lungs the hæmoglobin was fully reduced, in some instances after subjection to only 10 minutes anaerobiosis, and in all cases some reduction had occurred; while after 25 minutes it was,

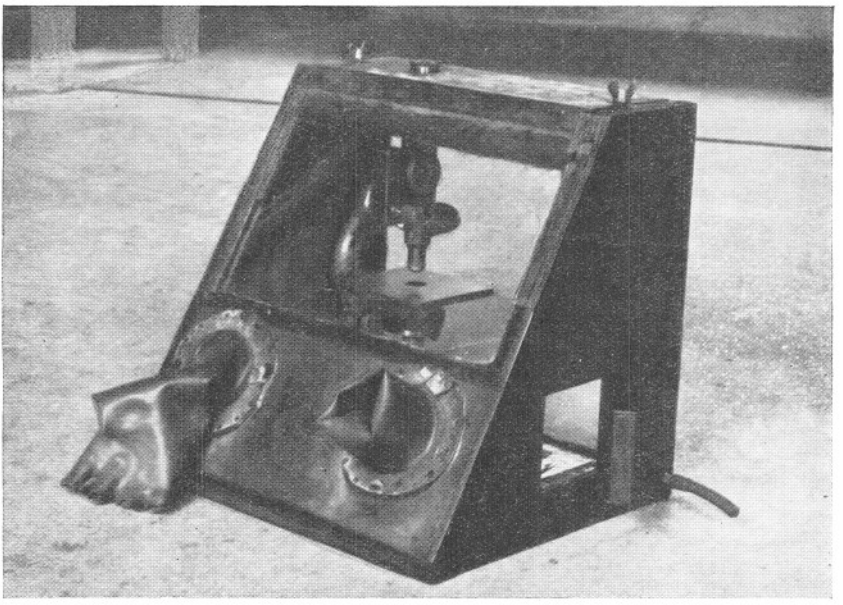

FIG. 2.

with two exceptions, fully reduced. If, however, the snails were used with their lungs full of air, the blood remained in the form of oxyhæmoglobin for 40 minutes, while between 40 and 80 minutes both the oxy- and reduced forms of hæmoglobin were found. After 80 minutes it was, with a few exceptions, completely reduced.

It is, therefore, clear that the total oxygen supply in the blood will last from approximately 20 to 25 minutes, and this is in fairly close agreement with the theoretically determined value of 18 minutes. The air in the lung will supply oxygen for 40 minutes, so that altogether Planorbis is well able to endure an hour's subjection to oxygen deficiency.

The experiments also substantiate Leitch's evidence that the combined oxygen is the last to be used by the animal but, whereas she found only

enough for three minutes and did not think it constituted a reserve, this investigation indicates that it may indeed be a reserve of some importance, since the oxygen supplied by the blood considerably prolonged the animal's survival in an anaerobic atmosphere.

(b) Under Aerobiosis following Anaerobiosis.

It was important with reference to subsequent oxygen debt experiments to ascertain if the animals, having been exposed to an anaerobic atmosphere, oxidised their hæmoglobin immediately on admittance to air. If

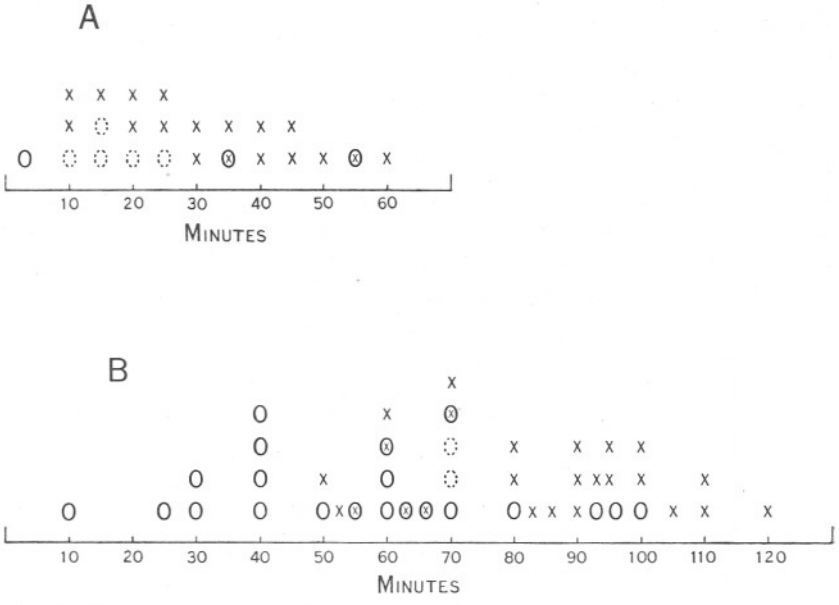

FIG. 3.—Diagram illustrating the time taken for the reduction of oxyhæmoglobin in Planorbis; A, in snails in which air had been removed from lungs; B, in snails with air in lungs. Separate animals were examined at frequent intervals. O, indicates presence of oxyhæmoglobin; ◌, presence of partially reduced hæmoglobin; ⊗, presence of almost completely reduced hæmoglobin; X, presence of reduced hæmoglobin.

N.B. The condition designated as partially reduced hæmoglobin was that in which the bands of oxyhæmoglobin were very faint; that of almost completely reduced hæmoglobin in which the faint oxyhæmoglobin bands were almost entirely masked by a weak reduced hæmoglobin band.

oxidation were not almost instantaneous the amount thus used would be included in the oxygen intake, thus giving a false value to the oxygen debt.

These experiments were, therefore, undertaken to measure the time taken by the animals for oxidising their hæmoglobin. For this purpose it was again necessary to carry out in the nitrogen-box the procedure of

exposing the animals to oxygen deficiency until the blood was reduced. They were then admitted to air in groups of two for varying periods, the blood being, however, collected and examined under anaerobic conditions. An additional piece of apparatus, a small stoppered bottle, placed on the floor of the nitrogen-box, was so arranged by means of an inlet tube that it could be connected directly with either the nitrogen supply or compressed air, while an outlet tube, extending to the exterior of the box, provided an escape for whatever gas was run into the bottle.

The experimental technique was as follows : nitrogen having been run into the box and into the bottle sufficiently to expel the air, the outlet tubes were closed and the animals placed in the box, the flow of nitrogen being continuous.

The blood from several snails was inspected until the hæmoglobin was found to be reduced ; two were then exposed to a current of air in the bottle for a definite time, at the end of which they were removed and the blood examined. Before removing the snails, however, the air in the bottle was expelled by a flow of nitrogen so that there was no introduction of air into the nitrogen-box. The details of a typical experiment are given in Table V, and the collective results in Figure 4.

TABLE V.

R indicates reduced hæmoglobin ; O, oxyhæmoglobin.

No.	Period of Anaerobiosis in min.	Time in Air in min.	Condition of Hæmoglobin.
1.	60	0	R
2.	62	0	R
3.	65	2	R
4.	65	2	R
5.	90	5	R
6.	90	5	R
7.	105	10	R
8.	105	10	R
9.	135	30	O
10.	135	30	O

During the above experiment the partial pressure of oxygen in the box was estimated after 45, 75, and 120 minutes, the values obtained being respectively 0·60, 0·70, and 0·53 mm.

From an examination of Figure 4 it will be seen that Planorbis does not oxidise its hæmoglobin immediately on exposure to air. Oxidation starts after 10 minutes and is complete within 20 minutes.

5. Oxygen Debt Experiments.

This investigation was undertaken to find if Planorbis went into oxygen debt when the period of anaerobiosis exceeded that provided for by its reserve of oxygen. The evidence so far obtained indicated that the reserve was sufficient for approximately one hour.

The presence of an oxygen debt following an anaerobic period would be marked by an increase in the oxygen consumption equivalent to the oxygen used by the animal at rest during the same period in air.

The method of measuring the oxygen debt in these experiments was as follows: one snail was weighed and placed in the Barcroft apparatus with

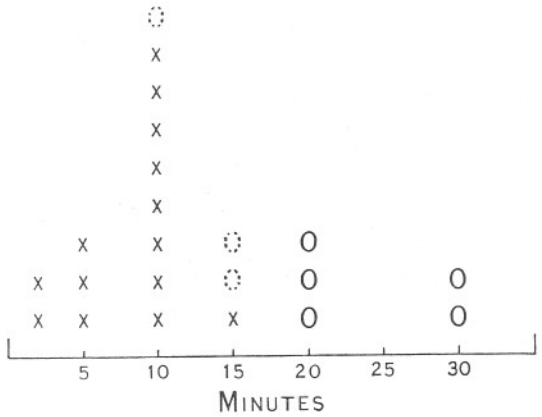

Fig. 4.—Diagram illustrating the time taken for oxidation of the hæmoglobin in separate animals (Planorbis). O, represents the presence of oxyhæmoglobin; ◌, the presence of partially oxidised hæmoglobin; X, the presence of reduced hæmoglobin.

one cubic centimetre of water and some caustic soda to absorb carbon dioxide. The apparatus was kept shaking in a water-bath, at 16° C. Observations were made on the animal's oxygen intake over a period of two to three hours, then by means of pressure tubing connecting the apparatus with the nitrogen supply, suction pump and pressure gauge the apparatus was emptied of air and refilled several times with nitrogen, the snail being left in this anaerobic atmosphere for whatever length of time was required. At the completion of the anaerobic period the apparatus was refilled with air and the oxygen intake again noted for several hours. Commercial nitrogen, before being introduced into the apparatus, was filtered through alkaline hydrosulphite and washed in several alkaline solutions of pyrogallol. Although these precautions were taken to purify the gas a trace of oxygen, amounting to a partial pressure of about 0·5 mm.,

was always present. This did not, however, appear to upset the experiments.

It is important to remember when interpreting the results, that the observed increase in respiration will be due in part to the oxidation of the hæmoglobin and that this amount must, therefore, be subtracted before the true value of the oxygen debt can be ascertained.

Since the average blood volume was estimated at 0·58 c.c. per gm. of snail; the oxygen capacity of the hæmoglobin at 0·013 c.c. per c.c. of

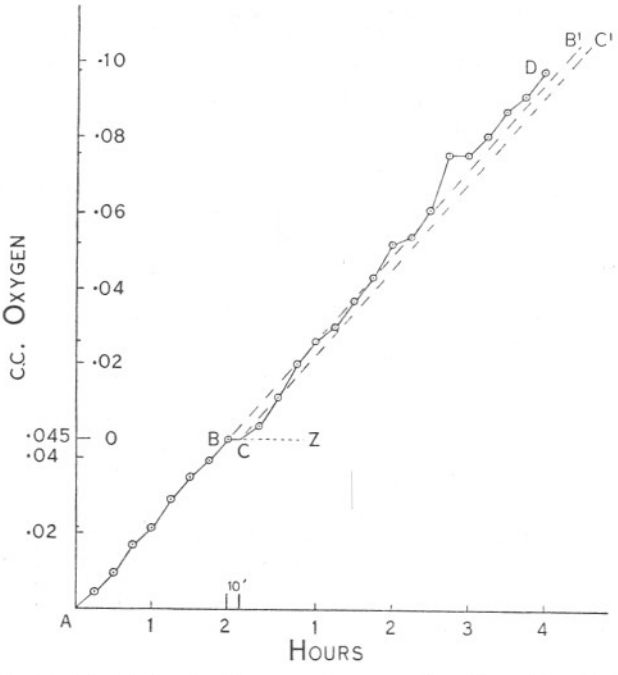

Fig. 5.—Graph showing the oxygen consumption of a snail weighing 0·48 gm. The period of experimental anaerobiosis was 1 hour; the period of true anaerobiosis, 10 minutes; temperature 16·5° C.

blood, it follows that the combined oxygen of the hæmoglobin, 0·0075 c.c. per gm. of snail, will be the amount needed for the oxidation of the hæmoglobin. It was also necessary to calculate the time the combined oxygen would last the animal, this being done for each on the basis of the normal oxygen intake during the experiment. This amount, plus 40 minutes for the supply of oxygen in the lung, was then deducted from the period of experimental anaerobiosis. Thus, if a snail were subjected to two hours oxygen deficiency and the hæmoglobin estimated to have enough oxygen for 20 minutes, the period of true anaerobiosis would be one hour; and from the observed oxygen intake following anaerobiosis was subtracted the

amount needed for oxidation of the hæmoglobin. These corrections were applied to all experiments.

Figures 5, 6, 7, and 8 illustrate typical experiments. The line AB shows the normal oxygen intake before anaerobiosis ; BZ the period of experimental anaerobiosis ; BC the period of true anaerobiosis estimated by deducting from BZ the length of time for which the oxygen in the lung

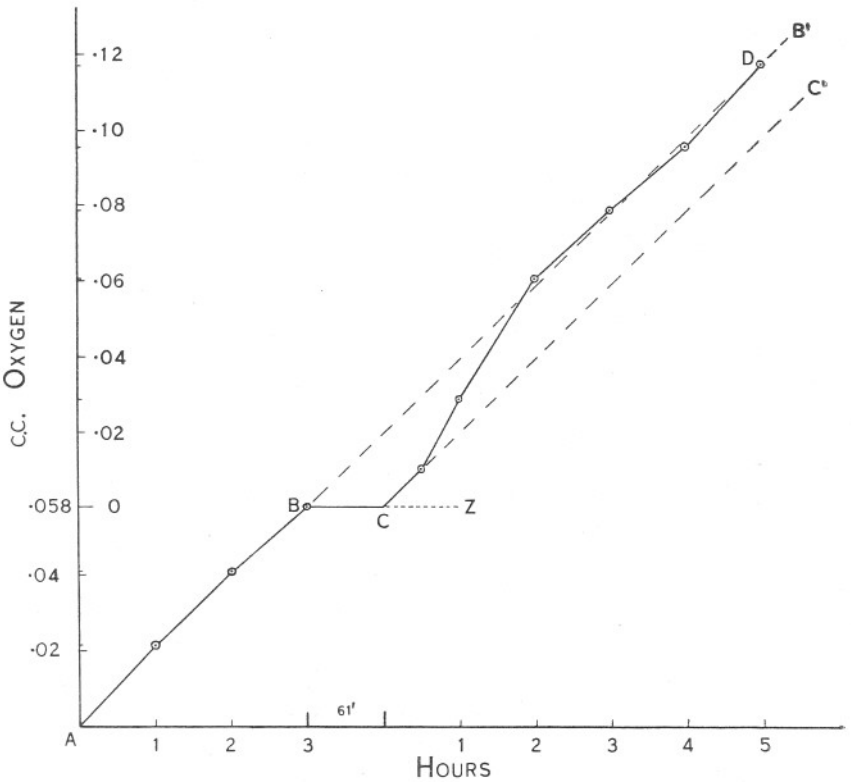

FIG. 6.—Graph showing the oxygen consumption of a snail weighing 0·82 gm. The period of experimental anaerobiosis was 2 hours ; the period of true anaerobiosis, 61 minutes ; temperature 15° C.

and that combined in the blood would last the animal. The broken line BB′ represents the amount of oxygen it is assumed the animal would have used had it not been subjected to anaerobiosis ; the broken line CC′ is that along which post-anaerobic respiration would have proceeded had it been equal to the normal resting value. The line CD shows the oxygen consumption after anaerobiosis less the estimated amount needed for oxidation of the hæmoglobin.

It will be seen from Figures 5, 6, and 7 that when the anaerobic period

has ended, the animal takes up more oxygen than it normally requires, the excess being equal to the amount it would have used during the time it was in nitrogen. Figure 8 illustrates an experiment in which the period of anaerobiosis did not extend beyond the time for which the animal was provided with oxygen by its lung and there was, therefore, no debt.

The results show that for short anaerobic periods up to approximately one hour, the extent to which anaerobiosis was carried, Planorbis went

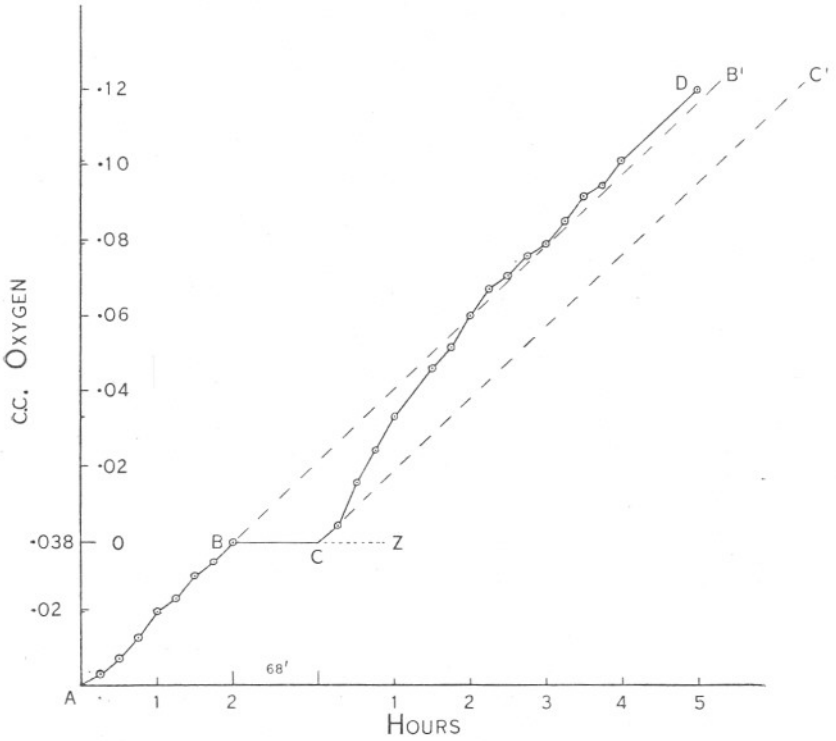

Fig. 7.—Graph showing the oxygen consumption of a snail weighing 0·50 gm. The period of experimental anaerobiosis was 2 hours; the period of true anaerobiosis, 68 minutes; temperature 16° C.

into debt for oxygen. The magnitude of the debt was proportional, within the limits of experimental error, to the time of anaerobiosis; the period of recovery was longer.

6. Discussion.

Planorbis inhabits rivers, canals, ponds and marshes, the water of which may be deficient in oxygen during periods of drought and stagnation. It has been shown by Leitch (1916) that normally enough oxygen is supplied to the snail by diffusion through the surfaces exposed to the

water. When the oxygen pressure falls below that necessary for diffusion the hæmoglobin is reduced and, to facilitate the oxidation of the blood, the animal renews the air in its lung by rising frequently to the surface. The present investigation shows that the combined oxygen is sufficient

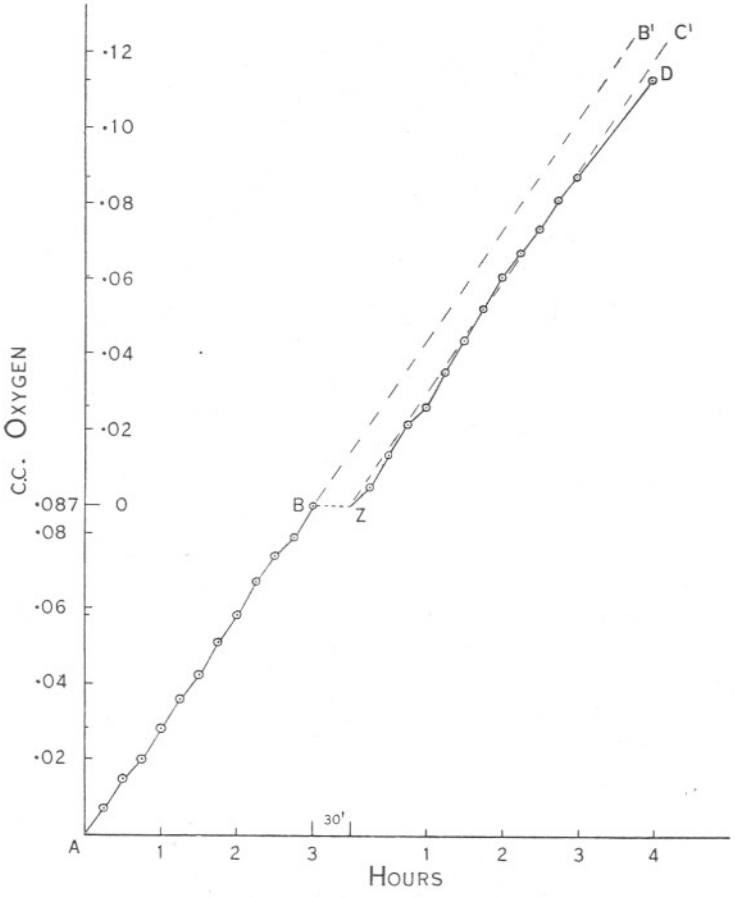

Fig. 8.—Graph showing the oxygen consumption of a snail weighing 0·50 gm. The period of experimental anaerobiosis was 30 minutes. There was no period of true anaerobiosis. Temperature 16° C.

for approximately 25 minutes. Leitch's evidence that the combined oxygen is the last to be used by the animal is further substantiated.

Barcroft (1928) has shown that the main dissociation of Planorbis blood occurs between oxygen pressures of 1 to 10 mm. of Hg.

It is concluded that the hæmoglobin functions primarily as a transporter of oxygen at low pressures. The combined oxygen may be considered as a reserve only in the sense that it supplements the oxygen held

in the lung, with the result that the animal is for a time independent of reduced oxygen pressures in the water. The significance of the hæmoglobin is, therefore, that it furnishes the means whereby oxygen is secured and transported to the tissues at times of lowered oxygen pressure.

The importance of the lung should not be overlooked as, in addition to facilitating the oxidation of the blood, it provides a mechanism by which the animal can obtain oxygen as long as it has access to air.

The investigation establishes the ability of Planorbis to put up an oxygen debt. Planorbis appears, therefore, to be especially well adapted for survival in an environment at times deficient in oxygen.

B. *ARENICOLA MARINA.*

1. Normal Rate of Respiration.

The experimental procedure for the estimation of the oxygen consumption of Arenicola differed only slightly in detail from that already described for Planorbis. Measurements were carried out in Haldane's blood gas apparatus which was kept shaking in a water-bath, the temperature of which ranged between 10° and 12° C., the variation of the temperature for each experiment not exceeding 0·5° C. Carbon dioxide was absorbed by small strips of filter paper moistened with 10% sodium hydroxide solution. The measurements were made on worms varying in weight from 2 to 9 gm., one worm being used at a time and readings taken over a period of six hours. Except for rhythmic contractions of the body wall the worm remained quite still.

The results of six determinations are given in Table VI and show that the average oxygen consumption is of the order of 0·031 c.c. per gm. per hour. The large animals appear to use less oxygen than the small, but yet adult, animals. It seems, therefore, that in the case of Arenicola there may be a relationship between body weight and oxygen intake.

TABLE VI.

No. of Animal.	Weight in gms.	Oxygen Consumption in c.c. per hour. 1	2	3	4	5	6	Average, c.c. per gm. per hr.
1.	2·4	0·080	0·070	0·085	0·100	0·097	0·098	0·037
2.	3·6	0·170	0·150	0·150	0·152	0·118	0·132	0·040
3.	4·3	0·130	0·136	0·140	0·100	0·114	0·115	0·028
4.	5·2	0·125	0·100	0·120	0·090	0·115	0·090	0·020
5.	7·1	0·260	0·240	0·206	0·250	0·220	0·220	0·034
6.	9·5	0·315	0·273	0·252	0·265	0·255	0·245	0·028

In Figure 9 the general character of the results is exemplified by the curve which represents the oxygen used per hour at 11·6° C, by a worm weighing 5·2 gm.

2. Blood Volume.

The blood volume of Arenicola was determined by the same colorimetric method as that outlined for Planorbis. The manner of bleeding the worm was as follows : the worm was opened along the mid-dorsal line to expose the body-cavity : the cœlomic fluid allowed to drain out and the cavity dried as thoroughly as possible : the heart and blood vessels were punctured and the escaping blood removed from the body-cavity with a pipette. In this way it was possible to obtain about 0·5 c.c., the rest of

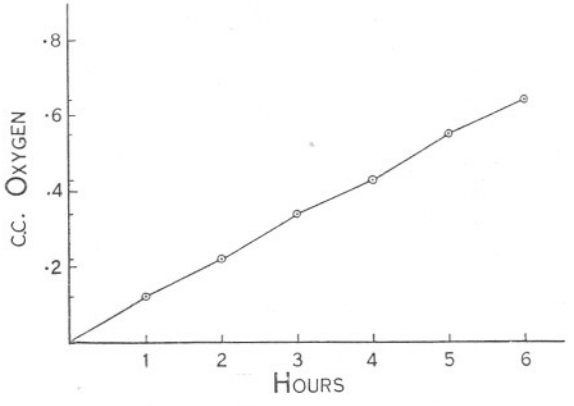

Fig. 9.

the blood being extracted by suction through a Buchner filter after the chopped-up worm had been left standing for some time under water.

In Table VII are given the results from which the average blood volume was estimated to be 0·382 c.c. per gm.

TABLE VII.

No.	Weight of Worm gm.	Volume of Blood c.c.	Volume of Blood per gm. of Worm.
1.	6·65	2·57	0·386
2.	6·87	3·43	0·500
3.	7·49	2·33	0·312
4.	7·70	2·56	0·333

It cannot be claimed that the colorimetric method is absolutely accurate and these results should be considered to be only roughly approximate to the true value. The presence of the black pigment from the epidermis rendered accurate colour comparison difficult.

3. Oxygen Capacity of the Blood.

Estimations of the total oxygen content of Arenicola blood were carried out in the Barcroft and in the Van Slyke apparatus, the procedure being identical with that already described for the experiments on Planorbis blood.

The results given in Table VIII show the oxygen capacity of the hæmoglobin to be 0·087 c.c. per c.c. of blood, the total oxygen content 0·097 c.c. per c.c. of blood.

TABLE VIII.

Estimations made on 1 c.c. of Blood at N.T.P.

Combined Oxygen by Barcroft's Apparatus c.c.	Total Oxygen Capacity of Blood by Van Slyke's Apparatus c.c.
0·097	0·098
0·085	0·097
0·084	0·097
0·085	0·096
—	0·099
—	0·096
Mean 0·087	0·097

The length of time that the total oxygen content of the blood will last the animal may be calculated as follows :—

Blood volume per gm. of worm	0·382 c.c.
Oxygen content per c.c. of blood	0·097 c.c.
Oxygen capacity of blood per gm. of worm	0·037 c.c.
Oxygen consumption per gm. per hour	0·031 c.c.

Hence, oxygen content of blood will last the animal 71 minutes.

4. Spectroscopic Examination of the Hæmoglobin.

(*a*) *Under Anaerobiosis.*

Arenicola blood was examined for the same purpose and by the same method as described for Planorbis. The worms were dried lightly on filter paper before being placed in the nitrogen-box. The process of obtaining the blood was as before, the worms being opened longitudinally, the blood vessels cut and a drop of blood transferred from the body-cavity to a glass slide and covered with a cover slip. The results are expressed in Figure 10.

The first sign of reduction occurred after 20 minutes, while after half an hour the hæmoglobin, although not completely reduced, was as nearly reduced as it was ever found. The analysis of the nitrogen atmosphere in the box showed a partial pressure of oxygen of about 0·5 mm., which

may perhaps explain the failure of the hæmoglobin to appear completely reduced. The dissociation curve of Arenicola hæmoglobin, as given by Barcroft and Barcroft (1924), showed that at this pressure the oxygen saturation of the blood is about 8%.

Since the hæmoglobin was never found in a state of complete reduction

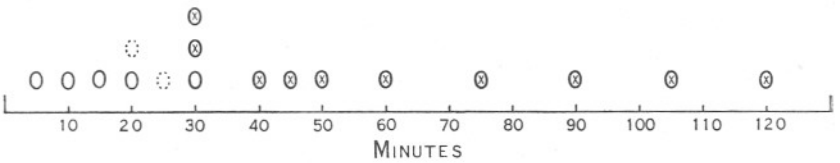

FIG. 10.—Diagram representing the time taken for the reduction of oxyhæmoglobin in Arenicola. Separate animals were examined at frequent intervals. O, indicates presence of oxyhæmoglobin; ⊙, presence of partially reduced hæmoglobin; ⊗, presence of almost completely reduced hæmoglobin.

it is impossible to arrive at any further conclusion concerning the time the oxygen supplied by the blood will last the animal. This investigation shows, however, that the supply is sufficient for at least 30 minutes.

(*b*) *Under Aerobiosis following Anaerobiosis.*

Figure 11 shows the results obtained for Arenicola, the methods being the same as those used for Planorbis and described above.

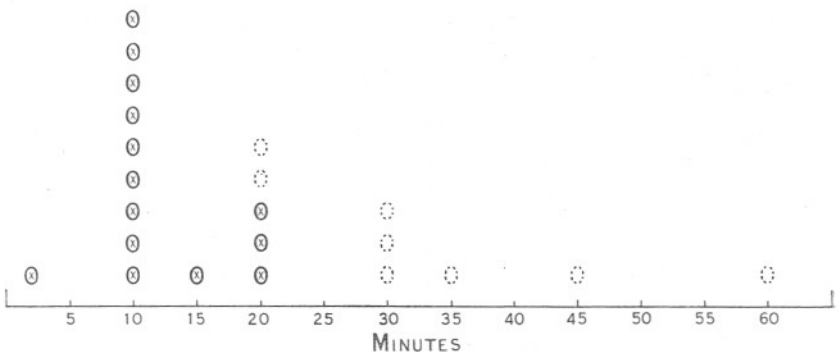

FIG. 11.—Diagram representing the time taken for the oxidation of the hæmoglobin in Arenicola. Separate animals examined at frequent intervals. ⊙, indicates that some oxidation has occurred though it is not complete; ⊗, presence of almost completely reduced hæmoglobin.

It is interesting to note that the hæmoglobin was still in the reduced state after 10 minutes exposure to air, while after 20 minutes, although some oxidation had occurred, well defined bands of oxyhæmoglobin were never found. The explanation for this may be that the temperature at which the experiments were conducted, 20° to 22° C., was higher than that of the

animal's normal environment at that time of the year, which was approximately 15°C. This, coupled with a fairly long exposure to almost complete anaerobiosis, injured the animals to such an extent that recovery did not take place during the time of the experiment.

5. Oxygen Debt Experiments.

Two series of experiments on the ability of Arenicola to put up an oxygen debt were made in the Barcroft apparatus. In the first, the weighed worm was placed in the respiration flask of the apparatus with 1 c.c. of sea-water, and a strip of filter paper moistened with 10% solution of NaOH, to absorb carbon dioxide, was placed in the reservoir, the anaerobic atmosphere being produced as before with nitrogen.

In the second series, hydrogen, washed through sodium hydrosulphite, pyrogallol and silver nitrate solutions, replaced nitrogen. No water was added, the flasks being simply rinsed with sea-water and used moist. Carbon dioxide was absorbed by a small rectangle of filter paper wet with 10% solution of KOH.

The measurement of the oxygen debt was made by observing the normal oxygen intake immediately before and after the period of oxygen lack, anaerobic conditions within the apparatus being attained as before. Analysis of the gas, whether nitrogen or hydrogen, revealed a partial pressure of oxygen of about 0·5 mm.

Observations made during the period of anaerobiosis showed that the volume of gas in the respiration flask gradually diminished, constant volume being attained after about 30 minutes, from which it was concluded that the worm used this small amount of oxygen and was not, therefore, under strictly anaerobic conditions until no more oxygen was available. In a few experiments constant volume was never attained and these were discarded. It was noted that the worm was capable of movement at the completion of the anaerobic period.

To estimate the period of true anaerobiosis allowance was made for the time taken by the worm to use the oxygen impurity in the apparatus and the combined oxygen in its blood. A mean value for the combined oxygen was obtained as follows :—

Volume of blood per gm. of worm	0·382 c.c.
Amount of oxygen combined with Hb per c.c. of blood	0·087 c.c.
Hence, amount of combined oxygen per gm. of worm	0·033 c.c.

The length of time that the combined oxygen will last is dependent on the animal's normal oxygen consumption.

To represent the true value of the debt a deduction was made from the increased oxygen intake following anaerobiosis corresponding to the amount needed by the animal for oxidation of its hæmoglobin. These

corrections were, at the best, only approximate, as they did not allow for individual variation in blood volume and concentration of hæmoglobin in the blood, nor for the fact that before constant volume was attained in the apparatus the worm must have been subjected to partial anaerobiosis.

Some typical results of the oxygen debt experiments are illustrated

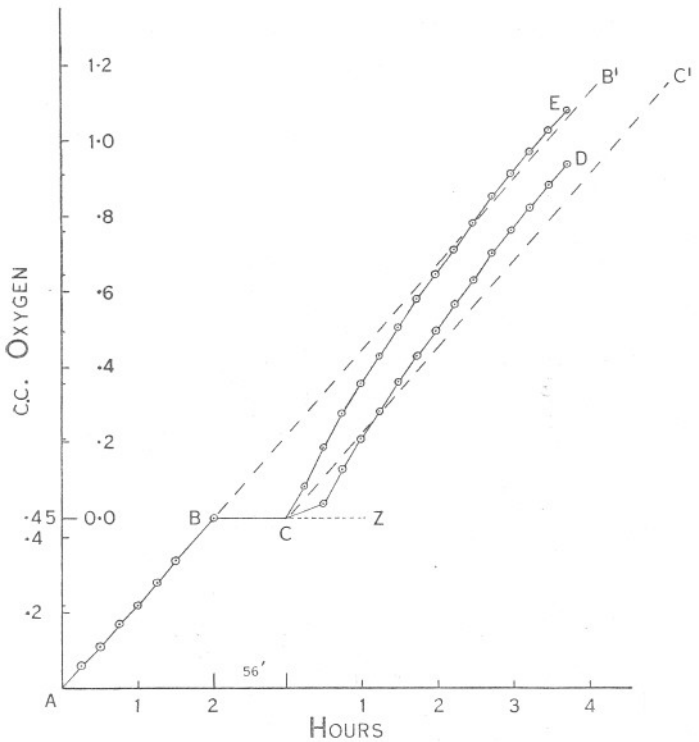

FIG. 12.—Graph showing the oxygen consumption of a worm weighing 4·5 gm. The period of experimental anaerobiosis in hydrogen was 2 hours; the period of true anaerobiosis, 56 minutes; temperature 13° C.

by Figures 12, 13, 14, and 15 in which AB represents the normal oxygen intake measured before anaerobiosis; BZ the period of experimental anaerobiosis; BC the period of true anaerobiosis estimated by deducting from BZ the length of time needed for constant volume to be attained within the apparatus and that for which the combined oxygen of the blood was calculated to last the animal. The broken line BB′ represents the oxygen it is assumed the animal would have used had it not been deprived of air; the broken line CC′ the oxygen intake equal to the normal resting value. The line CD shows the oxygen intake following anaerobiosis, the

correction for the oxidation of hæmoglobin having been applied ; while CE is the total oxygen intake following anaerobiosis as measured during the experiment.

Figures 12 and 13 illustrate experiments in which a partial debt was found. It will be noticed that the excess oxygen intake was equal to about half what the animal would have used during the same time in air. Figure 14 is typical of the results of the majority of experiments in which there appeared to be no oxygen debt. Figure 15 illustrates an experiment in which the period of experimental anaerobiosis was 30 minutes, the

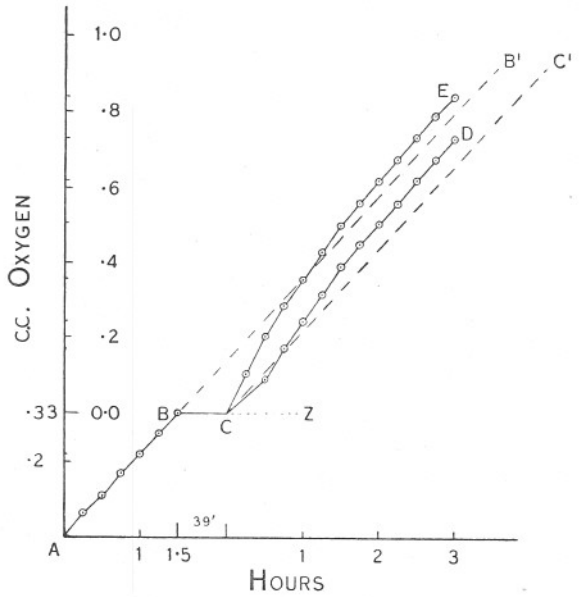

Fig. 13.—Graph showing the oxygen consumption of a worm weighing 3·4 gm. The period of experimental anaerobiosis in hydrogen was 1 hour 36 minutes; the period of true anaerobiosis, 39 minutes; temperature 14° C.

oxygen impurity in the apparatus enough for 3 minutes and the combined oxygen in the blood sufficient for 40 minutes. The worm was, therefore, not under anaerobic conditions as far as its blood was concerned, and thus there should be no debt, as was found to be the case when the amount needed for the oxidation of the hæmoglobin was subtracted from the observed oxygen intake.

The investigation on the ability of Arenicola to go into oxygen debt has given, on the whole, inconclusive results. The first series of experiments, in which nitrogen was used, indicate that the oxygen consumption after anaerobiosis was below normal. The second series of ten experiments

with hydrogen showed two instances of a partial oxygen debt. If, however, no deduction for the oxidation of the hæmoglobin is made, two out of the six experiments in which nitrogen was used show an oxygen debt, the remaining four a partial debt. Five of the experiments with hydrogen give a debt and four others only a partial oxygen debt.

It seems reasonable to conclude that Arenicola will oxidise its hæmoglobin in the course of one or two hours. Although the correction allowed for this may be too great, as is indicated by the experiments in which the

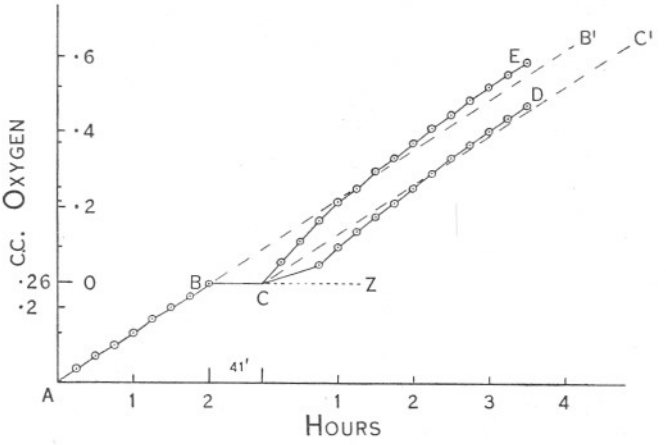

FIG. 14.—Graph showing the oxygen consumption of a worm weighing 3·6 gm. The period of experimental anaerobiosis in hydrogen was 2 hours; the period of true anærobiosis, 41 minutes; temperature 13° C.

corrected value for the oxygen intake falls below normal, the failure of the majority to show an oxygen debt cannot be entirely due to the error introduced by this correction.

6. The Habitat and Habits of Arenicola.

The worms used for this research were collected from a sandy beach forming part of Batten Bay, on the east side of Plymouth Sound. The area inhabited by Arenicola is uncovered between high and low tides for approximately three hours. The sand is black, with the exception of the surface layer, which is brown to a depth of one-quarter to one-half an inch. It is well known that black sand indicates the presence of sulphides from decomposing organic matter, while the brown colouration is the result of the oxidation of sulphides by the atmosphere. Arenicola burrows to a depth of one to two feet below the surface. The burrow, which is U-shaped and open at each end, is constructed by the animal pushing and eating its way through the sand. The entrance is not sealed at low tide by the castings. These are, in general, coiled in a heap around the opening in

such a manner that the latter is clearly visible. It was observed that whereas the surrounding sand is black that lining the burrows is brown, similar to the surface sand. The brown layer is approximately 1 mm. in thickness and extends throughout the entire length of the burrow.

The oxygen content of the interstitial water was determined as follows. Samples of the water from one foot below the surface were taken from a marked area on three occasions, each sample consisting of four lots of water collected at intervals of approximately one hour, so that the first was obtained just as the tide uncovered the area and the fourth just as the tide again reached the area. The boring apparatus used to obtain the

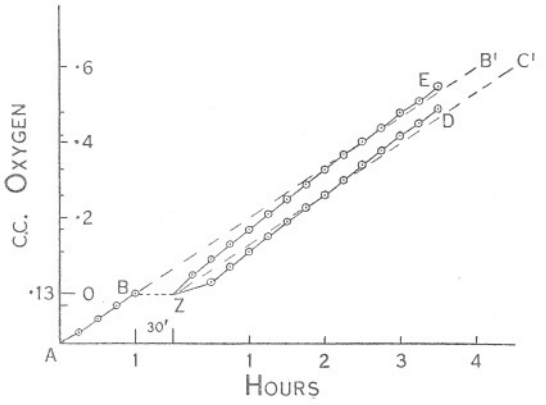

FIG. 15.—Graph showing the oxygen consumption of a worm weighing 2·8 gm. The period of experimental anaerobiosis in nitrogen was 30 minutes. There was no period of true anaerobiosis as the worm had a supply of oxygen sufficient for 43 minutes. Temperature 11° C.

samples consisted of a hollow iron tube, two inches in diameter and two and a half feet in length, closed at the bottom and terminating in a spiral spike. Near the bottom was a double row of holes, 5 mm. in diameter, blocked on the inside by means of a plunger which could be withdrawn as desired. The borer was forced into the sand to the required depth and the plunger then removed so that the water could drain in through the holes. The water was obtained by sucking it up into a large separating funnel the stem of which reached to the bottom of the borer. Three successive samples of water were thus collected and run into bottles of approximately 250 c.c. capacity. Precautions were taken to keep the water as free as possible from contact with air by sampling under liquid paraffin.

The estimation of oxygen was made in the laboratory by Winkler's method. Time was first allowed for the sediment invariably drawn up

with the water to settle. This was necessary as the sediment contained sulphides which on the addition of acid liberated hydrogen sulphide, the latter combining with the iodine from Winkler's reagents. The bottles were then opened and water free from sediment, drawn off from the upper layer, was transferred under oil to smaller bottles of 60 c.c. capacity. The estimations of dissolved oxygen were then carried out.

The remaining water in the large bottles was tested for hydrogen sulphide by adding acid to samples of water free from sediment and to other samples well mixed with sediment, and testing these with lead acetate paper. It was found that the water which had been shaken up with sediment generally gave a positive test for hydrogen sulphide, whereas that lacking sediment invariably gave a negative test. It was, therefore, concluded that the method of allowing sediment to settle before estimating the oxygen was sufficient to prevent the interference of hydrogen sulphide with Winkler's reagents.

Control experiments were devised to find the margin of error introduced into the oxygen estimations by the unavoidable handling of the water in the field. For this purpose sea-water was boiled to expel air and samples siphoned into several of the 60 c.c. bottles. The rest of the boiled water was then sucked up into the separating funnel, run into 250 c.c. bottles, and samples transferred from them to other 60 c.c. bottles under oil. The technique was as far as possible an exact reproduction of that employed in the sampling of water from the field. The oxygen concentration was determined by Winkler's method. The difference between that found in the siphoned samples and that in which the water was transferred by the separating funnel represents the error introduced by the handling of the water. The average error introduced by this method of sampling the water was found to be 0·44 c.c. of oxygen per litre. Table IX gives the oxygen content in c.c. per litre of the interstitial water.

TABLE IX.

Date of Sampling.	Oxygen content of water from sand in c.c. per litre at Exposure.	1 hour.	2 hours.	3 hours.
Oct. 24.	0·107	0·058	0·142	0·145
	0·066	0·151	0·137	0·034
	0·114	0·125	0·165	0·028
Nov. 7.	0·137	0·021	0·136	0·130
	0·126	0·055	0·124	0·197
	0·114	0·073	0·241	—
Nov. 10.	0·212	0·220	0·130	0·266
	0·199	0·135	0·151	0·125
	0·218	0·117	0·206	0·143

The highest value of oxygen found was 0·27 c.c. per litre, and as the experimental error was 0·44 c.c. per litre it is clear that there is practically no oxygen in the interstitial water at any time. The variation in the values of oxygen present in samples collected at a given time may, perhaps, be explained by the amounts of sediment in the bottles being different, and by the difference in the length of time the water was exposed to the sediment.

The data so far presented show that the worms burrow in black sand, the interstitial water of which at a depth of 1 foot lacks oxygen. The burrows, however, are lined with brown sand, indicating that oxidation has occurred.

A few observations have been made in the laboratory on the burrowing habits of Arenicola. It was noticed that in the process of burrowing the worms acted as small suction pumps, that is, by everting and inverting the proboscis water was drawn towards the anterior end from all sides. The worms begin their burrows when covered with water and it is clear that as they move into the sand water will flow in behind them, thus oxidising the lining of the burrow which consists of particles of sand held together with mucus and forming a layer about 1 mm. in thickness. It was noted in one case where a worm had died in its burrow and lost blood that the red colouration did not diffuse into the surrounding water. This indicates that the water in the burrows cannot be considered as part of the interstitial water.

It is presumed that when the tide is high the worms have no difficulty in obtaining oxygen, as they can either maintain a current through the burrow or come into direct contact with fresh sea-water by moving to the surface.

During the period of intertidal exposure they are most generally found at a considerable depth below the surface. It is probable that during this period, which lasts for approximately three hours, conditions approaching anaerobiosis will occur. The water in a completed burrow was observed in the laboratory to move and to change its direction of motion suddenly, as the worm alternately protruded and withdrew its proboscis. Fine particles of sediment were observed in motion within the burrow. It is, therefore, assumed that the movement of the worm within its burrow will keep the water in a state of constant motion, thus bringing it all into contact with the air at the surface. Since the openings are not more than 0·5 cm. in diameter the surface of water exposed to the air is obviously restricted and thus only a limited amount of oxygen can be dissolved in a given time. This amount will, however, be used by the worm as the dissociation of its blood occurs mainly at very low oxygen pressures. It is thought that the oxygen thus acquired, in conjunction with that already combined with the hæmoglobin, will be sufficient to satisfy the animal's requirements during low tide.

7. Discussion.

Barcroft and Barcroft (1924) have shown that the dissociation of Arenicola blood takes place mainly at oxygen pressures of between 1 and 3 mm. of Hg. It is evident that in well aerated water respiration is effected by the diffusion of oxygen through the gill filaments into the blood stream, the transport of oxygen by the hæmoglobin taking place only at reduced pressures.

The great affinity of the hæmoglobin for oxygen and the consequent low pressure at which it dissociates adapt Arenicola particularly well to its environment.

It is concluded that the primary function of the hæmoglobin is that of transporting oxygen during the period of lowered oxygen pressures to which the worms are probably subjected at low tide. The theoretically calculated amount of combined oxygen is enough for an hour and, while it is not suggested that the hæmoglobin functions chiefly as a storer of oxygen, the reserve it holds will be of great service to the animal.

The experiments on the ability of Arenicola to go into oxygen debt gave on the whole unsatisfactory results. In a few instances the oxygen intake following anaerobiosis was in excess of the normal. This would seem to indicate that Arenicola is able to go into debt for oxygen, but that its ability to do so is limited. The limiting factors may perhaps be a low buffering power on the part of the tissues and blood. The concentration of lactic acid was not estimated. In view of the results obtained this will be necessary before it is possible to conclude to what extent the mechanism of the oxygen debt is of use to the animal.

SUMMARY.

A study of the respiration and of the function of hæmoglobin in *Planorbis corneus* and *Arenicola marina* has been undertaken.

The oxygen consumption of Planorbis is of the order of 0·026 c.c. per gm. per hour, measured at 15° C.

The blood volume is approximately 0·581 c.c. per gm.

The combined oxygen of the blood is 0·013 c.c. per c.c. of blood, the total oxygen being 0·014 c.c. per c.c. The total oxygen capacity of the blood per gm. of snail is estimated to be 0·0081 c.c.

The oxygen supplied by the blood is calculated to last 18 minutes and is found by experiment to last 25 minutes.

The snail does not immediately oxidise its hæmoglobin after subjection to anaerobiosis. Oxidation begins after 10 minutes and is complete within 20 minutes.

Planorbis goes into debt for oxygen when subjected to short anaerobic

periods. The debt is proportional to the time of anaerobiosis, but the recovery period is longer.

This animal appears to be well adapted for survival in a habitat which at times may be deficient in oxygen.

The function assigned to the hæmoglobin is that of transporting oxygen.

The oxygen consumption of Arenicola is of the order of 0·031 c.c. per gm. per hour, measured at between 10° and 12° C.

The blood volume is approximately 0·382 c.c. per gm.

The combined oxygen of the blood is 0·087 c.c. per c.c. of blood, the total oxygen content being 0·097 c.c. per c.c. The total oxygen capacity of the blood is estimated to be 0·037 c.c. per gm. of worm.

The oxygen supply of Arenicola blood is calculated to last 71 minutes and is found by experiment to last at least 30 minutes.

Arenicola when transferred from anaerobic to aerobic conditions partially oxidises its hæmoglobin after 20 minutes. Instances of complete oxidation were never found.

The results of the oxygen debt experiments are not conclusive. A few instances of a partial debt were found. It is thought that the ability of the worm to go into oxygen debt is limited.

The sand at Plymouth, in which the Arenicola burrow, is black, while that lining the burrows is brown, similar to the surface sand. The burrows open to the surface at each end and the openings are not blocked by the castings. The amount of oxygen in the interstitial water is found to be negligible at all times. The water in the burrows is not considered to form part of the interstitial water. It is thought that the movements of the worm within the burrow keep the water in motion so that oxygen is being continually renewed at the surface.

The dissociation of Arenicola hæmoglobin occurring at low oxygen pressures of between 1 and 3 mm. of Hg. seems especially adapted to the needs of the animals. The significance of the hæmoglobin is that it functions as a carrier of oxygen during the period of lowered oxygen pressures to which the animals are liable to be subjected during intertidal exposure.

Acknowledgments.

This work was carried out in the Department of Zoology, University College, London, and at the University's table at the Laboratory of the Marine Biological Association, Plymouth. I wish to thank Professor D. M. S. Watson, F.R.S., and Mr. C. F. A. Pantin, who suggested this piece of work, for their advice and criticism. I should also like to express my thanks to Dr. E. J. Allen, F.R.S., and the members of his staff for placing the facilities of the Laboratory at my disposal.

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Hydroid Pigments. I. General discussion and pigments of the Sertulariidæ.

By

Nellie M. Payne.

INTRODUCTION.

Cœlenterate Pigments.

The literature on cœlenterate pigments is not large, but is rather scattered and somewhat difficult of access. In addition some pigment studies on squids and worms appear in the literature as researches on cœlenterates. An effort has been made in this paper to bring together the known results that have been secured in the study of cœlenterate colouring matter with the exception of such papers as deal with protective coloration, mimicry, and the like. Compilations are not listed unless they contained an original contribution either in methodology or view-point. Only papers where it could be clearly ascertained that the animal studied was a cœlenterate have been cited. In some of the older work done by non-zoologists, the scientific name has been sunk to a mere synonym and the description of the animal was insufficient even to place it to phylum.

The pigments of the cœlenterates include several types of compounds, some of which may be used in respiration. Blanchard (1882) described a blue, water-soluble pigment obtained from the circum-umbrellar region of *Rhizostoma cuveri*. The aqueous solution of this pigment showed three absorption bands in the red, yellow, and green respectively. Colasanti (1880) described a blue pigment from hydromedusæ, which colouring matter he considered as a compound of carotin and protein. Elmhirst and Sharpe (1920) found a light-sensitive pigment in *Actinia equina* and *Anemonia sulcata*. The intensity of the colour was proportional to the intensity of the light to which the Actinians were exposed. Elmhirst studied the environment in relation to the colour, and Sharpe the chemical properties of the pigments themselves. Sharpe came to the conclusion that in *Actinia equina* the red and brown pigments may be the same basic substance, the exact colour of which is due to the alkalinity or acidity of the medium in which the pigments occurs. This animal used blue and possibly violet-light rays; the light-sensitive pigment which it contains has properties similar to those of chlorophyll and is used in

respiration. *Anemonia sulcata* contained no hæmoglobin derivatives. It did contain small green algæ along the inner border of the tentacles and in the mesenteries. These algæ contained a colouring matter very similar to the chlorophyll of green leaves.

Fewkes (1889) described a case of pigment discharge by a hydroid medusoid. Fürth (1903) in his monograph on the physiology of lower animals classifies the pigments of cœlenterates into seven groups: (1) the blue pigment of the medusoid umbrella, (2) pelageine, (3) the blue colour of the coral *Heliopora cœrulea* and compounds related thereto, (4) the hæmatin series, (5) the red and purple pigments which include colouring matters such as actinochrome, purpuridin, and the floridines, (6) the lipochromes, and (7) the uradines, a sulphur-containing group, which are yellow in the live animal, but turn black on its death.

Fulton (1922) described a red pigment from *Actinia bermudensis*. The pigment is soluble in CS_2, methyl, ethyl, and amyl alcohol, petroleum ether, pyridine, and acetone. The pigment occurs in granules. Addition of HCl or valeric acid deepened the red colour, but alkali produced no change that was apparent. Geddes (1882) found that the "yellow cells" in cœlenterates were commensal organisms. These organisms, which were algæ, produced oxygen which was needed by the cœlenterate in its respiration. The chlorophyll-like pigment, found in the cœlenterate Anthea and in others, was thus due, not to the cœlenterate itself but to the alga. Griffiths and Platt (1895) obtained a violet pigment from the medusoid Pelagia, to which dyestuff they applied the name pelageine and ascribed the formula $C_{20}H_{17}NO_7$. Since the pigment was extracted in amorphous condition only, it seems scarcely possible that the formula suggested could be valid. Griffiths (1892) considered that the cœlenterate pigments had a respiratory function.

Haurowitz and Waelsch (1926) found a blue pigment in *Vellela spirans*, which on spectroscopic examination showed absorption in both red and violet, but no distinct bands. The pigment became reddish brown on drying, or with treatment with alcohol or toluol. Kropp (1931) extracted the colouring matter of *Vellela spirans* with water. The extract was opalescent with a reddish colour in reflected light. Near the neutral point it turned yellow, and successively pink and reddish as the solution became increasingly acid. An aqueous solution of the pigment showed diffuse absorption in the red, $\lambda = 655\ \mu\mu - 685\ \mu\mu$, and blue violet $425 - 475\ \mu\mu$, but no sharp bands.

The most comprehensive work that has been made on the cœlenterate pigments is that of Krukenberg (1880, 1882). He obtained a green pigment with a red fluorescence from *Anthea cereus*.* The alcoholic solution of this pigment varied from brown to green. The absorption spectrum

* = *Anemonia sulcata*.

of the alcoholic solution was figured. Addition of acid changed the green colour to blue and added a new band at the junction of yellow and green. This author pointed out the similarity between the green pigments of the cœlenterates and the chlorophyll in plants.

Lancaster (1873) examined the pigment found in the stalked protozöon, *Stentor cœruleus*, with a Sorby-Browning spectroscope. He found an absorption spectrum containing two bands, the darker in the red extending a little to the side of solar C line, and the second in the green. *Stentor mülleri* gave absorption spectra like those of Hydra and Spongilla. Since Stentor feed on Hydra, it served as a concentrating agent for the hydroid pigment. Liversidge (1898) found a blue nitrogen containing pigment in the coral *Heliopora cœrulea*. The pigment from "dead coral" dissolved readily in alcohol and acetic acid. Heating a concentrated residue of coral extract produced an odour similar to that of burned fish. Liversidge tested the solubility of the material in a large series of compounds both inorganic and organic. Acetic acid proved to be one of the best solvents. An alcoholic solution of coral contained more organic matter than an acetic acid solution. The pigment was insoluble in kerosene, the pure paraffines, in CS_2, CCl_4, or petroleum ether. Solutions were either blue or green, depending on the solvent used, e.g. a sodium acetate solution was green; a formic acid solution blue. The pigment did not appear to be either a natural indicator or a reducing agent.

M'Kendrick (1881) described pigments that occurred in small granules in several of the cœlenterates. He did not study the chemistry but mentioned a yellow pigment in Chrysaora, a blue one in Cyanea, and a pink in Aurelia. He gave simple methods for pigment extraction.

MacMunn (1885, 1890) found colouring matters in cœlenterates which resembled these of vertebrate blood. *Actinia mesembryanthemum** contained a pigment which could be transformed either into hæmochromogen or hæmatoporphorin. This pigment was not actinochrome, which dyestuff is widely distributed in the Actiniæ. In *Sargartia parasitica* occurred a colouring matter in both reduced and oxidised states. This pigment did not occur in any of the Actiniæ. A green pigment which gave all the reactions of biliveridin was found in the mesenteries of *Anthea mesentherium*. A yellow pigment which differed from chlorophyll occurred in the tentacles of *Anthea cereus*,† *Bunodes balii*, and *Sargartia bellis*. In these species were both luteins and a pigment that gave absorption bands in the red and violet part of the spectrum.

Merejowski (1881) described a carotin-like substance from cœlenterata which he designated as tétranérythine.

Mosely (1873) found a pigment, the so-called actiniochrome, in *Actinia mesembryanthemum*‡ which is a pale olive or merely a dirty white colour

* = *Actinia equina*. † = *Anemonia sulcata*. ‡ = *A. equina*.

in muddy water. This colouring matter also occurred in *Bunodes crassicornis* which is a transparent green. In some specimens of *B. crassicornis* the tips of the gonidial tubercules were bright red. Mosely determined the absorption band for the red pigment but lost the drawing. He found no similar colouring matter in *Actinia mesembryanthemum** or *Actinia rosea*. In 1877 Mosely found a hematine-like pigment in *Bunodes crassicornis*. Teissier (1925) described an interesting case of pigment development which paralleled the embryonic. This author believed that the appearance of pigment in the eggs of *Clava squamata* was due to the liberation of carotin from a compound of carotin and protein.

General Chemical Literature.

The nomenclature for the various pigments differs from author to author. In the foregoing literature summary, the original term used by the investigator in question has been quoted. Lypochromes, luteins, and carotin belong to the group of carotinoids as the term is defined by Palmer (1922). In this paper the nomenclature of Palmer will be followed. This worker summarised the preceding work on carotinoid pigments and has also made valuable contributions of his own to the study of chromatology. Schertz (1925) described an accurate method for obtaining crystalline carotin. He extracted the pigment with a highly purified ether kept over sodium. Crystalline carotin kept in an ice box oxidised very slowly and could be stored some months without deterioration. Wheldale (1916) classifies plant pigments into two general groups : the plastid pigments which include chlorophylls, xanthophylls, and the carotinoids, and the pigments distributed throughout the cell or the anthocyanins, and their derivatives, the flavones. The anthocyanins and flavones are characterised by their water solubility. In the plant kingdom there are two yellows, one type soluble in water, the other in fat solvents. Wheldale also pointed out that many white flowers contain a pigment made apparent in alkaline solution. The flavones are natural indicators, being white in neutral or acid solution, and yellow to orange in alkaline. The flavones are oxidation products of the anthocyanins. The flavone group forms characteristic salts with $FeSO_4$, $FeCl_2$, $FeCl_3$, and $Pb(COO)_2$.

The ultimate source of the coelenterate pigments may be the plant kingdom. Thus far, to the author's knowledge, there has been no clear example of either chlorophyll or carotin being a direct product of animal metabolism. Geddes (1882) and others have demonstrated the algal origin of cœlenterate chlorophyll. An interesting paper by Palmer and Knight (1924) describes the transfer of potato carotin into the blood of the

* $=A.$ *equina*.

potato beetle, *Leptinotarsa decimlineata* Say, and from this insect to the predaceous plant bug, *Perillus bioculatus Fabricius*, in which the carotin was in part deposited in the exoskeleton. Thus far the origin of the cœlenterate pigments other than chlorophyll is unknown. It is altogether possible that both carotin and flavones are of algal origin.

Materials and Methods.

The hydroids studied by the present writer belonged to two distinct groups, one including those bearing carotinoid pigments, namely, the Antennulariidæ and Haleciidæ; the other including the Sertulariidæ which carried water-soluble yellow and brown pigments.

The characteristic of the colouring matters in these two groups, respectively, was so different that the same method of treatment of the hydroids previous to extraction could not be used. The caratinoid-bearing group, of which *Antennularia antennina*, *A. ramosa*, *Aglaophenia pluma*, *A. tubulifera*, and *Halecium halecinum* were studied, were washed in fresh water repeatedly before their pigments were extracted. The hydroids thus freed of debris were dried in an incubator to air-dry state and then extracted with CS_2, CCl_4, or ether. The pigments in each of the species studied was more soluble in CS_2 than in any other of the solvents used. Those used included CS_2, CCl_4, ether, absolute alcohol, pyridine, petroleum ether, and chloroform. Details of the methods will be given in a later paper.

The colouring matter of the Sertulariidæ with the exception of the brown of *Sertularia pumila* was so extremely soluble in fresh water that the hydroids could not be freed of the usual debris and dirt clinging to them by washing in fresh water. The most practical way of cleaning hydroid material in these groups was washing in sea-water. The long stems were then cut into small pieces and extraction made in either fresh or dried condition. Alcohol or distilled water was the solvent used. A higher yield of pigment was obtained from fresh than from dried material. The crude extracts were allowed to evaporate, and during the evaporation were stirred. Since the pigments were less soluble in cold than in warm water, the extracts were chilled with ice to promote crystallisation. Crystals were obtained with great difficulty. Acid solutions of pigments from *Sertularella gayi* Lamaroux and *S. polyzonias* Linnæus yielded a small crop of crystals.

Although crystals of the pigments themselves were difficult to procure, it was relatively easy to procure their salts in crystalline form. Lead and iron salts of the pigments in the Sertulariidæ studied resembled the flavone salts of the plant flavones.

The species studied were *Sertularia pumila* Linnæus, *Sertularia argentea*

Ellis and Solander, *Sertularella gayi* Lamaroux, *Sertularella polyzonias* Linnæus, and *Thuiaria articulata* Pallas.

Results Obtained.

The nature of the pigments in the Sertulariidæ had first to be studied from a purely negative view-point. They were not soluble in the fat solvents, CS_2, CCl_4, or petroleum ether, therefore they were not carotinoids. Tests for free sulphur were negative, although the hydroids turned black in death. The species *Sertularia argentea*, *Sertularella gayi*, *S. polyzonias*, and *Thuiaria articulata* blackened readily on exposure to air. The yellow pigments found did not reduce Fehling's solution, nor did they present the other characteristics of chrysomphanic acid. The pigment in the Sertulariidæ is not distributed evenly throughout the tissues but occurs in small patches. This is especially true of the yellow species. The brown species *Sertularia pumila* apparently has more nearly uniform distribution of colouring matter.

No pigment solutions blackened on exposure to air. The blackening of the hydroid might be due to some enzyme adsorbed on the tissues, and not dissolved with the pigment. It is also interesting to observe that the one intertidal species studied, namely, *Sertularia pumila*, did not blacken on exposure to air. The other species used are normally covered at all times by sea-water. The blackening may possibly be that of a pigment not soluble in the same solvents as are the flavone-like pigments.

The yellow colouring matter in *Sertularella gayi* Lamaroux and *Sertularella polyzonias* Linnæus were extremely soluble in distilled water. An animal immersed in either distilled or tap water began to lose colour from the instant it was placed in the solvent. In neutral or alkaline aqueous solutions the pigment was a lemon-yellow. The gonophores were especially rich in colouring matter. Extracts from fresh material often had a greenish yellow cast. Rhomboid pigment crystals were obtained from etherial solutions. By salt formation, type of crystal, or differential solubility tests, the pigments from these two species, *Sertularella polyzonias* and *S. gayi*, could not be separated. It is possible that these closely allied species bear a common pigment. A determination of the chemical constitution of the pigments in question is necessary before it can be said definitely whether there are one or two pigments involved.

Nearly allied to the colouring matter in the Sertularellas is the chromatophore group in the white or colourless species *Sertularia argentea* Ellis and Solander. This hydroid can be used as indicator for hydrogen ion concentration. It is colourless in neutral and acid solutions. The aqueous extract of the chromatophore is colourless at pH 7, yellow at pH 8, orange at pH 8·5, and finally brown in pH 10. Extracts of these chromatophore

Species.	Colour in Nature.	Solubility.			Colour of metallic salts.			Influence of pH on pigment colour.		
		Water.	Alcohol.	Ether.	$Pb(COO)_2$	$FeCl_3$	$FeSO_4$	Neutral pH 7.	Alkaline pH 8.	Acid pH 6·5.
Thuiaria articulata Pallas	orange-brown	readily	readily	moderately	blue	brown	greenish	brown	lemon-yellow	colourless
Sertularia argentea Ellis and Solander	white or colourless	readily	readily	slightly	blue	blue	greenish	colourless	yellow (at pH 8·5 orange)	colourless
Sertularella gayi Lamaroux	lemon-yellow	readily	readily	moderately	blue	greenish	blue	yellow	yellow	colourless
Sertularella polyzonias Linnæus	lemon-yellow	readily	readily	moderately	blue	greenish	blue	yellow	yellow	colourless
Sertularia pumila Linnæus	brown	moderately	readily	slightly	greenish	greenish	blue	brown	brown	yellow (at pH 4 white)

in ether or alcohol were also colourless. The presence of the pigment became apparent when KOH or NH_4OH was added to the solutions. The pigment or rather the chromatophore group was insoluble in CCl_4, CS_2, or petroleum ether, but was slightly soluble in ether. The presence of the pigment group in this colourless hydroid can be demonstrated by holding the hydroid over NH_4OH fumes. It was by this simple method that Wheldale (1916) demonstrated the flavone in the white snapdragon.

The pigment in the *Sertularia pumila* was distinctly less soluble in water than were the pigments from the other species. It was insoluble in CS_2, CCl_4, and petroleum ether, even after long standing in contact with these solvents. *Sertularia pumila* is also a natural indicator for pH, but its colour changes lie on the acid side of neutrality. Characteristic salts of the pigment were obtained with $Pb(COO)_2$, $FeCl_3$, $FeSO_4$.

The orange-brown species *Thuiaria articulata* Pallas contained a pigment, also a natural indicator, which was readily soluble in water. Crystals were obtained from slightly acid solutions. Addition of small quantities of HCl to water, alcohol or ether solutions made them turbid. From these turbid solutions rhomboid crystals were obtained. The pH of such solutions must be controlled, for at pH 6·5 the pigment was decolorised. Characteristic salts were formed with $Pb(COO)_2$, $FeCl_3$, and $FeSO_4$. In solubility, crystal type, and salt formation the pigment of *Thuiaria articulata* resembles that found in the Sertularellas.

The accompanying table gives the chief results obtained with the pigments of the Sertulariidæ. Each of the species studied contained a water-soluble colouring matter. The pigments were all natural indicators. In solubility, crystal type, and salt formation the colours from *Sertularella gayi*, *S. polyzonias*, *Sertularia argentea*, and *Thuiaria articulata* showed marked similarity. *Sertularia pumila* contained a pigment which possessed properties similar to the flavones, but was distinctly less water soluble than the others studied.

SUMMARY.

1. The yellow colours of the hydroids include at least two groups, the carotinoids found in the Antennulariidæ and Haliciidæ and the flavone-like pigments that occur in the Sertulariidæ. From the literature a third group, the uradines, may be added.

2. The flavone pigments and their relatives are all water soluble and are thus distinguished from the carotinoids which are not water soluble, but may be dissolved in the usual fat solvents.

3. In the Sertulariidæ studied, a graded series of chromatophore groups and pigments was found which ranged from the colourless species *Sertularia argentea* Ellis and Solander, through the yellow of *Sertularella gayi*

Lamaroux and *S. polyzonias* Linnæus, to the orange-brown of *Thuiaria articulata* Pallas. The brown of *Sertularia pumila* is probably also a flavone derivative.

4. The flavones and related pigments occur extensively in the plant kingdom. It is probable that the flavone-like pigments found in the Sertulariidæ are of plant origin.

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Muds of the Clyde Sea Area. II. Bacterial Content.

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With 2 Figures in the Text.

Introduction.

An important factor in the economy of the sea is the presence of bacteria, which are found not only in the sea-water itself, but in the mud and sand of the sea bottom. The parts of the sea which are most important biologically are (i.) the upper twenty metres of water in these latitudes, and (ii.) the uppermost layer of the sea floor in regions where the water is less than a few hundred metres deep. The first is of interest as the zone inhabited at the proper season by autotrophic organisms, chiefly phytoplankton. It is here that the products of photosynthesis are largely formed ; upon these heterotrophic life in the sea is ultimately dependent. Except in shallow water, there is insufficient light at the sea bottom for photosynthesis, and the organisms inhabiting the sea floor are of necessity heterotrophic. These organisms, among which are protozoa and the majority of bacteria, derive their foodstuffs directly or indirectly from the already organised proteins and carbohydrates of dead organic matter accumulated on the sea floor. The bacteria found in this zone include the following representatives of different physiological groups :—

(i.) Simple heterotrophs, which can utilise the proteins of dead organisms, and which liberate ammonia as waste metabolite.

(ii.) Nitrifying organisms of the two types, (*a*) those which oxidise ammonia to nitrite, and (*b*) those which oxidise nitrite to nitrate (**14**). These bacteria thus assist in the regeneration of nitrate from ammonia. This is important, because although ammonium-nitrogen can be utilised by some algæ and by higher plants, nitrate-nitrogen is in general more readily assimilated by autotrophic plants. Now the low concentration of nitrate is a limiting factor to plant growth in the sea, so it is desirable to know what bacterial changes in the sea may result in its formation.

(iii.) Denitrifying bacteria. These are simple heterotrophs with a special mechanism for reducing nitrate and nitrite to elementary nitrogen, the oxygen thus liberated being used for respiration (see p. 762).

(iv.) Nitrogen-fixing bacteria, which fix elementary nitrogen by synthesising nitrogenous compounds, possibly ammonia. These have been isolated from algal slime along the coast-line (**5**, **6**), but not from true bottom deposits.

(v.) Sulphur bacteria, which oxidise hydrogen sulphide to free sulphur (**16**).

The physiological importance of these and other groups will naturally depend upon their numbers, and accordingly the experimental work described below was undertaken (i.) to determine the approximate numbers of bacteria present in samples taken from different types of bottom deposits in the Clyde Sea Area, and (ii.) to make a preliminary investigation into the different types of micro-organisms found.

Historical.

The earliest record of the bacteria in marine mud is that of Russel (**13**), who noted that there were many more micro-organisms in the mud than in the supernatant water. Drew (**2**) found that the exceptionally high bacterial content of shallow coastal waters in the tropics was due to the fact that the mud flats below were unusually rich in bacteria. These appear to be the only general records of mud bacteria.

Other workers have studied special groups of organisms isolated from marine muds. Nitrifying bacteria of both types were isolated by Thomsen (**14**) at Kiel from bottom deposits close to the shore. According to Issatchenko (**4**), nitrate-forming bacteria are found in northern seas in bottom deposits, but their number depends on the nature of the sea bottom ; he found that they were absent from black muds, present in clay deposits, and more abundant in calcareous sandy deposits.

Experimental.

(a) *The Area Investigated.*

The samples examined were all from the Clyde Sea Area, a brief description of which is given by Marshall and Orr (**12**) ; the stations used for mud sampling are described by Moore (**9**, **10**). The bottom deposits are chiefly muds, with some sands ; these are classified into four types by Moore (**10**), and stations representative of each of these four types were selected for bacteriological analysis as under :—

(i.) *Loch-head Type :* Station 10, Loch Striven Head. Depth 24 m.

(ii.) *Mid-loch Type :* Station 11, Clapochlar. Depth 73 m.

(iii.) *Deep-water Type :* Station 7B, Garroch-Corrie. Depth 166 m.

(iv.) *Sandy Type :* Station 1B, Kames Bay. Depth 25 m.

(b) *Sampling.*

The samples were obtained by means of the apparatus described by Moore and Neill (**11**). The sampling tube is a cylinder which is sent down open at both ends ; thus the water through which it passes streams through the tube and may deposit bacteria on the inside of the glass tube. However, any error thus introduced is negligible, since (i.) it appears that there is practically no streaming of mud up the sides of the glass tube when the sample is pushed through, (ii.) the number of bacteria in the muds is very much higher than that in the water above, and (iii.) the sub-samples were taken from the centre of the core, which had not been in contact with the glass.

(c) *Laboratory Technique.*

The mud samples were transported ashore in the sampling tubes. They were taken below deck in order to keep them cool during the interval between sampling and examination, and they were kept in the dark by means of cardboard sheaths. The time interval between sampling and plating depended on the distance of the sampling station from the laboratory, and varied from half an hour to four hours. On arrival at the laboratory the cylindrical tube was marked off into centimetre lengths, and at selected intervals two sub-samples (*a*) and (*b*) were taken from the mud. One sub-sample was used for determination of the interstitial water, and the second was used for estimating the bacterial content.

This portion of the work was carried out in conjunction with Mr. Moore, and the author wishes to acknowledge his kindness in taking the samples, in dividing them into sub-samples, and in determining the amount of interstitial water present in each sub-sample.

Sub-sample (*a*) was placed in a tared watch glass and weighed ; it was then dried to constant weight at 100° C. The difference between the first and the final readings gave the total amount of contained water. From these the figures the amount of water contained in sub-sample (*b*) was calculated. Sub-sample (*b*) was placed in a tared sterile Erlenmeyer flask and weighed ; filtered sea-water, sterilised by autoclaving for 30 minutes at 30 lbs. pressure, was then added to make up a volume of 100 c.c. ; the pipettes used were sterilised by heating to 150° C. for 30 minutes. The whole was then shaken very thoroughly to disperse the constituent mud particles. In the first series of dilutions (Station 7B, 14/4/30 and Station 1B, 10/4/30), lead shot was used to facilitate the

breaking up of the mud. The use of lead shot was then discontinued, on account of the toxic action of metals on most bacteria. It was difficult to disperse the mud particles in sub-samples from the lower layers of mud, which contained less interstitial water.

The diluted sample was then plated out on agar and on gelatine according to the procedure previously described by the writer (**7**). Four agar cultures and four gelatine cultures were made, a known volume of the diluted sub-sample being added. In the first samples examined, the amounts of inoculum were 1·0 c.c., 1·0 c.c., 0·5 c.c., and 0·5 c.c., but it was found that the colonies which developed were too crowded for convenient counting, and in the later work the following amounts were used : 0·5 c.c., 0·5 c.c., 0·1 c.c., and 0·1 c.c.

The plates were incubated at room temperature (15° C.) for five days, and then the bacterial colonies visible to the naked eye were counted. Tables I–IV give the results of the counts ; from these the average number of bacteria per c.c. in each diluted sub-sample was calculated. From this average the number per gram of dry mud was calculated approximately to the nearest thousand.

In estimating the bacterial content of mud the following difficulties occur :—

(i.) The relative amounts of water and of solid matter in sub-samples from different depths in any one series vary very much. The bacteria are present both on the particles and in the interstitial water, but since the organic matter in the mud is the source of their food supply, they will naturally be more densely crowded on the solid particles. It was decided to follow the procedure adopted in soil bacteriology (**15**), and to estimate the number per gram of *dry* mud.

(ii.) Some bacteria, such as the nitrogen-fixing bacteria and the nitrifying bacteria, do not grow readily on ordinary culture media, and the figures given below therefore do not include these.

(iii.) Slow-growing forms, such as certain Spirilla, form very small " pin-point " colonies, which are not easily seen with the naked eye when counts are made. For these reasons the bacterial content is probably underestimated.

The numerical work was supplemented by some descriptive and diagnostic study of the species isolated ; for this the ordinary bacteriological routine technique was adopted. In the course of this work many hundreds of different strains were isolated. Only a few of these could be identified as known species, and of the many unknown forms, only a few were studied in any detail.

TABLE I.

Estimations of Bacterial Content of Mud Samples, Station 10, Loch Striven Head.

	Depth of sub-sample in cm.	Agar Cultures, c.c. 0·5	0·5	0·1	0·1	Gelatine Cultures, c.c. 0·5	0·5	0·1	0·1	Average per c.c. of 1 : 100 dilution of wet sample.	Wt. of wet sample in gm.	No. of bacteria in thousands per gm. of wet mud.	Wt. of dry sample in gm.	No. of bacteria in thousands per gm. of dry mud.
16/4/30	0–1	255	330	86	40	207	330	187	88	635	1·10	58	0·37	171
	10–11	166	96	36	38	270	244	11	10	362	0·84	43	0·43	84
27/5/30	0–1	869	689	238	452	1005	940	379	241	2005	2·47	81	0·88	227
	2–3	673	463	190	241	611	443	214	93	1219	2·97	41	1·50	81
	6–7	139	247	153	88	221	225	114	91	532	1·72	31	0·92	57
	10–11	266	274	144	149	433	417	67	60	754	1·55	49	0·82	91

TABLE II.

Station 11.

16/4/30	0–1	158	186	39	38	285	226	29	46	419	0·86	49	0·14	300
	2–3	244	298	192	176	607	641	220	57	1014	1·88	54	0·58	175
	10–11	205	148	—	53	263	323	31	26	456	1·00	46	0·38	120
	25–26	107	162	37	29	195	146	51	45	321	1·06	30	0·44	73
27/5/30	0–1	576	684	226	139	431	244	148	95	1059	2·70	39	0·75	140
	2–3	596	517	241	203	*	507	295	126	1307	2·13	61	0·73	180
	10–11	324	237	84	118	326	518	74	38	716	1·28	56	0·39	184
	24–25	153	250	188	214	374	360	83	116	724	1·92	38	0·84	87

* Colonies too crowded for counting.

TABLE III.

Estimations of Bacterial Content of Mud Samples.

Station 7B.

	Depth of sub-sample in cm.	Agar Cultures, c.c. 1·0	1·0	0·5	0·1	Gelatine Cultures, c.c. 1·0	1·0	·05	0·1	Average per c.c. of 1 : 100 dilution of wet sample.	Wt. of wet sample in gm.	No. of bacteria in thousands per gm. of wet mud.	Wt. of dry sample in gm.	No. of bacteria in thousands per gm. of dry mud.
14/4/30	0–1	582	448	306	0	743	585	370	48	593	2·39	24	0·73	81
	10–11	434	547	230	56	353	432	195	18	435	0·97	45	0·39	110
	27–28	215	187	128	9	355	312	239	12	280	1·16	25	0·51	55
	Depth of sub-sample in cm.	Agar Cultures, c.c. 0·5	0·5	0·1	0·1	Gelatine Cultures, c.c. 0·5	0·5	0·1	0·1					
3/6/30	0–1	147	29	22	43	119	137	198	145	350	1·12	31	0·31	113
	1–2	72	62	34	29	133	37	—	108	206	0·94	22	0·30	69
	2–3	59	25	21	25	122	134	102	155	267	1·00	27	0·33	81
	3–4	40	27	31	38	81	—	77	110	212	0·69	31	0·23	92
	4–5	87	71	49	70	53	57	71	58	215	0·91	24	0·31	69
	6–7	33	17	18	60	96	129	81	53	202	0·71	29	0·24	84
	12–13	24	44	33	45	*	*	114	101	257	0·77	33	0·29	89
	20–21	27	47	34	50	124	119	84	47	221	0·80	28	0·32	69
	29–30	41	44	39	31	*	185	46	115	263	1·05	25	0·45	58

TABLE IV. Station 1B.

	Depth of sub-sample in cm.	Agar Cultures, c.c. 1·0	1·0	0·5	0·1	Gelatine Cultures, c.c. 1·0	1·0	0·5	0·1					
10/4/30	0–1	*	*	328	103	*	*	622	150	1002	2·24	44	0·93	107
	5–6	297	372	102	59	*	*	*	*	320	1·89	17	1·16	28
	10–11	*	*	120	35	*	*	168	68	325	1·11	29	0·70	46
	Depth of sub-sample in cm.	Agar Cultures, c.c. 0·5	0·5	0·1	0·1	Gelatine Cultures, c.c. 0·5	0·5	0·1	0·1					
27/5/30	0–1	334	343	105	111	220	189	131	109	642	1·97	33	0·91	70
	2–3	362	418	154	219	*	*	31	87	908	2·59	35	1·42	63
	6–7	301	—	151	205	539	—	181	181	1112	2·59	43	1·65	69
	10–11	418	—	93	70	466	—	116	239	1001	3·15	32	2·11	47

* Colonies too crowded for counting.

RESULTS.

(*a*) Quantitative Work.

Station 10, *Loch-head Type.* In the sample taken on April 16th, the number of bacteria at the surface of the mud was greater than at a depth

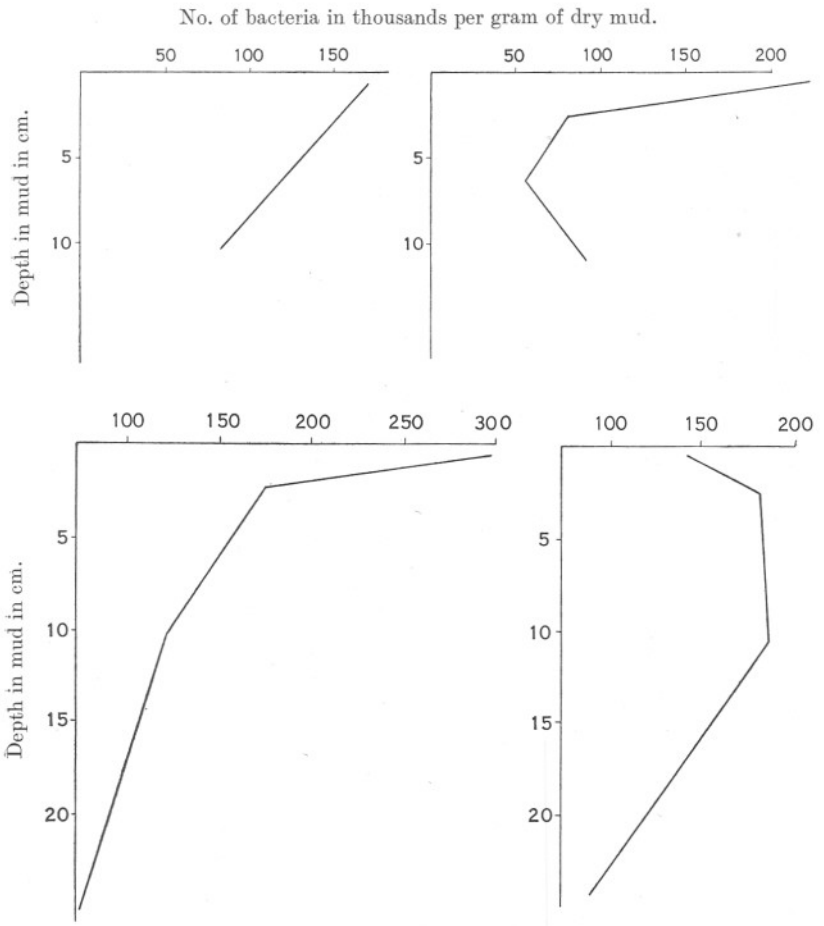

Fig. 1.—Bacterial Content of Marine Muds.
Above, Station 10, 16/4/30 and 27/5/30.
Below, Station 11, 16/4/30 and 27/5/30.

of 10–11 cm. (Fig. 1). A second sample, taken on May 27th, showed a surface increase from approximately 170,000 to 227,000 bacteria per gram of dry mud. It showed also a progressive decrease from the surface down to 6–7 cm., and an increase at 10–11 cm.; at this depth there was

relatively little change in the bacterial content in the interval between the first and second sampling (Table I).

Station 11, *Mid-loch Type.* The first sample taken on April 16th showed a progressive downward decrease in the number of bacteria. After five weeks, a second sample showed a surface decrease from 300,000 to 140,000, so that there were then fewer bacteria at the surface than at 3–4 cm. and at 10–11 cm. At 24–25 cm. there was a slight increase in numbers (Fig. 1 ; Table II).

Station 7*B*, *Deep-water Type.* At this station mud samples from the greatest depth of water were examined. The first sample, taken on April 14th, was marked by higher bacterial content at 10–11 cm. than at the surface : at 27 cm. the numbers were much lower. In order to determine more precisely the vertical variation in bacterial content, the second sample taken on June 3rd was divided into sub-samples at closer intervals. It was found that the number was highest at the surface, but there were two zones, at 3–4 cm. and 12–13 cm. respectively, where the bacterial content increased. Below that level the numbers gradually diminished (Fig. 2, Table III).

Station 1*B*, *Sandy Type.* The first sample, taken on April 10th, had a moderately high surface number, but at 5–6 cm. an abnormally low bacterial content—the lowest for any mud examined from this area ; there were almost twice as many bacteria per gram at 10–11 cm. as at 5–6 cm. The second sample, taken some six weeks later, showed a great decrease in the number of bacteria at the surface, a slight decrease at 2–3 cm., a slight increase at 6–7 cm., and a decrease at 10–11 cm. (Fig. 2, Table IV).

Summing up these results (see Table V), it is seen in general that the number of bacteria is in most cases greatest at the surface, that there is usually a progressive decrease with increase in depth, that the number fluctuates very widely near the surface of the mud, but that it remains fairly constant at the greatest depths for any given station.

(*b*) Description of Mud Bacteria.

In view of the large number of strains isolated, it was not found possible to study the physiology and morphology of all the forms. Certain species with special cultural or physiological characteristics were selected as types for further study, and those organisms having many characters in common were grouped together.

The marine muds examined were found to contain micro-organisms belonging to the following groups :—

(i.) The most frequent organisms were small bacilli similar to those found commonly in sea-water, and resembling the genera *Achromobacter*

Bergey and *Chromobacterium* Bergey (**1**), which appear to be common in fresh water. These organisms are true water bacteria.

TABLE V.

SUMMARY OF BACTERIAL CONTENT OF MUD. THE FIGURES REFER TO THE NUMBER OF BACTERIA IN THOUSANDS PER GRAM OF DRY MUD, APPROXIMATED TO THE NEAREST THOUSAND.

Depth in cm.	Station 10.		Station 11.		Station 7B.		Station 1B.	
	16/4/30	27/5/30	16/4/30	27/5/30	14/4/30	3/6/30	10/4/30	27/5/30
0–1	171	227	300	140	81	113	107	70
1–2						69		
2–3		81	175	180		81		63
3–4						92		
4–5						69		
5–6							28	
6–7		57				84		69
10–11	84	91	120	184	110		46	47
12–13						89		
20–21						69		
24–25				87				
25–26			73					
27–28					55			
29–30						58		

Morphologically, they are non-sporing and Gram-negative, and may be motile or non-motile. On agar they form moist, raised, more or less circular colonies similar to those of the colon-typhoid group, but they are usually slower-growing, and they vary in colour from white or cream to yellow or light brown. Physiologically, they were found to be extremely inert. They grow as readily on the ordinary peptone-containing media as on media prepared from fish extract, but they do not form indol from peptone, and do not readily ferment sugars, not even dextrose. They are thus physiologically much less active than terrestrial saprophytic bacteria under the experimental conditions tried ; it is of course possible that this group depends for its nutrition, not directly on the tissues of dead marine organisms, but on the simple nitrogenous compounds and carbohydrates dissolved in the water between the mud particles.

The bacteria of this class isolated from the mud samples have low oxygen requirements. The colonies in cultures used for the quantitative work were frequently found growing down into the medium away from the surface. Although they prefer anaerobic cultural conditions, they are facultative ærobes, for after repeated sub-culture they grow equally readily in well aerated parts of the culture medium. Most of these organisms were also able to utilise nitrates as a source of oxygen by reducing the nitrates to nitrites. Some strains carried the reduction a stage further, with evolution of gaseous nitrogen ; such denitrifiers were easily recognised because of the ease with which they reduced nitrates to nitrogen even in the

presence of some free oxygen. The occurrence of denitrification depends not only on the physiological specificity of the organism concerned, but

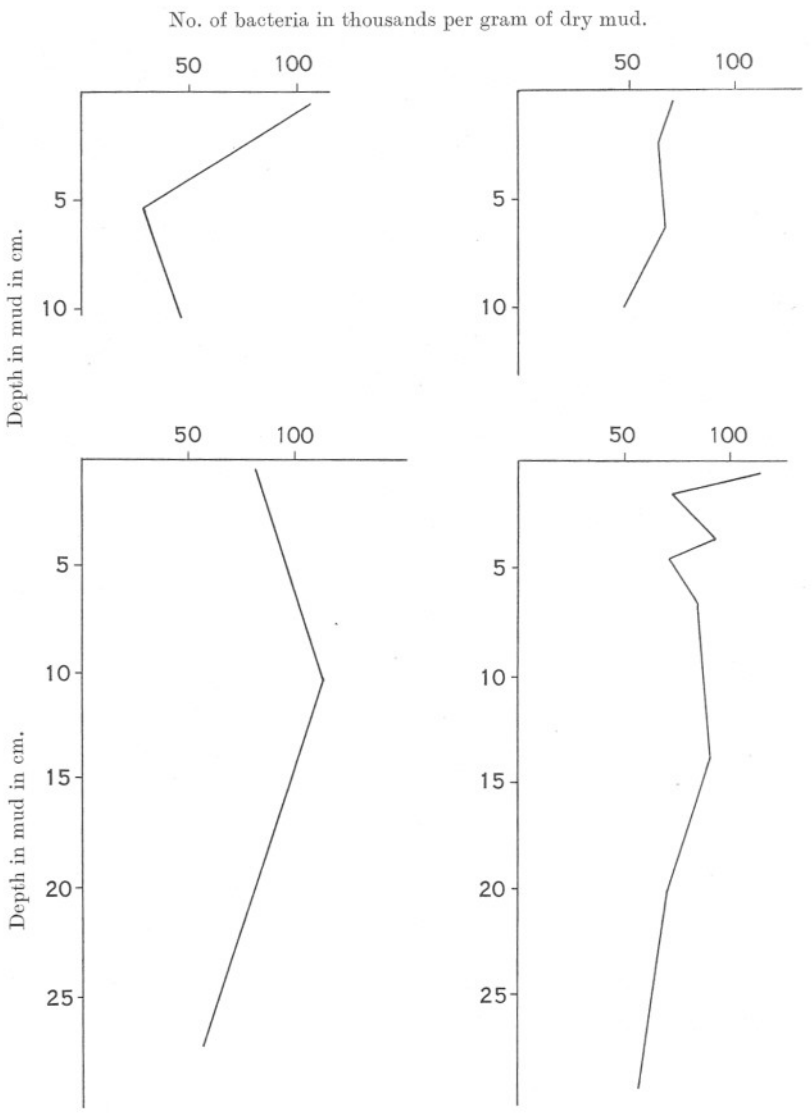

FIG. 2.—Bacterial Content of Marine Muds.
Above, Station 1B, 10/4/30 and 27/5/30.
Below, Station 7B, 14/4/30 and 3/6/30.

on such external conditions as temperature, hydrogen ion concentration and initial concentration of nitrate (8).

(ii.) There occurred in the samples a small proportion of small Gram-negative diplococci and sarcinæ forming cream, yellow or brown colonies. They resembled physiologically the first group, but were morphologically distinct. However, since morphologically bacteria are extremely plastic, it is possible that these are stages in the life history of members of the first group.

(iii.) The second group in order of numerical importance was found to consist of relatively large, spore-forming bacilli similar to the forms common in soil. Microscopically, they are often seen adhering in long chains. Culturally, they are recognised by their white slightly raised colonies, with a matt surface and irregular, dendritic or radiating outline. Physiologically they are more active than the preceding group, for they ferment the common sugars more readily; dextrose and sucrose are commonly attacked by these organisms, and a few are even lactose fermenters. Some strains produced indol from peptone. Under favourable conditions most of the members of this group reduced nitrates to nitrites, and a few reduced nitrates to gaseous nitrogen.

These organisms form a much larger proportion of the bacteria of the muds than of the water above, and they present many resemblances to the common spore-forming soil organisms. It is therefore necessary to consider whether they are species peculiar to marine muds, or whether they are terrigenous. It is not known whether they exist in the mud in the spore state or in the vegetative state.

(iv.) A small proportion of spirilla occurs. They grow only slowly on ordinary media, and the quantitative counts therefore often omit them. They may, however, be found in a mud dilution by first sedimenting the larger mud particles and then centrifuging the suspended micro-organisms and finer mud particles. Large colourless spirilla containing sulphur globules were occasionally found.

DISCUSSION OF RESULTS.

From the foregoing it is seen that in the Clyde Sea Area the bacterial content of the sea bottom is higher than that of sea-water, even of the water immediately overlying the mud. These results do not necessarily represent the total number of bacteria, since it is highly probable that there are many forms which do not grow on ordinary media, and therefore escape notice. The bacteria of the mud may be affected by the following factors :—

1. *Oxygen.* It appears that there is no free oxygen in the mud itself, and that oxygen cannot penetrate far below the surface. This has a marked effect upon the distribution of the fauna ; Moore has shown elsewhere in this Journal (**10**) that the oxygen-loving Copepods are restricted to the

top few centimetres, while the Nematodes, on account of their lower oxygen requirements, can penetrate deeper. It is evident that bacteria are not as a class thus restricted, for they occur in very large numbers even at a depth of 30 cm. These bacteria thus live normally under anærobic conditions, though when cultures are made they grow quite readily in air. It is possible that the muds contain in addition many strict anærobes, whose presence would not be revealed by the ordinary counting technique. However, some preliminary experiments with anærobic cultures made from mud samples did not show any conspicuous anærobe.

The terms "ærobe" and "anærobe" have become increasingly unsatisfactory, since it has been shown that the difference is only one of degree, and that the so-called anærobic bacteria are really organisms which require a low oxygen pressure. Some of these so-called anærobes can utilise combined oxygen; the most important of these are the denitrifying bacteria, which will reduce nitrates, using the oxygen for respiration, and liberating the nitrogen as waste metabolite. There is no direct experimental evidence to show that denitrification occurs in muds.

Hitherto it has been thought that in temperate latitudes the destructive effect of denitrifying bacteria on the nitrate in the sea was negligible, for the following reasons:—(i.) the number of bacteria in the sea-water is relatively low (**7**), and of these only a certain number are denitrifiers, (ii.) free oxygen is present in sufficient amount to inhibit nitrate-destruction (**3**), and (iii.) the low temperature prevents denitrification (Gran, **3**). The last condition is the only one that applies to the muds, however, for the number of bacteria is extremely high, and the aeration insufficient. The hydrogen ion concentration, the low nitrate concentration, in fact, all conditions except temperature, favour denitrification, so that on theoretical grounds it would appear that loss of nitrate by bacterial action is much more likely to occur here than in the sea-water above.

2. *Hydrogen ion concentration.* There is a slight downward decrease in pH value in the muds (**10**), and there is also a downward decrease in the bacterial content. However, although many micro-organisms are extremely sensitive to changes in hydrogen ion concentration, the range of variation here is too slight to account for the progressive downward decrease in the number of bacteria.

3. *Temperature.* The rate of multiplication of bacteria increases with temperature up to the optimum for any given species. No data for the temperature of the muds are available, but the low temperature of the bottom waters—from 7° to 14° C. in Loch Striven—(**12**) suggests that the rate of multiplication of bacteria on the sea bottom is limited by this factor.

4. *Light Intensity.* With increasing depth of overlying water there

is diminished light intensity at the mud surface. This does not appear to have any effect on the bacterial numbers ; there is no apparent relation between the bacterial content at the mud surface and the depth of overlying water. This is confirmed by the fact that at the mud surface the numbers are usually greater. In any case, even the surface of the mud does not receive the short light waves, which are bactericidal in their action.

4. *Food Supply.* The most important factor affecting bacterial numbers is the amount of available foodstuffs. The chief source of food supply to the mud bacteria is the accumulated dead plankton. This is subject to seasonal variations, for the amount of organic matter deposited on the sea floor depends upon the flora and fauna in the waters above. In the lochs of the Clyde Sea Area the sedimentation of phytoplankton after the spring diatom increase is most important : Moore has shown (**10**) that this seasonal deposition of diatoms forms well-marked layers in the muds of undisturbed stations.

Such zones would be layers of intense bacterial activity, and would have a much higher bacterial content than the intervening layers ; these zones would continue to have a high bacterial content until such time as the food supply was exhausted by the bacteria or other organisms competing for the same food supply. That bacterial zonation occurs in the mud is shown diagrammatically in Figure 2, where at Station 7B there are between the surface and 7 cm. four zones of alternating high and low bacterial content. A more detailed examination of the mud samples would probably show a better correlation between the diatom layers and the zones of high bacterial content, but this so far has not been done ; it would be necessary to take many more samples, in order to ensure that such variations were not chance variations.

Although the surface numbers are high, they are irregular, and do not show any definite relation to the spring increase. For instance, the Lochhead and Mid-loch types show a great difference in bacterial numbers, though at these two places the spring increase is parallel, and of almost equal intensity.

In the deeper mud layers, the food supply is gradually exhausted, but the fauna becomes progressively reduced in numbers downwards, so that bacteria are in all probability the predominant organisms at the greatest depth.

It has already been pointed out that there are great fluctuations in bacterial numbers at the mud surface. These fluctuations would depend partly upon the varying amount of foodstuffs present, and also upon the numbers of organisms such as protozoa which feed upon the bacteria.

The spring diatom increase at all stations was over by April 1st, 1930 ; the accumulation of diatoms at the bottom then follows, the time interval

depending upon the depth of the water. An accumulation of plankton rain does not necessarily imply a sudden increase in the bacterial population at the bottom. Different species may develop according to the ordinary population curve with an initial lag period, a maximal growth period, and a period of decay due to diminished food supply and accumulation of toxic metabolic products. Different groups of bacteria may follow one another, but there is at present no experimental evidence for this. At the bottom of the sea, however, conditions are complex and cannot accurately be reproduced in the laboratory, so that it is difficult to gain exact knowledge of the growth and physiology of mud bacteria under natural conditions.

In conclusion, the writer wishes to acknowledge the help received from members of the Station staff at Millport.

SUMMARY.

1. The bacterial content of mud deposits in the Clyde Sea Area has been investigated.

2. The number of bacteria is found to decrease from the surface downwards.

3. The numbers fluctuate very much in the top mud layers, and there is some evidence of bacterial zonation.

4. In the deeper mud layers the bacterial content for any given station is fairly constant.

5. The predominant organisms were found to be water bacteria of the *Achromobacter* and *Chromobacterium* type, and large spore-forming bacilli similar to common soil bacteria.

6. The factors affecting the bacterial content of the muds are discussed.

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The Vertical Distribution of Marine Macroplankton. XI. Further Observations on Diurnal Changes.

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With 7 Figures in the Text.

On June 3rd–4th, 1926, a further series of observations was made on the vertical migrations of plankton animals by means of collections with the 2-metre stramin ring-trawl. Thus, with the observations made on one night in July, 1924 (**1**), and on two nights in June, 1925 (**2**), we now have data for four nights.

Since so few observations of this nature have been made at sea it seems desirable that the results obtained on this fourth night should be published.

The collections were made in the same way as on the previous collections and the log, giving full details of conditions at the time of collecting, has been given in a previous publication (**3**) in which the behaviour of the young fishes is described.

The collections are noteworthy for the very large numbers of animals caught, catches as large as over 120,000 organisms for a ten-minute haul being recorded. Swarms of *Calanus finmarchicus* and Crab zoeas were chiefly responsible for these high numbers. It is also interesting to record the presence in the catches at night of numbers of small Portunid crabs up to about a size of 4 mm. in carapace breadth. Of thirty-eight specimens examined all were *Portunus depurator*.* Small *Pandalina brevirostris* and Crangonids also migrated at night into layers well above the bottom. Many of the animals living in the upper water layers in the daytime were much nearer the surface on the morning of June 4th than they were on the previous afternoon. This is possibly due to the light intensity being cut down by the enormous swarms of Calanus and Crab zoeas present on June 4th ; it has already been shown that many of the young fishes were affected in the same way (**3**, p. 833).

On the whole, however, the results are so confirmatory of the other observations that it is unnecessary to deal with the data as fully as in the two previous papers. They are therefore here given only in the form of

* I am greatly indebted to Mr. R. Palmer for the identification of these young Portunids.

diagrams for the many species (Figs. 1 to 7, pp. 776 and 782) and as a Table setting out the complete catches of all organisms (Table I, pp. 783 and 784).

Comparison of Results of Four Series of Collections.

It is now possible to compare the results of the four series of collections and on pages 771 to 775 are given in summary form the types of behaviour shown by the more important species on the four nights in question, namely July 15–16th, 1924, June 17–18th, and 18–19th, 1925, and June 3–4th, 1926.

It must be realised that for most species we are dealing with a mixed population, composed of individuals of different ages and perhaps sexes; this point has been emphasised in a recent publication (**4**) in which the behaviour of Sagitta of different sizes is studied. It must also be borne in mind that, in the method of collecting, the catches from the different depths have not been made simultaneously (see **2**, pp. 81 and 82). We cannot hope, therefore, to attempt to draw conclusions on the fundamental factors controlling the behaviour of the animals. The time has now come when a number of simultaneous collections must be made in rapid succession during the hours of changing light intensity at dusk and dawn, and attention must be given to the behaviour of each stage of development of the species caught.

Nevertheless these four series of collections have given us a very good picture of how the larger plankton animals behave as a whole throughout the twenty-four hours in June and July in the waters off Plymouth.

After a careful study of the available data it is evident that whatever be the physical and chemical conditions of the environment that control the behaviour of the animals and provide the necessary stimuli, there are two factors inherent in the animals themselves which are largely responsible for the type of distribution shown by any species during the night, namely :—

1. The depth at which the animal has been living during the previous daylight.
2. The speed at which the animal is capable of swimming upwards.

In the report on the first night's observations in 1924 (**1**, p. 779) the types of behaviour shown by the different species were grouped under the following four headings :—

1. Those that definitely migrated to the surface at night from the deeper layers in which they dwelt by day, showing a very large increase in numbers on the surface with a corresponding decrease in the deeper layers.

2. Those that did not show a definite migration to the surface at night, but merely extended their distribution into the surface layers, which they avoided by day. In this case a diminution in numbers was shown at the region of maximum intensity in the daytime, so that the distribution from surface to deeper layers was more or less uniform.
3. Those forms whose daytime distribution altered little or not at all at night.
4. Those that showed a movement upwards from the bottom, appearing in large numbers at night at a level about 10 fathoms from the bottom.

Actually it seems probable now that these groups cannot be separated, but that one merges into the other and a complete gradation can be obtained in the different types of behaviour, depending largely on the depths at which the animals are living in the daylight and the rates at which they can swim upward. In the present paper the figures giving the diagrams of vertical distribution for the different species (Figs. 1–7, pp. 776 and 782) have been arranged in order to give more or less a complete gradation from a species such as Leuckartiara (=Turris) which migrates rapidly to the surface at dusk, to Mysids and other bottom-living animals which have time only to reach the layers up to 20 metres below the surface. Good examples also are given showing how in one group of animals differences in activity will produce different behaviour at night. The diagram in Figure 6, for instance, shows that Mysids, chiefly *Leptomysis gracilis*, do not apparently have time during the night to migrate in numbers above 20 metres, whereas *Anchialus agilis*, as its name implies, is able rapidly to migrate right to the surface in considerable numbers (Fig. 5). A comparison of these figures with Figures 5 and 6 in the previous publication (**1**) shows that in 1924 these two species of Mysids showed exactly the same difference in their behaviour, the diagrams for the same species being almost identical. Figure 7, p. 782, shows the behaviour of two Cumacean species* at night ; *Diastylis rostrata*, like Leptomysis, did not appear in numbers above 20 metres, but *Bodotria scorpioides*, like Anchialus, migrated right to the surface. It is interesting to record as on a previous occasion (**1**, p. 797) that many of the Diastylis taken above the bottom at night were females. The young swimming crabs also were able to mount right to the surface in the dark, whereas the young of *Pandalina brevirostris*, like Leptomysis, could not migrate in numbers above

* I am greatly indebted to Dr. W. T. Calman, F.R.S., and Dr. Isabella Gordon for the identification of these two species as *D. laevis* Norman (=*D. rostrata* (Goodsir) in "Plymouth Marine Fauna") and *Bodotria* (=*Cuma*) *scorpioides* (Montagu) (=*C. edwardsi* of Sars', "Crustacea of Norway"). *B. scorpioides* is recorded for the first time at Plymouth.

the 20-metre level. Many other examples can also be seen, such as *Themisto gracilipes* as opposed to bottom amphipods. It is possible even that some species, e.g. perhaps Bougainvillea and Steenstrupia, which show no marked change in their distribution during the night hours, are prevented from doing so by their inability to swim quickly.

A study of pages 771–775, in which the results for the three years are compared, shows that for a great number of species almost identical types of behaviour were shown for all three years. For other species differences were shown, the animals behaving differently in one year from the other two. In no case did a species behave in a different manner in all three years. It is noteworthy that the majority of species showing the same type of behaviour in all three years were those which lived deep down or very near the bottom in the daytime, and whose depth is limited by that of the bottom. For animals of this class power of movement may be said to be almost more of a conditioning factor in their type of distribution at night than such factors as light intensity. For animals living nearer the surface, however, daylight may control the ultimate night distribution more, in that it affects the daytime distribution of the animals, which are not so limited in the depths to which they descend as are those which normally live very near the bottom. It is therefore more likely that differences in behaviour will be shown by those animals living nearer the surface in the daytime (see **4**, p. 404).

Differences in vertical distribution due to season also may affect the behaviour of the animals ; Tomopteris, for instance, in June lives very near the bottom in the daytime and its diurnal behaviour consequently appears very different from that shown in July when they are well up in the water during daylight.

At the same time the different animals are not all quite consistent in their behaviour. For instance, it has been shown that Sagitta in 1925 (**4**, p. 404) was living very near the bottom in the daytime, possibly being forced down by strong light owing to the clearness of the water, whereas in 1924 and 1926 Sagitta was well up in the water in the daytime. There is no evidence, however, that some of the other animals were affected to so marked a degree. Such phenomena can only be understood when we have far more observations carried out in greater detail.

A comparison of the four nights shows also that more of the deep-living animals reached the layers up to the surface in the nights in June, 1925, than they did on either of the nights in July, 1924, or June, 1926. It seems possible that owing to the scarcity of plankton animals on the nights in 1925 their passage upward was less impeded by obstructing animals. The presence of other animals in large numbers must in itself cause modification of the behaviour to be expected of an animal in perfectly uninhabited water. Both avoiding reactions and feeding reactions must

tend to divert an animal from its pure responses to physical and chemical environmental stimuli.

Summary of Observations on Four Nights.

Steenstrupia nutans.* 1924. "No marked vertical movements at night": numbers rather low.

1925. First night—numbers rather low.
Second night: "in the dark there had been a decided movement into the layers above 20 metres": did not extend in numbers much above 12 m.

1926. No marked vertical movement at night; slightly higher in water at dawn.

Leuckartiara octona.† 1924. "By 9 p.m. the majority were caught above a depth of 10 metres, and at midnight they were taken in greatest numbers right at the surface."

1925. "On both nights—but more markedly on the first—there seems to have been an active migration to the surface itself at dusk, followed by a downward movement at night in the dark and a further upward migration at dawn."

1926. Although the numbers rather point to encountering horizontal swarms there was a marked migration to surface at dusk, followed by a descent in the dark and a further upward migration at dawn. The medusæ remained high in the water the following day.

Obelia sp. 1924. "It cannot be said that there was any marked movement towards the surface at night."

1925. "The catches of Obelia were very small, and appear to indicate little co-ordinated movement."

1926. Entirely absent at night: no indication of movement at dusk.

Phialidium sp. 1924. "showed no signs of being affected by changes in light intensity."

1925. "There appear to be definite indications of an upward movement on the part of these medusæ at night."

1926. No very marked movement at night shown.

Cosmetira pilosella. 1924. "it would seem that here is shown a definite migration to the surface at night." Numbers rather low: present at surface at dusk.

1925. On both nights were evenly distributed from surface downwards in the dark: no movement at dusk.

1926. Same as 1925.

* All specific names used are those adopted in the *Plymouth Marine Fauna*, 2nd edition. 1931. Previously recorded as *S. rubra*. † = *Turris pileata* in previous papers.

Saphenia gracilis. 1924. "Present at the surface both at 9 p.m. and at midnight, and absent from there at other times." Numbers low.

1925. "the impression gained is that in its diurnal behaviour Saphenia resembled Cosmetira, except that in the daytime it went possibly deeper."

1926. Resembled Cosmetira in its behaviour, except fewer at surface itself.

Tomopteris helgolandica. 1924. Present in numbers right at the surface at dusk and at night, but they were already high in the water in the daytime, when the region of maximum abundance was at about 20 metres.

1925. On both nights Tomopteris appeared in numbers on the upper layers at dark and dawn, being probably very near the bottom in the daylight.

1926. Very similar behaviour to 1925, the majority probably living very near the bottom in the daytime.

Sagitta sp. These have been dealt with separately in another publication (**4**), the populations having been divided up into different size groups. There was, however, a very definite difference in the behaviour in 1925 from that shown in 1924 and in 1926. This would seem to be explained by the fact that in the daytime in 1925 the Sagitta were almost on the bottom, whereas in the other two years they were well up in the water layers in daylight.

Calanus finmarchicus. 1924. A definite migration to the surface at dusk, followed by an even distribution from the surface downwards in the dark.

1925. "By dusk there had been a marked upward movement in the water. . . . In the dark they were mostly distributed between the surface and 25 metres. The movements . . . were not as marked on the second night as on the first."

1926. Adult females: Slight upward movement at dusk followed by fairly even distribution from surface downwards in the dark. Larger concentration at 5 metres at dawn.

Adult males: Being lower in the water in daytime than the females hardly any had reached the surface by dusk, and the majority were still deep in the water at night.

Candacia armata. 1924. Definite migration to the surface at dusk, followed by fairly even distribution at night.

1925. Definite migration to the surface in the dark, but not at dusk, as the majority were living very deep down in the daytime.

1926. Same as 1925.

Mysids : Mostly *Leptomysis gracilis.*

1924. Appeared in larger numbers at night, but majority did not rise above 20 metres.

1925. Similar behaviour to 1924 but rather more taken in surface layers.

1926. Behaviour same as in 1924.

Anchialus agilis. 1924. "Unlike the other Mysids, which never rose much above 20 metres from the bottom, this form exhibited a very sudden migration towards midnight right to the surface."

1925. Similar to 1924 though fewer at surface and more evenly distributed.

1926. Behaviour same as in 1924.

Cumaceans. Showed the same type of behaviour in all three years, appearing only in upper layers at night. It was noticeable that the Diastylis species, probably *D. rostrata*, were not caught in numbers above 20 m. at night, but that Bodotria sp. were able to reach the surface (see page 769).

*Themisto gracilipes.** 1924. "A marked migration to the surface at midnight."

1925. Very rare.

1926. Same behaviour as 1924.

Apherusa sp. 1924. "Exhibited no marked movement at night."

1925. Marked movement on both nights, being evenly distributed from surface downwards.

1926. Probably same behaviour as 1925, though numbers at night rather low.

Bottom Amphipods showed same type of behaviour in all three years, appearing in upper layers at night only.

Pandalid larvæ. 1924. "Did not . . . show any marked change. . . . There is perhaps a slight tendency to rise at midnight, but the larvæ never appeared in numbers in the surface layers."

1925. There was a definite indication of an extension into the upper layers at night.

1926. Rather similar behaviour as in 1924.

Crangonid larvæ and *post-larvæ.* 1924. Appeared in upper layers at night, but were still most abundant below 20 metres.

1925. Same as 1924. but larger numbers extending to surface.

1926. Same as 1925.

Phyllosoma larvæ. 1924. Marked movement right to surface by dusk : but entirely absent at night.

* *Parathemisto oblivia* in "Plymouth Marine Fauna."

1925. Same as 1924 : still present throughout upper water layers at night.

1926. Same as 1925.

Galatheid larvæ. 1924. " At dusk and at midnight they tended to become more evenly distributed from the upper layers downwards, but were at no time very abundant on the surface."

1925. Upper layers filled up right to the surface at night.

1926. Same as 1925 but not so marked, as they were living higher in the water in the daytime.

Galatheid post-larvæ. 1924. Appeared in numbers at night in upper layers, but still most abundant below 20 metres.

1925. In numbers right to surface itself at night.

1926. In numbers right to surface itself at night.

Porcellana zoeas. 1924. " had spread out by 9.30 p.m. into all layers, and were still distributed in this manner at midnight."

1925. " The midnight behaviour on these two nights was apparently very unco-ordinated, but may possibly have been upset by the presence of swarms."

1926. Same as 1924, but more massed in upper layers in dark.

Porcellana post-larvæ. 1926. Similar behaviour to that of Galatheid post-larvæ, but rather slower going down at dawn.

Upogebia larvæ. 1924. " By 9 p.m. they were present in all layers from the surface to 30 metres. At midnight by far the majority were taken on the surface."

1925. " By dusk they were extending their distribution up to between 10 and 15 m., and in the dark they were most abundant actually at the surface." On second night "the surface itself was not fully populated as on the previous night."

1926. By dusk many had already reached surface, and at night biggest catch was just below the surface at 4 metres.

Pagurid larvæ. 1924. " There was a very slight rise at midnight, but no increase in numbers at the surface."

1925. A very marked movement, the surface layers being filled from the surface downwards at night.

1926. Definite extension into surface layers at night.

Pagurid glaucothoë. 1924. " At midnight they were taken on the surface, but in greatest numbers at 20 and 30 metres."

1925. " In the dark they moved up into the upper water layers as far as the surface itself, though the largest catches were still below 25 m."

1926. Same behaviour as 1924.

Crab zoeas (mostly Portunids). 1924. "Extending into the upper layers and surface at dusk and midnight."

1925. "A considerable increase in numbers in the layers above 15 to 20 m. on both nights, an increase which was pronounced also at the surface itself."

1926. Same as 1924.

Crab megalopas (mostly Portunids). 1924. "At midnight . . . appeared on the surface in large numbers, being distributed from top to bottom."

1925. A marked movement to the surface in the dark on both nights.

1926. A marked movement to the surface in the dark. Although at the surface in the daylight they were mostly below 10 to 15 metres at dusk.

SUMMARY.

1. Details are given of the results of a series of hauls with the 2-metre stramin ring-trawl fished at six different depths in daylight, at dusk, in the dark, at dawn and again in daylight on June 3rd–4th, 1926.

2. A comparison is given of the results obtained on the four nights July 15–16th, 1924; June 17–18–19th, 1925, and June 3rd–4th, 1926.

3. The importance is stressed of the effects on the type of behaviour shown by any animal produced by the depth at which it is living in the daylight and the speed at which it can swim upwards.

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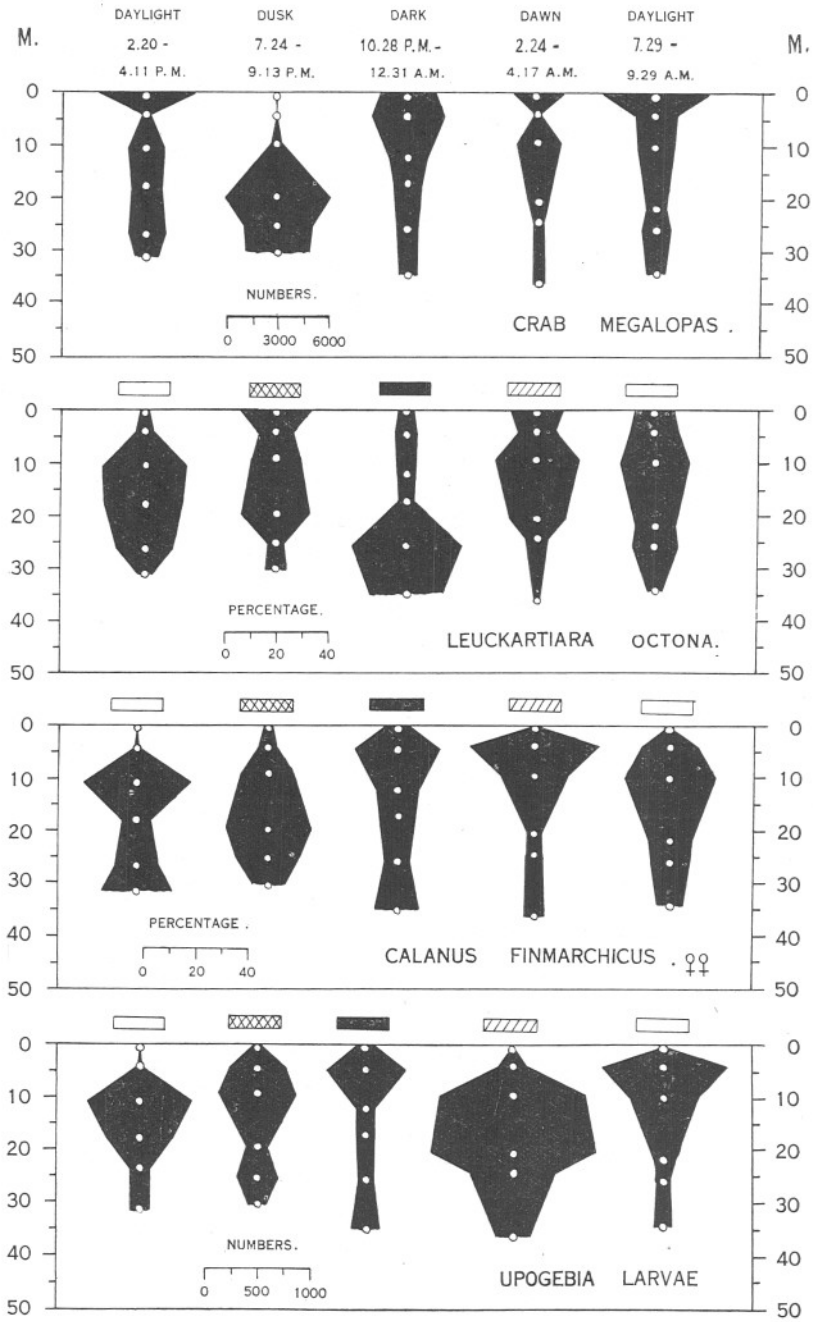

FIG. 1.—The vertical distribution of Crab megalopas (mostly Portunids), *Leuckartiara octona* (=Turris), *Calanus finmarchicus* adult females, and Upogebia larvæ at the times shown on June 3rd–4th, 1926. The plain, cross-hatched, black, and shaded rectangles represent "daylight," dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

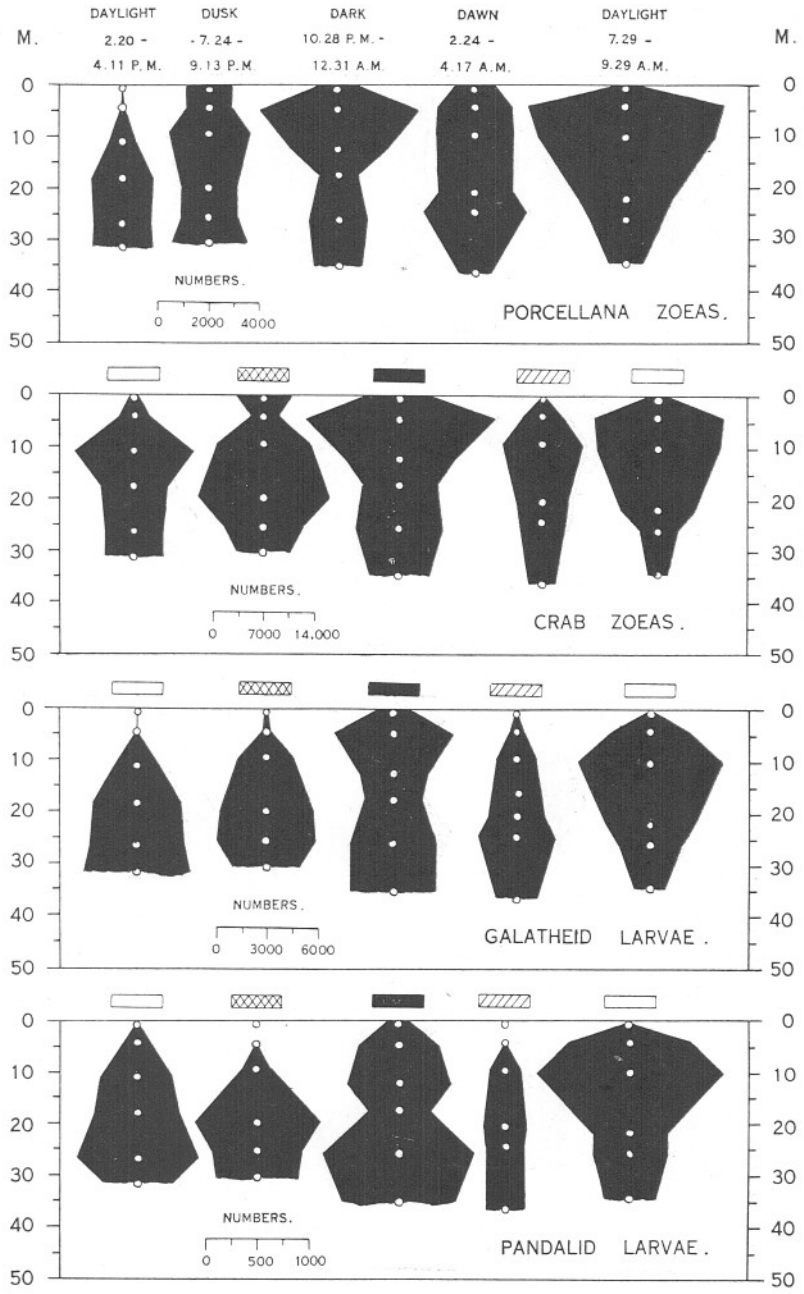

FIG. 2.—The vertical distribution of Porcellana zoeas, Crab zoeas (mostly Portunids), Galatheid larvæ, and Pandalid larvæ, at the times shown on June 3rd–4th, 1926. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

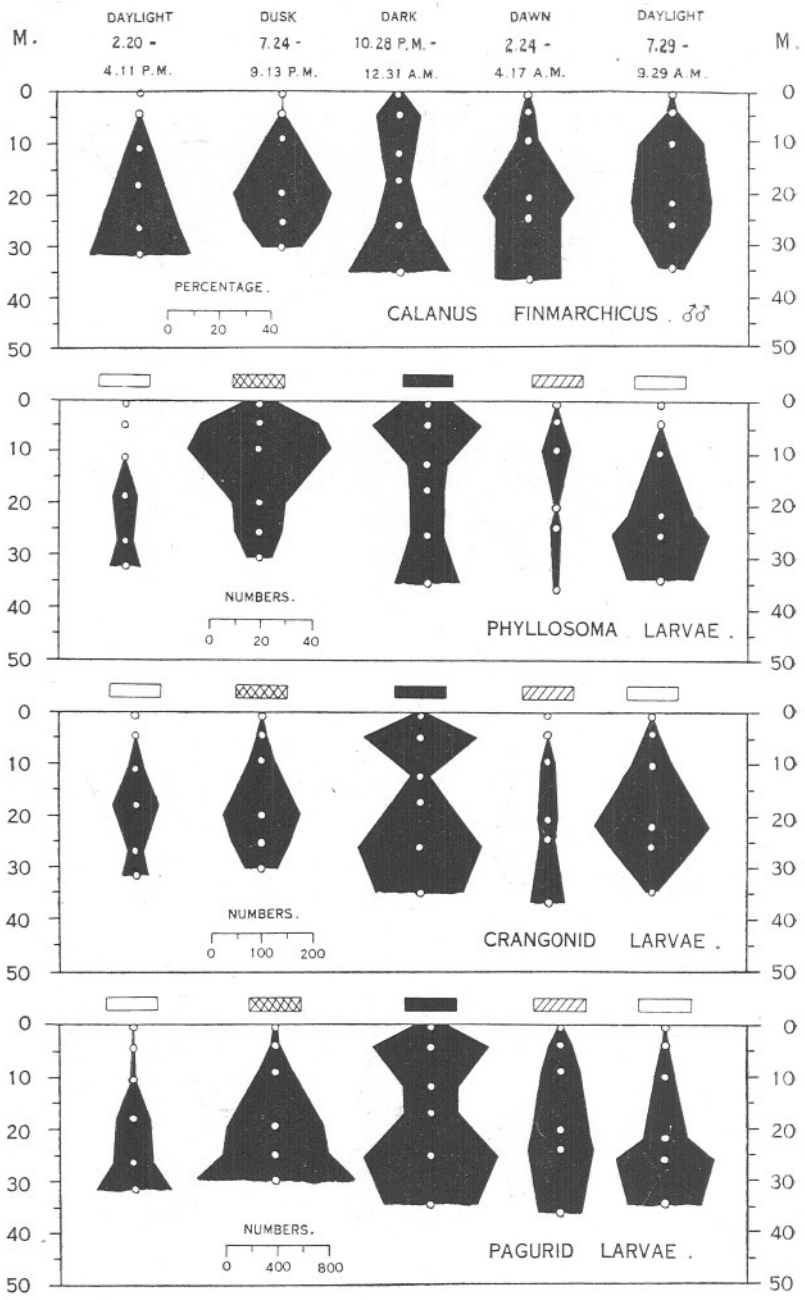

FIG. 3.—The vertical distribution of *Calanus finmarchicus* adult males, Phyllosoma larvæ, Crangonid larvæ, and Pagurid larvæ at the times shown on June 3rd–4th, 1926. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

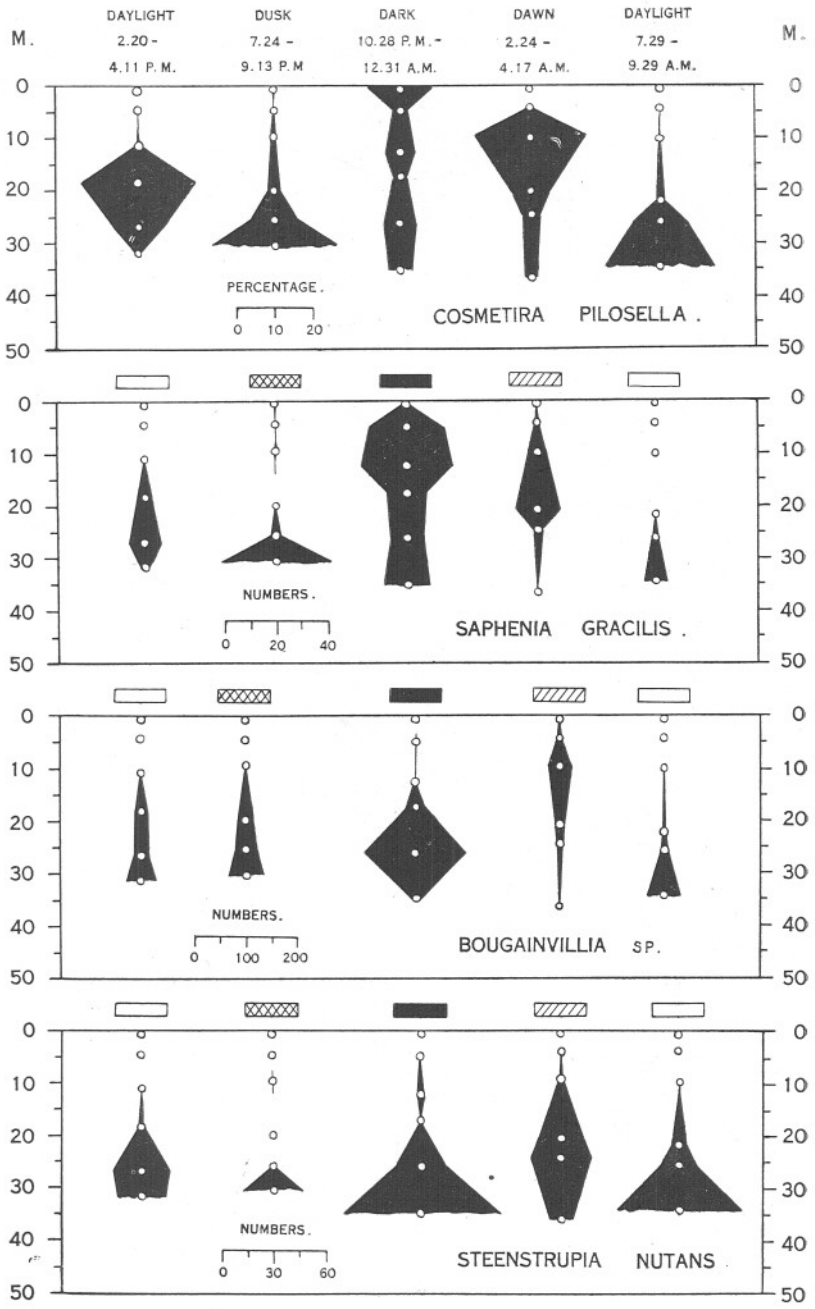

FIG. 4.—The vertical distribution of *Cosmetira pilosella*, *Saphenia gracilis*, Bougainvillea sp., and *Steenstrupia nutans* at the times shown on June 3rd–4th, 1926. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

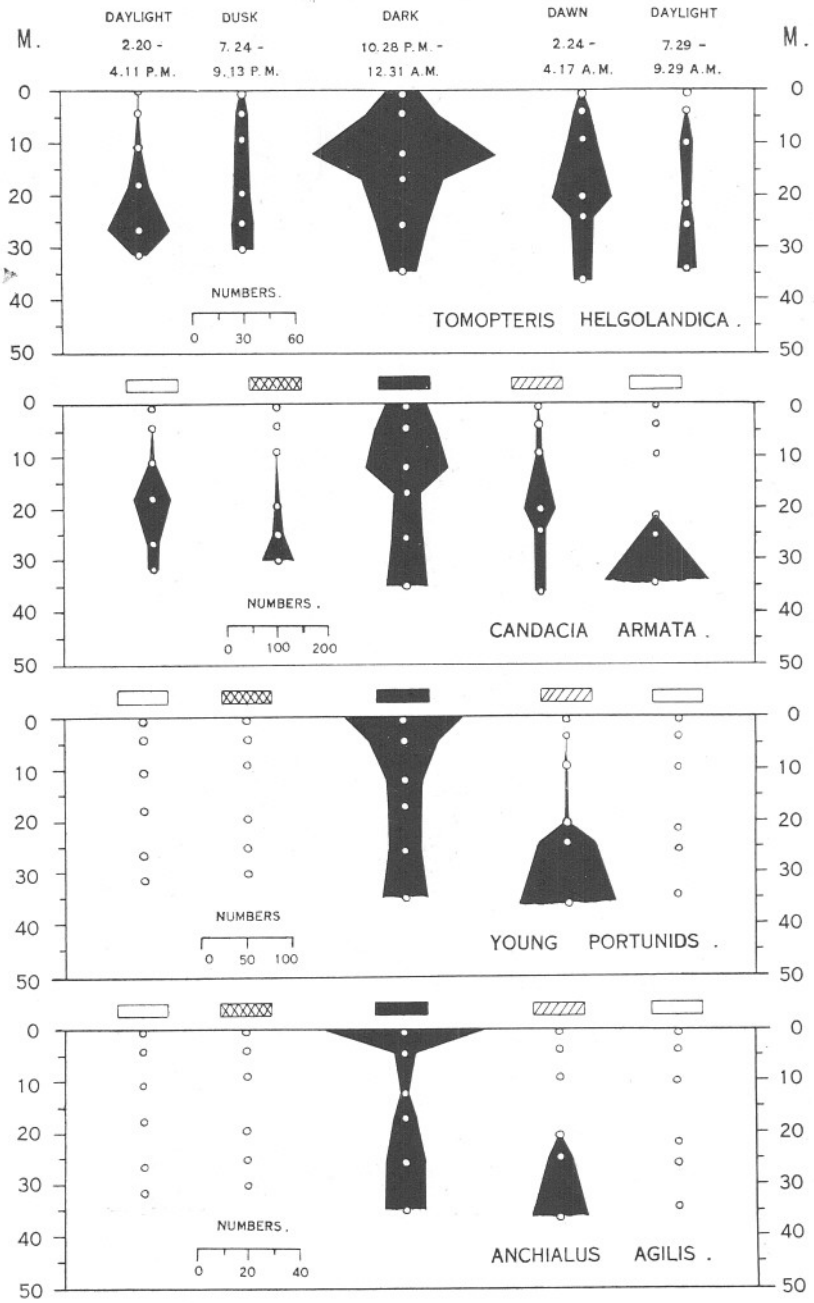

FIG. 5.—The vertical distribution of *Tomopteris helgolandica*, *Candacia armata*, Young Portunids, and *Anchialus agilis* at the times shown on June 3rd–4th, 1926. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

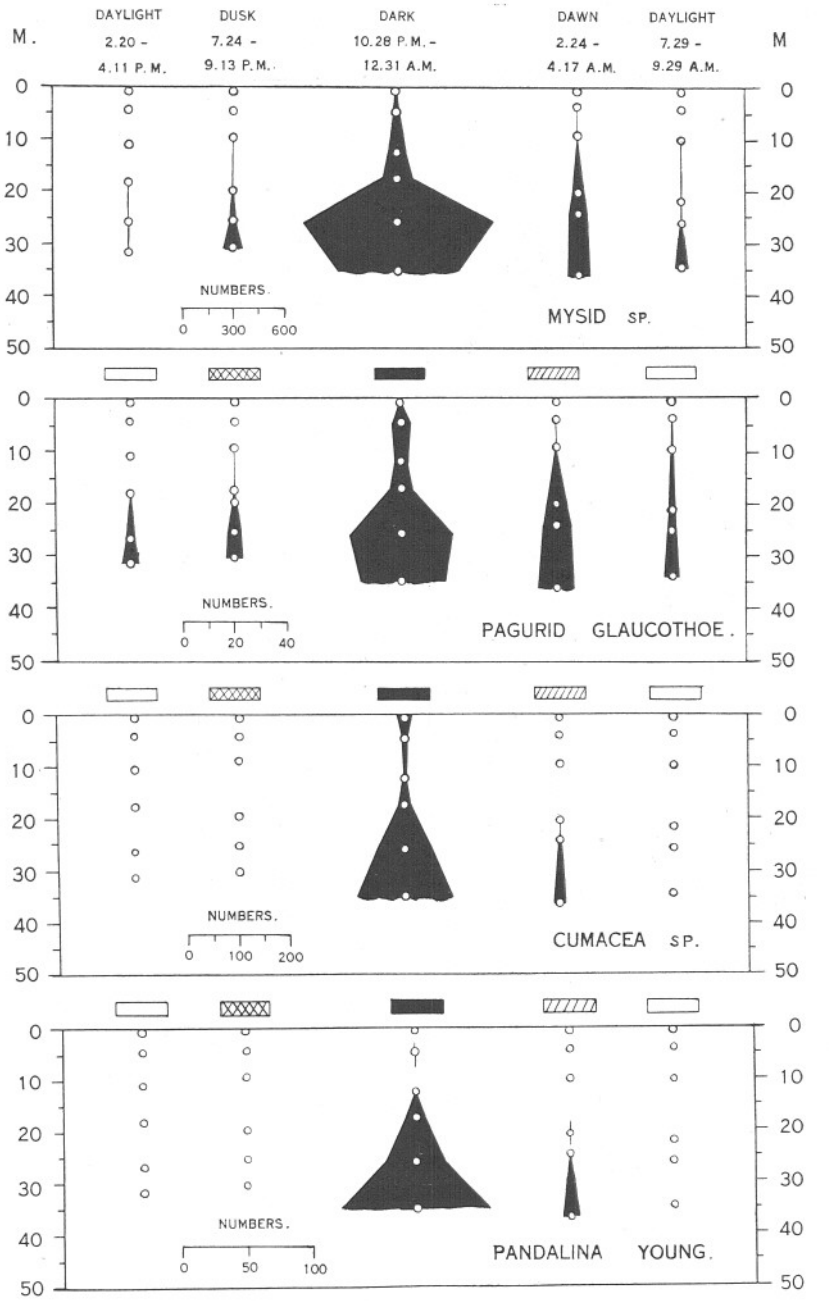

FIG. 6.—The vertical distribution of Mysids (chiefly *Leptomysis gracilis*), Pagurid glaucothoë, Cumacea, and young *Pandalina brevirostris* at the times shown on June 3rd–4th, 1926. The plain, cross-hatched, black, and shaded rectangles represent "daylight," "dusk," "dark," and "dawn" respectively. The white spots and black circles indicate the average depths at which hauls were taken.

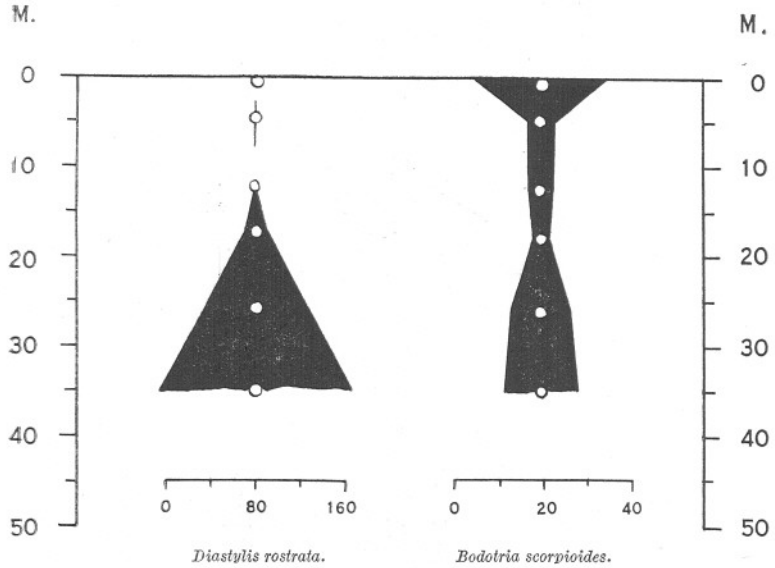

FIG. 7.—The vertical distribution of *Diastylis rostrata* (left) and *Bodotria scorpioides* (right) in the dark on June 3rd–4th, 1926. The white spots and black circles indicate the average depths at which hauls were taken. The scales give the actual numbers caught.

NOTES ON TABLE I.

SERIES 1.

Leuckartiara octona. At surface and 4·25 m. in first daylight series these were all small medusæ; the larger medusæ being in the deeper layers.
Tomopteris helgolandica from surface, 4·25 and 10·75 m., were all in a damaged state.
Nyctiphanes. Series one—all juvenile.
Mysids were very small stages.

SERIES 2.

Crab zoeas. Surface and 4·4 m. Mostly very small specimens.
Galatheid l. Surface, small.
Porcellana zoea. Surface, small.
Pandalid l. 4·4 m. Very small.
Crangonid l. 4·4 m. Very small.
Hyperiid at surface = *H. alba.*
Nyctiphanes. All juvenile.

SERIES 3.

Leuckartiara octona. Surface. Small.
4·6 m. Half small.
12·3 m. Most small.
11 m. Small.
rest=some small.

Young Portunids. Thirty-eight examined at 25·9 m. by R. Palmer= all *P. depurator.*

Young crangons up to 15 mm. long. At 25·9 there were two and at 35 m. three *Philoceras bispinosus* in berry 12 and 15 mm. long.

SERIES 5.

Leuckartiara octona. Surface to 10 m. Many small: larger deeper.

TABLE I. Ring-Trawl Catches. June 3rd–4th, 1926.

Time.	*Depth in metres.*	Steenstrupia nutans.	Slabberia halterata.	Bougainvillea sp.	Amphinema dinema.	Leuckartiara octona.	Cosmetira pilosella.	Obelia sp.	Phialidium sp.	Saphenia gracilis.	Cyanea lamarcki.	Pleurobrachia pileus.	Peachia larvae.	Arachnactis larvae.	Tomopteris helgolandica.	Pœcilochætus larvae.	Sagitta elegans.	Sagitta setosa.	Calanus finmarchicus ♀	Calanus finmarchicus ♂	Calanus finmarchicus St. V.	Metridia lucens.	Candacia armata.	Anomalocera Patersoni.	Labidocera Wollastoni.	Caligus sp.	Mysid spp.	Anchialus agilis.	Haplostylus Normani.	Nyctiphanes.
4.1 p.m.	*S.*	–	–	–	–	7	–	–	90	–	–	–	3	–	1	–	40	13	117	6	–	–	–	2	2	–	–	–	–	–
3.44 ,,	*4·3*	–	–	–	–	12	–	–	320	–	–	–	3	–	1	–	92	49	2,000	43	107	–	–	–	20	1	–	–	–	–
3.25 ,,	*10·8*	–	–	2	3	58	35	50	790	–	–	–	4	1	4	–	1028	92	40,437	3,145	1,338	–	10	2	100	3	–	–	–	3
3.3 ,,	*18*	3	–	27	6	57	2271	4000	2360	6	–	–	7	1	12	4	1117	83	10,876	6,296	1,908	–	70	1	?	2	3	–	–	4
2.42 ,,	*26·6*	33	1	29	4	38	982	2700	3710	12	–	12	16	1	36	4	3784	167	16,585	10,120	1,405	–	20	–	50	1	5	–	–	3
2.20 ,,	*31·5*	28	2	60	2	10	119	810	1340	3	–	13	8	2	8	2	4090	120	26,441	12,591	2,938	–	20	–	140	2	4	–	–	8
9.3 p.m.	*S.*	–	–	–	–	393	33	–	120	1	3	1	–	–	2	–	513	677	3,046	90	1,344	–	–	–	10	8	–	–	–	–
8.46 ,,	*4·4*	–	–	–	–	183	5	–	190	–	2	–	–	–	6	–	392	288	5,474	805	1,771	–	–	1	–	7	–	–	–	–
8.28 ,,	*9·3*	1	–	3	–	271	38	–	310	1	1	–	3	–	7	1	755	745	16,832	7,088	5,610	–	–	3	20	3	1	–	–	–
8.9 ,,	*19·7*	–	–	31	–	373	140	20	320	1	–	1	7	1	9	3	1318	252	26,603	18,929	5,628	–	10	–	70	2	8	–	–	7
7.48 ,,	*25·3*	1	–	43	–	83	296	220	1520	4	1	6	21	1	13	–	766	464	20,401	14,572	1,457	–	20	–	10	4	29	–	–	1
7.24 ,,	*30·3*	35	1	63	3	118	1249	3730	4150	42	–	19	43	–	12	2	1530	550	10,597	7,308	365	–	60	2	10	2	101	–	–	3
12.21 a.m.	*S.*	–	–	–	–	11	848	–	30	1	1	2	–	–	18	–	143	287	13,798	2,123	1,769	–	80	2	–	1	2	63	4	9
12.1 ,,	*4·6*	–	1	4	–	17	199	–	380	29	–	9	3	1	41	1	188	452	52,805	10,268	10,267	–	120	3	–	2	30	8	2	72
11.36 p.m.	*12·3*	4	–	5	–	14	402	–	840	35	3	17	11	2	105	1	108	412	27,276	8,142	5,292	–	160	4	20	1	104	3	4	77
11.13 ,,	*17·2*	1	–	33	–	11	167	–	550	15	–	10	5	–	47	2	156	264	23,991	5,511	2,918	30	50	3	30	1	172	9	4	47
10.51 ,,	*25·9*	29	1	196	–	76	440	–	910	13	1	12	11	–	30	3	124	317	17,039	11,025	5,346	20	60	4	20	–	1106	16	1	83
10.28 ,,	*35*	91	1	15	–	52	292	–	1110	18	–	9	10	–	15	2	456	604	28,359	23,948	10,713	10	80	8	30	1	705	16	1	75
4.7 a.m.	*S.*	–	–	–	–	25	–	–	–	–	1	–	–	–	1	–	257	93	2,141	67	22	–	–	–	–	–	–	–	–	–
3.49 ,,	*4*	–	–	10	–	18	4	–	40	2	–	–	–	–	9	–	454	116	44,582	929	939	–	10	–	–	2	–	–	–	1
3.29 ,,	*9·5*	3	–	49	1	40	577	–	750	7	–	–	8	2	17	–	1152	338	23,842	1,340	1,608	–	10	–	20	1	4	–	–	5
3.8 ,,	*20·5*	27	1	18	2	27	196	1550	2310	17	–	2	17	–	35	3	993	207	5,630	5,755	1,125	–	60	–	100	2	68	–	–	17
2.47 ,,	*24·4*	35	1	11	–	12	92	460	720	3	–	3	6	1	13	1	388	172	6,458	4,066	1,436	–	20	–	10	2	107	9	1	16
2.24 ,,	*36·3*	13	2	8	1	3	61	390	170	–	–	3	2	–	9	–	507	72	7,118	4,163	2,149	20	20	–	60	1	129	21	–	8
9.19 a.m.	*S.*	–	–	–	–	123	–	–	30	–	–	–	–	–	–	–	117	13	529	76	25	–	–	60	20	–	–	–	–	1
8.59 ,,	*4*	–	–	–	–	156	–	–	10	–	–	1	–	–	–	–	347	244	37,375	3,602	4,053	–	–	3	50	1	–	–	–	2
8.38 ,,	*10*	–	–	–	–	223	9	–	100	–	1	4	–	–	7	–	852	107	58,660	19,003	4,957	–	–	–	20	2	–	–	–	7
8.17 ,,	*21·8*	9	–	10	–	120	61	20	120	–	5	4	1	–	4	1	1426	194	29,101	23,965	3,994	–	–	–	60	–	8	–	–	94
7.52 ,,	*25·7*	21	–	17	–	149	432	60	980	3	5	9	4	–	8	1	2428	272	25,327	22,347	1,986	–	60	–	–	1	11	–	–	48
7.29 ,,	*34·3*	72	1	61	–	43	864	220	1100	9	–	13	8	–	13	–	2112	808	17,563	8,376	1,081	–	200	1	–	2	63	–	–	33

TABLE I.—*Continued.*

Time.	*Depth in metres.*	Diastylis rostrata.	Bodotria scorpioides.	Themisto gracilipes.	Apherusa sp.	Bottom Amphipods.	Pandalid larvæ.	Pandalid post-larvæ.	Pandalina brevirostris.	Spirontocaris larvæ.	Leander larvæ.	Crangonid larvæ.	Pontophilus spinosus l.	Young Crangonids.	Palinurus phyllosoma.	Galatheid larvæ.	Galatheid post-larvæ.	Porcellana zoeas.	Porcellana post-larvæ.	Upogebia larvæ.	Pagurid larvæ.	Pagurid Glaucothöe.	Young Portunids.	Crab zoeas.	Crab megalopas.	Corystes megalopas.	Echinospira larvæ.	Limacina retroversa.	Total Organisms.
4.1 p.m.	*S.*	–	–	–	–	–	12	–	–	–	9	–	–	–	–	–	–	40	–	–	–	–	–	1,160	5490	–	–	–	**6,992**
3.44 ,,	*4·3*	–	–	–	–	–	280	–	–	–	9	–	–	–	–	130	–	180	–	50	10	–	–	4,200	530	–	–	–	**8,037**
3.25 ,,	*10·8*	–	–	–	10	–	670	–	–	140	25	30	2	–	–	2670	–	1020	10	1010	10	–	–	16,080	2030	–	10	–	**70,822**
3.3 ,,	*18*	–	–	1	40	–	830	–	–	60	5	90	26	–	10	5210	–	2360	10	680	260	–	–	8,980	1820	–	360	50	**49,906**
2.42 ,,	*26·6*	–	–	–	60	–	1180	2	–	70	10	30	16	–	6	5420	–	2200	30	200	310	3	–	7,870	2150	–	150	–	**59,425**
2.20 ,,	*31·5*	–	–	1	50	–	680	–	–	20	3	50	24	–	12	6210	–	2280	60	210	580	6	–	7,840	1490	–	20	–	**68,297**
9.3 p.m.	*S.*	–	–	1	–	–	–	–	–	–	3	–	–	–	12	180	–	1820	–	110	20	–	–	7,500	150	–	–	–	**16,037**
8.46 ,,	*4·4*	–	–	–	–	–	10	–	–	–	4	20	–	–	46	510	–	1750	–	560	70	–	–	3,910	90	–	10	–	**16,104**
8.28 ,,	*9·3*	–	–	–	150	–	270	–	–	–	19	50	–	–	56	3240	–	3130	20	750	260	–	–	12,720	650	–	40	10	**53,058**
8.9 ,,	*19·7*	–	–	–	170	–	1210	20	–	40	3	150	17	–	21	5580	10	2190	50	210	760	1	–	17,890	6230	–	70	20	**88,375**
7.48 ,,	*25·3*	–	–	2	220	–	880	–	–	40	8	110	4	–	19	5770	10	2200	90	400	820	5	–	10,790	4010	–	30	20	**65,361**
7.24 ,,	*30·3*	–	–	4	350	–	800	–	–	30	5	60	15	–	10	3920	10	2860	180	190	1220	6	–	7,250	3770	–	10	10	**50,695**
12.21 a.m.	*S.*	–	29	21	90	1	210	4	–	–	5	30	2	1	19	2220	160	1710	80	160	230	1	137	9,260	3370	1	20	40	**36,993**
12.1 ,,	*4·6*	2	6	4	40	7	780	18	1	60	11	220	6	34	42	6900	80	6180	240	760	900	7	82	25,700	4270	9	20	20	**121,301**
11.36 p.m.	*12·3*	–	5	–	60	5	1000	11	2	10	4	40	9	18	16	4060	220	3640	160	170	420	5	42	14,850	2210	14	50	20	**70,083**
11.13 ,,	*17·2*	21	3	3	–	3	620	12	15	10	5	110	9	42	14	3270	150	1540	90	170	420	9	40	10,340	1660	15	30	10	**95,680**
10.51 ,,	*25·9*	90	13	1	40	11	1470	15	47	40	–	240	30	44	13	5260	350	2230	220	150	1040	40	38	12,140	1240	12	50	10	**61,717**
10.28 ,,	*35*	170	16	2	–	21	1110	11	116	50	3	170	15	55	25	5070	320	1910	220	260	740	33	53	8,280	1140	14	90	–	**86,515**
4.7 a.m.	*S.*	–	–	–	20	–	20	–	–	–	10	–	–	–	–	50	–	1660	–	–	20	–	–	980	2800	–	–	–	**8,167**
3.49 ,,	*4*	–	–	–	50	–	40	–	–	–	9	–	–	–	4	1120	–	2960	10	270	170	–	–	5,260	440	–	–	–	**57,449**
3.29 ,,	*9·5*	–	–	–	70	–	310	–	–	30	11	30	5	–	11	2360	–	3020	120	1420	290	1	2	10,940	2540	–	70	–	**50,964**
3.8 ,,	*20·5*	–	1	–	30	2	430	1	1	30	4	40	4	–	1	3390	40	2870	480	1580	440	8	4	7,030	1180	–	90	–	**35,818**
2.47 ,,	*24·4*	2	1	–	40	16	380	2	–	30	4	30	5	19	4	4540	210	4140	470	790	490	11	65	6,510	680	3	30	–	**32,515**
2.24 ,,	*36·3*	12	5	2	20	29	390	3	13	–	1	70	4	17	1	2410	140	1240	360	330	330	14	112	3,720	850	5	30	–	**25,038**
9.19 a.m.	*S.*	–	–	–	30	–	10	–	–	–	5	–	–	–	–	380	–	1190	–	40	–	–	–	3,310	6080	–	–	–	**12,039**
8.59 ,,	*4*	–	–	–	90	–	1200	–	–	80	7	30	2	–	–	4630	–	7650	–	1190	60	–	–	17,570	2440	–	30	–	**80,823**
8.38 ,,	*10*	–	–	–	120	–	1820	–	–	40	2	80	15	–	8	8360	–	6820	–	660	160	1	–	16,920	2180	–	60	40	**121,238**
8·17 ,,	*21·8*	–	–	–	200	–	720	11	–	–	1	220	14	–	25	5300	20	3660	100	220	340	2	–	10,360	1160	–	20	–	**81,570**
7.52 ,,	*25·7*	–	–	2	280	–	720	16	–	–	2	160	9	–	38	3660	20	2880	60	140	760	3	–	5,120	1620	–	20	–	**69,679**
7.29 ,,	*34·3*	–	–	4	380	–	520	23	–	20	9	20	8	–	25	1820	100	1320	180	160	560	4	–	3,040	1180	–	40	–	**42,156**

Clione limacina in Plymouth Waters.

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With Plates I and II.

THE pteropod *Clione limacina* (Phipps), now regarded as one of the tectibranchs, occurs at times in the neighbourhood of Plymouth. In 1930, however, it was extraordinarily abundant, especially in the summer, and was breeding freely. Although not specially recorded it has been seen singly or in small numbers in almost any month of the year, and for some years the eggs and larvæ (not recognised at the time as belonging to Clione) have been seen in summer. So far it is known from the British coasts in the North Sea and the west and extreme south-west of England. Its distribution, as known up to 1908, is given fully for the area of International Fisheries Investigations by Paulsen (1910). There it is shown that it is an Arctic-boreal species, spreading southwards nearly to the Bay of Biscay, which is about its southerly limit. It is known to occur in the northern and mid North Sea, but not in the southern North Sea, and at that time was only recorded from the Channel in the extreme west. It is also common in the Atlantic. Paulsen was led to infer that *Clione limacina* did not enter the North Sea from the Channel, but its prevalence sometimes at Plymouth shows that it can come a long way up the Channel and, as few samples are taken to the east and in the southern North Sea, this view should be carefully reconsidered. It was also thought that the presence of *Clione limacina* indicated Atlantic water, but as it may be found in almost any month and breeds at Plymouth in summer, and as its large numbers do not specially coincide with any influx of Atlantic water, it seems more reasonable to suppose that it is a permanent member of the Channel plankton.

Paulsen (*op. cit.*) thinks that the nets used are too small for Clione, but at Plymouth the larvæ may be found in the finest tow-nettings (180 strands to the inch). It is perhaps more probable that the small larvæ, if present, are not generally recognised. At Plymouth the larvæ have been found in the tow-nettings of any mesh, and the adults in medium and course tow-nettings and in the ring-trawl.

Clione limacina usually occurs with *Limacina retroversa*, on which it probably feeds, as the usual food in Arctic waters is *Limacina arctica*, a closely related species. It also feeds on other plankton organisms, being extremely voracious and armed with powerful hooks, strong radula, tentacles, and head-cones. It is itself economically important, for not only does it form an important food for whales in Arctic waters, but is also largely eaten by mackerel and herring. Hardy (1924) states that in the North Sea *Clione limacina*, although of much less importance than Limacina, was taken in fair numbers in the summer of both 1922 and 1923 and formed about 0·21 per cent of the total year's food of the herring.

M'Intosh (1898) has described the late larvæ in various stages from St. Andrews Bay, all of which agree well with the Plymouth specimens. He shows that the southern examples are much smaller than the Arctic forms. Paulsen (*op. cit.*) is of the opinion that the Arctic form and the more southerly form are two distinct races. The Plymouth specimens are mature at 4 or 5 mm., the largest reaching to 12 mm. ; even at 3 mm. they may contain quite large eggs. M'Intosh's largest specimen measured 12 mm. The Arctic form reaches 40–41 mm. In support of Paulsen's view it is found that there are many more teeth in the radula of the adult Arctic form. The usual formula is 14–1–14 or 13–1–13, the side teeth being less in the younger individuals and gradually increasing with age (Pelseneer, 1886). In the Plymouth form the formula is 4–1–4 or 3–1–3 for all adults examined, ranging from 4 to 10 mm. in length. In no case have more than 4 side teeth been found. Thus the adults of the southern form have a radula formula similar to the young of the Arctic form. Another difference is the colour, which is much less intense than in the Arctic form, the hermaphrodite organ being a pale pinkish yellow instead of the brilliant orange-red of the Arctic form. It appears thus that we have truly a southerly form of *Clione limacina* differing from the northern form in size, radula formula, and colour.

In the Arctic regions *Clione limacina* spawns in shallow water ; in the Atlantic it spawns in the open sea. So far the breeding habits of the southern form have never been described.

Clione limacina may occur at Plymouth in any month of the year. The largest specimens have been seen in February and March and in August. The greatest number were seen in the summer of 1930 when all through June until the middle of August they were abundant, adults, young, and eggs were to be found in the plankton both from the outside waters and inside the Sound. Mr. O. D. Hunt notes that it also occurred abundantly in the neighbourhood of the River Yealm, going up the river, and that they reached 10 mm. in length. They were not seen to breed except in the summer months and at this time nearly every individual from 3 mm. in length carried eggs. If one of these laid eggs in a bowl, more eggs were seen

inside, indicating more than one brood. Moreover, development takes place very quickly, and probably only a few months are needed for quite a large size to be attained. It is very likely that those eggs laid in the summer yield mature animals the following summer.

If placed in a bowl on the Laboratory bench the mature individuals will nearly always lay eggs overnight. From these eggs some of the larvæ were reared until the stage in which the shell was lost and the three circlets of cilia were formed.

The later larvæ of *Clione limacina* have often been described, but the younger larvæ which are provided with a shell are not so well known, although very young larvæ of other species of the Clionidæ have been briefly described (Krohn, 1860). From the work of Fol (1875) we know the general form of the spawn of various pteropods, which appears to be of the same character in all species, both thecate and naked. The eggs are minute and laid in a perfectly transparent gelatinous ribbon, which is sometimes free and sometimes entangled in any light hairy object which may be floating in the plankton. There seems to be no reason to think, as Paulsen (*op. cit.*) has suggested, that they are laid on the bottom, for the eggs of both Clione and Limacina frequently appear in the plankton at Plymouth. The eggs are placed in the gelatinous ribbon at regular intervals, arranged differently in the different species, and are themselves perfectly transparent and begin to develop when only a few hours old, emerging as larvæ, with or without a shell according to the species.

Clione limacina has been described many times, the chief works being those of Eschricht (1838), Souleyet (1852), Boas (1886), Wagner (1885), Pelseneer (1886) and Meisenheimer (1906). All these treat mainly of the purely Arctic form. M'Intosh's (*op. cit.*) description of the southern form from St. Andrews Bay shows the differences between the two.

The eggs of *Clione limacina* are laid in a clear oblong or square gelatinous mass, sometimes more elongated, the matrix being very elastic and catching in any light obstacle which may be floating about. A typical mass may measure about 1 mm. to 1·2 mm. across, the perfectly colourless eggs being scattered about irregularly, of an oval shape, and measuring about 0·09 mm. by 0·08 mm. (Plate I, Figs. 1 and 2). In two or three days the larvæ emerge. The newly-hatched larva has a thimble-shaped shell, usually slightly irregular, measure about 0·15 to 0·16 mm. in length and 0·11 mm. in breadth. The shell is very thin and perfectly transparent, slightly pointed at the end, with the mouth widening a little. The larva is fixed to the shell by longitudinal muscles reaching from near the tip to the mouth of the shell (Plate I, Figs. 3, 4, 5). There is a well-developed bi-lobed velum edged with large cilia and a ridge below edged with small cilia, the two forming a groove to the mouth. The whole animal, including

the velum, is capable of complete retraction into the shell. The beginning of the foot sticks out between the velar lobes and is ciliated all over, stomach, intestine, and liver are seen and there are two conspicuous otoliths. The larva grows rapidly ; two or three days after hatching the shell has increased in length to about 0·18 mm. and the margin of the shell is finely striated longitudinally (Plate I, Fig. 6). The velum projects far out of the shell when the animal is swimming. In the next few days the shell rapidly increases, very soon almost doubling its original length. It has now reached the maximum size (Plate I, Figs. 7–8). Spicules can be seen lining the stomach and in it remains of food. The larvæ in the bowls were given a pure culture of Nitzschia and the spermatozoids of Fucus, but the food inside the stomach was not usually recognisable. The dinoflagellate *Prorocentrum micans* was once seen in the œsophagus of a larva which had lost its shell. There is strong ciliation down the intestine, œsophagus, and round the mouth region. The shell now disappears. It was not possible to be certain whether it was cast off or absorbed, but it is probable that it was cast off, as empty shells were found in the bowl. There are now three circlets of cilia round the larva, one at the neck, just below the velum, one near the centre of the body, and one at the hind end (Plate I, Fig. 10 ; Plate II, Figs. 1–6). The whole body is covered with very fine cilia. Beginnings of the radula can now be seen and the tentacles and head-cones begin to form ; the foot shows a small hind lobe and the velum very soon disappears. The larvæ were reared in the finger-bowls until the disappearance of the velum when they were 17 and 18 days old and measured about 0·32 mm. in length. After this they died. They were still quite colourless and transparent. Larvæ were then collected from the plankton, the earlier stages corresponding exactly with those reared in the bowls. From this stage onwards the internal organs gradually move forward so that, as has been noted by many workers, in the adult they occupy only the fore part of the body, leaving the hind part for the developing ova. Larvæ from the plankton slightly older than those reared in the bowls and measuring 0·48 mm. in length had head-cones, tentacles and hooks well developed, the radula present, the wings beginning to form behind the foot ventrally (Plate I, Fig. 11). The liver and intestinal mass has begun to move forward. At about 0·9 mm. to 2 mm. the wings are still more developed and at 2 mm. they may project well beyond the sides of the body. Whilst they are developing the ring of cilia at the neck becomes irregular as it is interrupted ventrally by the foot and wings. At 2 mm. the intestinal mass lies almost entirely in front of the middle ring of cilia (Plate II, Figs. 1–6). At 2·8 mm. all the cilia may have disappeared and the wings are well developed, the penis showing at the right side. The last row of cilia may however persist even when the animal is breeding. In a specimen 3 mm. long all the organs are formed,

and it may now lay eggs. One specimen, 2·8 mm. long, had eggs nearly ripe occupying the hind end of the body (Plate II, Fig. 7) and one of 3 mm. laid eggs in the Laboratory. Fol (*op. cit.*) notes that a young *Clione aurantiaca* Fol. from Messina which still retained the last ring of cilia was full of eggs. Pelseneer (*op. cit.*) suggests that this is *Clione flavescens*. The animals have gradually been acquiring red and orange pigment in parts, and although the adult is fairly transparent it is much less so than in the young stages. The head end is bright orange-red, especially the head-cones and tentacles and round the mouth, also orange-red at the extreme hind end, the penis being pinkish yellow. The liver which surrounds the intestinal mass is dark brown and very conspicuous, the gonad sometimes pinkish yellow or sometimes colourless and the wings a pale pink.

In 1930 Clione was unusually abundant in the neighbourhood of Plymouth, but it had also been noticed in fair numbers, though not specially recorded, in the previous years. In 1931, however, it was not seen after January until late in August, when it was plentiful in the outside grounds. It is evidently irregular in its appearances. The following records from 1930 to September, 1931 (when it was last seen), are given, showing that it has been observed every month during one year :—

1930. *January, February, March, April, May*—in ring-trawl, from outside, fairly large specimens, especially in February. In tow-nettings occasionally both inside and outside Sound.

June. Abundant all through the month. Many adults and young, especially from outside. Eggs just seen in fine tow-net from W. of Eddystone on June 30th.

July. Eggs, young of all ages, and adults very plentiful, inside and outside. On July 17/18 one specimen of 4 mm. laid eggs during the night in a finger-bowl. Many more did the same all through July.

August. Many in early part outside and inside, eggs, young and adult, gradually dwindling, very few in latter part.

September. Very few. A few still breeding.

October 28*th*. One 1·9 mm. long, with hind circlet of cilia, from beyond Eddystone.

November 6*th*. One with 3 circlets of cilia, from outside. *November* 17*th*. Two with 3 circlets of cilia, 4 miles south of Penlee. *November* 21*st*. One larva with 3 circlets of cilia. Between New Grounds and Breakwater.

December 3*rd*. Three larvæ with 3 circlets of cilia, off Eddystone. *December* 4*th*. One with 3 circlets of cilia, off Rame. *December* 18*th*.

Three with 3 circlets of cilia, from Sound. *December* 19*th*. Two with 3 circlets of cilia, off Mewstone.

1931. *January* 19*th*. Two with 3 circlets of cilia, off Mewstone.

August 25*th*. A few mature specimens and one larva with 3 circlets of cilia, outside Sound. Some laid eggs in the Laboratory which hatched.

26*th*. About 150 mature specimens and many larvæ from Station E 2 between Eddystone and Ushant.

28*th*. A few adults, one larva with 3 circlets of cilia, near Eddystone. Two larvæ from inside the Sound.

September 3*rd*. Many adults and larvæ with 3 circlets, near Eddystone.

9*th*. A few adults and larvæ, near Eddystone.

16*th*. Two adults and a few late larvæ, near Eddystone.

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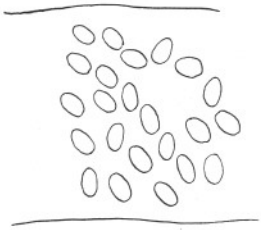
KEY TO FIGURES.

(Scale B is 6 times the scale of A.)

PLATE I. (Fig. 1 Scale A., 2–11 Scale B.) *Clione limacina.*

FIG. 1.—Ribbon of eggs, laid in finger-bowl, 30.6.30.
FIG. 2.—Egg a few hours old, 0·11 mm. long.
FIG. 3.—Empty shell of newly hatched larva, 0·14 mm. long.
FIG. 4.—Shell of newly hatched larva with animal retracted, 0·16 mm. long.
FIG. 5.—The same, side view, swimming.
FIG. 6.—Young larva, five days old, reared in Laboratory, 0·32 mm. long.
FIG. 7.—Empty shell of larva 12 days old, reared in Laboratory, 0·28 mm. long.
FIG. 8.—Larva 14 days old, reared in Laboratory, 0·38 mm. long.
FIG. 9.—Larva 16 days old, reared in Laboratory, having lost its shell, 0·35 mm. long.
FIG. 10.—Larva 18 days old, reared in Laboratory, having lost its velum, 0·32 mm. long.
FIG. 11.—Larva from plankton, 0·48 mm. long, side view.



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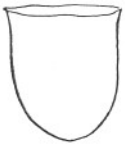

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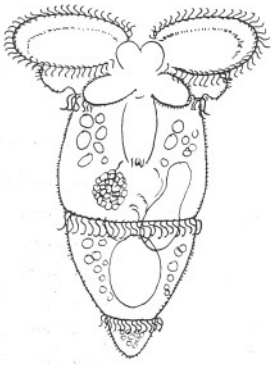

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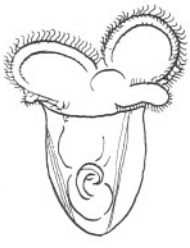

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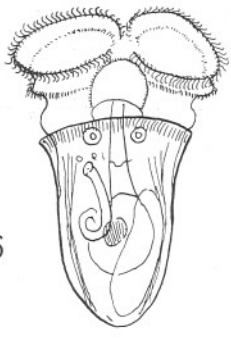

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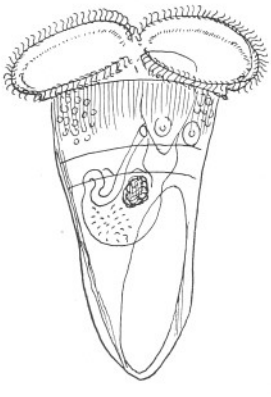

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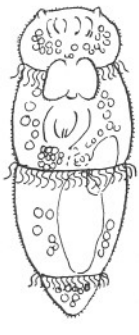

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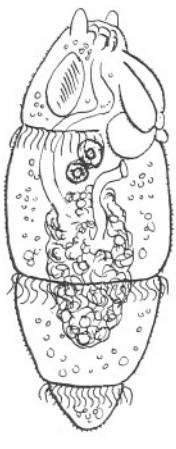

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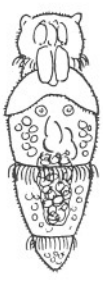
PLATE II. (Scale A.) *Clione limacina* from plankton.

FIG. 1.—Larva 0·96 mm. long, side view.
FIG. 2.—Larva 1 mm. long.
FIG. 3.—Larva 1·44 mm. long, ventral view.
FIG. 4.—Larva 1·6 mm. long, side view.
FIG. 5.—Larva 2 mm. long, dorsal view.
FIG. 6.—Larva 2 mm. long, ventral view, older than Fig. 6.
FIG. 7.—Larva 2·8 mm. long, with developing eggs.
FIG. 8.—Head of adult showing radula protruded.



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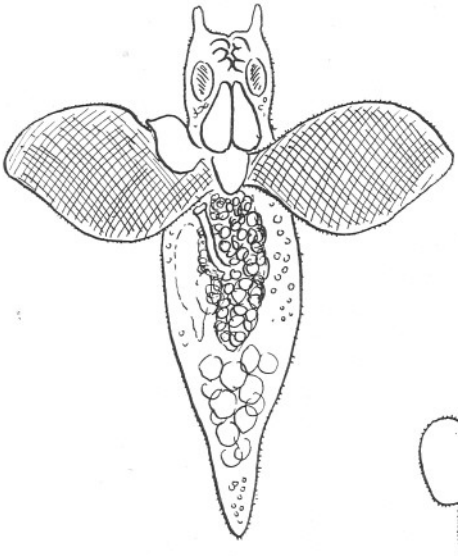

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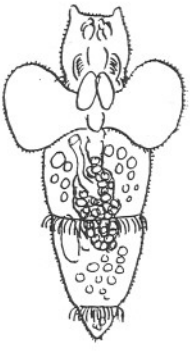

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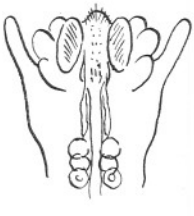

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The Larval Stages of *Nassarius reticulatus* and *Nassarius incrassatus.*

By

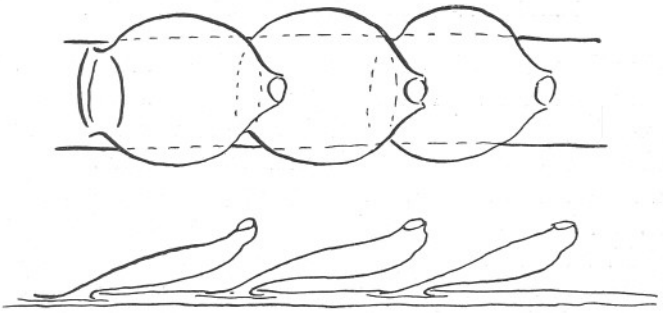
Marie V. Lebour, D.Sc.

Naturalist at the Plymouth Laboratory.

With 3 Figures in the Text and Plates I–V.

THE two species of Nassarius (usually known as Nassa), *N. reticulatus* and *N. incrassatus*, are both common at Plymouth. *N. reticulatus*, the larger species, occurs from low water usually to a depth of a few fathoms, more rarely from the waters outside the Breakwater, *N. incrassatus* occurring between tide-marks and extending into deeper water, even to 46 fathoms.

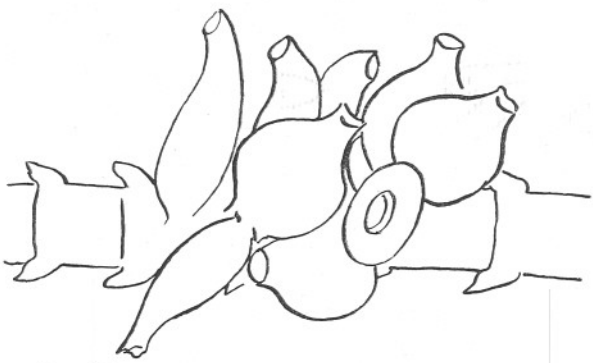
The egg capsules of both are well known. It is necessary, however, to modify a general statement present in most popular mollusc and natural history works (for instance, Cooke, 1895, p. 125), quoted by Flatteley and Walton (1922, p. 272), that "*Nassa reticulata* lays egg capsules in shape like flattened pouches with a short stalk. . . . *Nassa incrassata* deposits solitary capsules which are shaped like rounded oil-flasks."



TEXT-FIG. 1.—Egg capsules of *Nassarius reticulatus* on Zostera.

In reality both lay egg capsules like flattened pouches, the general shape being much alike, but those of *Nassarius reticulatus* are nearly three times the height of those of *N. incrassatus ;* the pouch is flattened in one direction and almost round in the other, that of *N. reticulatus* being rather flatter than *N. incrassatus*. The adhesive base is broad in *N. reticulatus* and hardly to be called a stalk, whilst in *N. incrassatus* it

is narrower and more stalk-like. The mouth of the pouch is more pronounced in *N. incrassatus*. The capsules have a slanting position, the flat surface uppermost (Plate I and Text-figures 1 and 2). Both species may lay the capsules on Zostera, but this is usual in *N. reticulatus* and there are generally many in a row. There may, however, be only one, two or three, and occasionally they are laid in clusters of rows on hydroids or on Bryozoa. *N. incrassatus* usually lays the capsules irregularly in clusters on some rough surface, especially on hydroids or on Bryozoa, but occasionally they are to be found singly and sometimes on Zostera. When on Zostera they are more usually clustering in crevices near the roots, but as many as three in a row have been found on Zostera leaves. In support of this statement we find that Fischer (1892), who was the first to describe the capsules of what is almost certainly *N. incrassatus*,

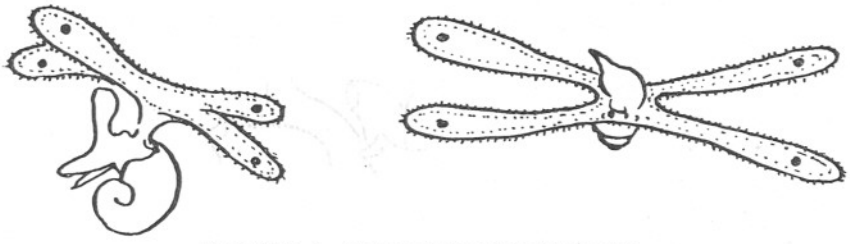


TEXT-FIG. 2.—Egg capsules of *Nassarius incrassatus*.

states that they occurred two or three at a time on Zostera. His figure shows a broader base than in the Plymouth specimen, but the size (not over 2 mm.) and the fact that *N. incrassatus* was common where he collected the eggs make the identification almost certain.

From 50 to 100 eggs, sometimes less, sometimes more, are laid in the capsules. *N. incrassatus* usually lays from 50 to 80, rarely more, in each capsule, *N. reticulatus* usually upwards of 100. Usually all the eggs develop and there are no "nurse eggs," which are devoured by their neighbours, as is the case in certain other gastropods, notably *Buccinum undatum*, *Nucella* (=*Purpura*) *lapillus*, *Natica catena* and *Rissoa membranacea*. There is thus an enormous number of young hatched out and swimming about in the sea as veligers, both species hatching with well-formed shell and bilobed velum. Up to this stage the larvæ, especially those of *N. reticulatus*, are well known, and it is apparently usually supposed that they have a short free-swimming life and soon settle down to be like their parents.

Pelseneer (1911) gives an account of the eggs and larvæ of *N. reticulatus* up to the time of hatching, but he could not rear them longer than two or three days. He describes and figures the developing embryos and newly-hatched larvæ and his descriptions agree very well with the Plymouth specimens. He also figures the egg capsules and larval shell in Lankester's *Treatise of Zoology; Mollusca*, 1906, pp. 130, 135, and the egg capsules again in his paper of 1926, in which he describes the egg-laying. Recently Ankel (1929) has investigated the laying of the egg capsules in *N. reticulatus* and given photographic illustrations of these. The following notes will show that both species have a long free-swimming period lasting for two months or more (at any rate under Laboratory conditions) and grow to a large size before losing the velum. For this



TEXT-FIG. 3.—Larvæ of *Nassarius incrassatus*.

reason they are a very important constituent of the plankton both inshore and outside, and they must form a large part of the food of the larger plankton-eating animals.

In late spring and summer a larval gastropod is always conspicuous in the Plymouth plankton, occurring in the water outside the Breakwater more commonly than any other mollusc (except the pteropod *Limacina retroversa* which may be present at the same time in very large numbers) and it is also common in the inshore plankton. The later stages of this larva, and it is these which commonly occur outside, show an enormously developed four-lobed velum. By keeping these in a plunger-jar it was found that they grew into *Nassarius incrassatus* (Plate IV, Fig. 8; Text-figure 3). Adults were then collected, eggs obtained and the larvæ reared to a certain stage. Eggs of *N. reticulatus* were obtained from the Zostera, hatched and reared until they began to crawl. This took two months. There is every indication that the free-swimming period is even longer in *N. incrassatus*.

It is now possible to give an account of the life-history of both these species from experiments and observations in the Laboratory and from freshly collected material from dredge, trawl and tow-net.

Methods.

Eggs of both species were collected whenever possible and plankton hauls investigated continually. The two species of Nassarius were placed in aquaria, aerated glass vessels, plunger-jars and Laboratory tanks.

Although later on some were found to be depositing eggs in the tanks, in none of these cases did *N. reticulatus* lay eggs in captivity, but *N. incrassatus* laid them easily in plunger-jars on the glass, on Zostera roots and on pieces of Bryozoa and hydroids. The eggs of *N. reticulatus* laid on Zostera were collected, the capsules removed from the Zostera and placed in a plunger-jar. These hatched out early and were kept in the same vessel for over two months without change of water. A pure culture of Nitzschia was added to the water, and this diatom, together with others which appeared naturally in the water, served as food for the larvæ. Unfortunately towards the end of the two months the flagellate Phæocystis appeared in the jar, and although this was eaten by the larvæ to a certain extent it soon became too dense and killed everything off. Some of the larvæ had, however, reached the crawling stage. From the first it could be seen that diatoms and other minute objects were in the stomachs of the larvæ, the contents always in a violent state of agitation owing to the ciliated lining of the stomach. Later on larger diatoms could be detected and the larvæ ate *Skeletonema costatum* and *Thalassiosira gravida* besides Nitzschia. These were the main forms growing in the jar and it was interesting to note that chains of Skeletonema and Thalassiosira were to be seen in the stomach and not only separate cells. That Skeletonema, which is one of the commonest diatoms, one of the easiest to culture, and one which is always penetrating into other cultures, should be a common food for a larval mollusc is an interesting and important fact. It is evident that diatoms form the chief food of these larvæ throughout their free-swimming life.

The larvæ of *N. incrassatus* were also fed in the same way, but they did not live so long and intermediate stages were collected from the plankton. In all cases when examined for food the natural food of both species in the free-swimming stage was essentially diatom material. The late larvæ of *N. incrassatus* were put into a plunger-jar provided with diatoms. As they grew and began to crawl, small mollusc larvæ from the plankton, chiefly bivalves, were introduced and evidently served well as food for those which had lost the velum. A stage exists in both species in which the velum is still retained although the foot is well developed. The mollusc can thus crawl or swim at will. It is apparently still a plankton feeder for some time and continues to eat diatoms, but when the velum begins to disappear, and afterwards, it is apparently carnivorous. Small bivalves, especially Anomia, settled down on the glass sides of the plunger-

jar and these were eaten by the young Nassarius, some of which were actually seen to attack them. In this way *N. incrassatus* was reared to the adult stage.

The water for rearing was taken from outside the Breakwater where there were many diatoms, and these diatoms naturally present were eaten quite as much as the Nitzschia which was introduced. In all cases the food was chiefly Skeletonema, Thalassiosira and Nitzschia, always mixed with small indistinguishable particles, probably both organic and inorganic.

Characters of the Two Species.

The egg capsules are a light horn colour, transparent, and the eggs visible through the wall of the capsule (Plate I). About a month is the usual time taken from the deposition of the eggs to the time of hatching. This is the time given by Pelseneer, and it is much the same in the Laboratory, the eggs of *N. reticulatus* from very early capsules hatching in from three to four weeks, those of *N. incrassatus* newly laid in the Laboratory hatching in twenty-three to thirty days. The ages of the larvæ when known and the sizes given are all under the ordinary Laboratory conditions of temperature. A comparison with those from the plankton shows much the same state of development at the same size. Some time before hatching the larvæ are moving about as veligers inside the capsule, with the shell already formed, much yolk being inside each larva, and when all the yolk is absorbed the larva hatches, escaping from the top of the capsule where a thin covering is broken through.

The newly hatched larva (Plate II, Figs. 1, 2; Plate III, Fig. 1; Plate IV, Figs. 1, 2) has a smooth unsculptured shell, very transparent, consisting of one whorl. The outer lip is slightly drawn out at the centre, curving inwards so that two hollows are formed to support the velum. This projection grows into a conspicuous tooth bent inwards and the hollows deepen as the velum grows (Plate III, Fig. 2; Plate V, Figs. 3, 7). The animal has a bilobed velum, rather longer across than the greatest breadth of the shell, with the usual ciliated margin and ciliated ridge below forming a groove to the mouth. The general method of feeding in a veliger is for the food to be collected whilst the animal is swimming. This is done by means of the velum. Round the margin of the velum is a thick rim edged with large cilia. On the underside and somewhat internal to the margin is another smaller ridge edged with smaller cilia. These two ridges form a groove in which the food is collected and brought to the mouth (Plate V, Fig. 6). The mouth is also ciliated and the united workings of the cilia on the velum and round and inside the mouth bring a constant supply of small food to the animal. Mucus appears to be secreted in the groove and if the particles are not suitable the animal

swims away from them, leaving them behind entangled in a stream of mucus. However large and elaborate the velum may be, the process of feeding seems to be the same. As the foot grows and crawling begins the radula has been forming and soon a different method of feeding may come into use, until finally the velar method is abandoned and the ordinary adult carnivorous method substituted.

At first the paired eyes are at the base of very short tentacles. Sometimes, as Pelseneer (1911) points out, but not always, only one tentacle is developed, the other not appearing till later. There are paired otoliths at the base of the foot. The ventral mouth just below the velum, œsophagus, stomach, intestine and anus are all visible, the liver lobes occupying the apex of the shell, the kidney is present and the heart beating. The stomach is ciliated and food material always moving about inside. The rectum and anus are on the right side (Plate III, Fig. 5 ; Plate V, Fig. 5). The veliger moves quickly by means of the long cilia on the velum which is fully expanded. Later the flapping of the lobes helps in the movement.

The larva grows quickly, but has a long free-swimming period. After a few weeks the velum becomes four-lobed and the colour, if not already present, is accentuated in certain regions, the shell begins to be spiral and the shell siphon or canal is formed (Plate II, Figs. 2–11 ; Plate III, Figs. 3–5 ; Plate IV, Figs. 3–8 ; Plate V, Figs. 2–5). The velum may remain only slightly four-lobed (*N. reticulatus*, Plate II, Figs. 8–9), or the lobes may grow out to an enormous length (*N. incrassatus*, Plate IV, Fig. 8 ; Text-Fig. 3). The foot, situated behind the velum, is ciliated on the whole of its surface ; at first a very small projection narrowing behind, but always provided with an operculum, it soon lengthens and a few large cilia project at its hind end. In later stages the front of the foot grows forward into a flexible process, still ciliated (Plate II, Figs. 7–9 ; Plate IV, Figs. 7–8). The tentacles grow longer and are also ciliated, the tips having a few large cilia and the whole surface covered by minute cilia. Pigment appears on the base of the foot and round the mouth. In *N. reticulatus* there is from the first a border of brown pigment round the velum, in *N. incrassatus* the velum is at first colourless, then brown pigment appears and gradually concentrate with a large spot at each corner of the four lobes. After some weeks the shell has from three to four whorls and the canal (the shell siphon) is fully formed, containing the siphon proper. When the animal can crawl there are from three to four whorls, the larval shell mouth has no longer the projecting tooth but the margin is simple with a slightly crenulated edge (Plate II, Figs. 12–14 ; Plate V, Figs. 8–9). The head end projects slightly and the front of the foot is provided with two horns. The foot itself is elongated and the siphon very long. Ribs may begin to appear on the shell. The animal is

now outwardly like the adult except for the sculpture on the shell, and probably attains maturity in a year or less.

Nassarius reticulatus (L.).

(Plates I, Figs. 1–2 ; II and III : Text-Fig. 1.)

The eggs are laid in spring and summer, usually from March to August, more rarely in autumn and winter, in the inshore waters ; occasionally further out in deeper water. Records of eggs show that they may be laid every month, except October and November (*Plymouth Marine Fauna*, new edition, 1931). Probably a few eggs could be found in any month of the year. Breeding is usually finished by the end of September, but three capsules were found on Zostera from Cawsand Bay, 28.1.31, perhaps the earliest of the season. The best localities for the egg capsules are the Zostera beds in Cawsand Bay and off Drake's Island. One large mass from outside waters in June, 1931, consisted of many clusters of rows laid in a tangle of Antennularia and Sertularella.

The capsule measures about 4·8 to 5 mm. in height and about 4 mm. across the widest part. The newly laid egg measures about 0·16 mm. across, but grows rapidly and is much bigger as the embryo develops. The newly hatched larva measures about 0·28 mm. to 0·30 mm. across at its widest part, which is across the body whorl to the outer lip. The velum measures about 0·29 to 0·32 mm. across and has a continuous reddish brown border just inside the margin. The outer lip of the shell is conspicuous in its projecting centre curving inwards, forming almost immediately the characteristic tooth (Plate II, Figs. 1, 2 ; Plate III, Figs. 1, 2, 3). The shell and velum both grow quickly, the shell at five days old measuring about 0·32 mm. across, the velum 0·45 mm. across. The tentacles are well developed and there is a small amount of brown pigment on the ventral surface of the foot. At about three weeks old the shell measures about 0·4 mm. to 0·5 mm. across, the velum being about 0·48 to 0·55 mm. across. The outer lip is now drawn out posteriorly, forming the canal or shell siphon, and the spire begins to project. The foot is perceptibly longer and the dark pigment round the mouth is conspicuous. The larva now begins to show an alteration in the velum, and when about twenty-five days old there is an indentation at each side, the the first indication of the four lobes, and the width across grows larger. The animal now looks like a butterfly with outspread wings. The velum in *N. reticulatus*, however, is never so large, nor the lobes so long as in *N. incrassatus*. When about five weeks old the shell has from two to three whorls and measures about 0·56 mm. across, the velum being about 1·3 mm. across. The reddish-brown border to the velum is very conspicuous throughout the larval life. At about six weeks there are three

whorls to the shell and the velum, sometimes larger anteriorly, may measure about 2 mm. across. The foot has now grown out into a squarish lobe in front and there is much brown pigment. The tentacles are long. The size may vary and a rather later stage may be smaller than a younger one, as in Figs. 8 and 9 of Plate II. After this the anterior lobe of the foot expands into two horns and the animal is able to crawl. It may now measure 0·72 mm. to 0·8 mm. across from the outer lip margin to the body whorl ; the outer tooth-like process has disappeared and the edge slightly crenulated (Plate II, Figs. 10–14). There is a long siphon, the foot projects some way beyond the spire when crawling and the tentacles are like the adult. It now crawls or swims at will, but the velum soon dwindles and then probably disappears altogether in a few weeks. At the first crawling stage *N. reticulatus* (about 0·8 mm. long) is decidedly smaller than *N. incrassatus* (about 1 to 1·2 mm.), although the latter species is so much smaller when adult.

All the stages are usually to be found in the inshore plankton in spring and summer and are seldom seen outside. They are exceedingly common inside the Sound.

Nassarius incrassatus (Ström.).

(Plate I, Figs. 3–4 ; Plates IV and V : Text-Figs. 2–3.)

The *Plymouth Marine Fauna*, new edition, 1931, records a mass of the egg capsules taken when the animal was actually depositing them on tufts of Antennularia, 25.1.09. Other records show that eggs were found every month except July. It is probable that a few may be found any month of the year, but the larvæ are much the commonest in spring and summer and are rarely seen in the autumn except when very young. Several adults were collected and placed in a plunger-jar in October and November, 1930, and on the 5th and 6th of November some capsules with eggs nearly ready to hatch were found in the jar attached to a mass of Cellaria on which were some eggs of *Parasepia elegans*. There were also capsules on the Parasepia eggs. Later in November and through December, January and February capsules were found on the sides of the glass jar, again on Cellaria and on pieces of Sertularella placed there for the purpose, and, later, from February to April, they were laid in clusters in crevices at the roots of Zostera floating in the jar. Very rarely they were laid on the Zostera leaves. Egg capsules were also found through May and June. All through June, July and August the late larvæ were abundant in the inside and outside plankton, and in winter, spring, summer, and more rarely in autumn the early larvæ could be found in the inshore waters. The younger forms are seldom seen far out. It is probable that most of the large larvæ come from inshore where the adults are so plentiful and they are so strong and large that they survive

when the smaller larvæ would perish. The length of larval life and their propensity for being carried out to sea would account for the very wide distribution and large numbers of this common species.

The egg capsules measure about 1·5 mm. to 2 mm. in height, the greatest breadth being rather less than the height. The eggs when newly laid measure 0·16 mm. across, which is the same size as those of *N. reticulatus*, although the newly hatched larvæ are smaller than in that species. The newly hatched larvæ are at first like *N. reticulatus*, but without any pigment on the velum. The shell measures 0·18 mm. to 0·2 mm. across and the velum about 0·2 mm. to 0·24 mm. across. At first growth and development take place in a similar way to *N. reticulatus*, but the pigment on the velum only appears after a few days.

Although the early larvæ are at first smaller than *N. reticulatus* at the same stage, yet in the later stages they are larger and the velum grows out into four very long lobes.

It was unfortunately not possible to rear these larvæ for longer than three weeks, but intermediate stages were collected from the plankton and the later stages were reared in a plunger-jar to the adult. Three of these which were placed in the jar in August, 1930, when they were free-swimming veligers, are now fully grown (July, 1931).

In about fourteen days the larvæ reared from the egg measured about 0·32 mm. across. Pigment may or may not be present on the velum at this stage, but at about three weeks old there are irregular masses of brown pigment which soon concentrate to form a large spot at each corner. The velum also begins to be four-lobed and shaped much like that of *N. reticulatus* at a slightly older stage, and when the shell is about 0·5 mm. across the lobes are much more divided than in the latest stage of *N. reticulatus*, at 0·8 mm. the lobes of the velum are about at their longest and each lobe is quite twice as long as the shell (Plate IV, Fig. 8). When the shell is about 1·2 mm. the animal can either crawl or swim and at about 1·5 mm. the velum is lost. It is probable that the larva of *N. incrassatus* remains in the free-swimming stage even longer than *N. reticulatus*, which takes two months under Laboratory conditions to reach the crawling stage.

These late veligers collected from the plankton were watched in the plunger jars. Here they could be seen swimming. Sometimes they remained still, the velum outspread upwards, the shell hanging down, or else the velar lobes were flapping and the movement was like that of the wings of a pteropod (Text-Fig. 3). When the lobes are spread out the animal is moving very slowly, and it is then that the food is directed into the mouth.

We have now ascertained the life-histories of both the Plymouth

species of Nassarius which can be recognised in all stages in the plankton and distinguished from one another and from other larval gastropods found with them. The unsculptured shell and the prominent tooth on the outer lip, which is apparent almost directly, distinguish the Nassarius larvæ from others of the same size. Later on the half-grown larvæ of *N. incrassatus* have a four-lobed velum with four spots much like a commonly occurring larva belonging to Natica (probably *N. catena*). The Natica, however, has no shell siphon and is always to be distinguished.

The two Nassarius larvæ are to be recognised in the following ways :—

N. reticulatus.	*N. incrassatus.*
All its larval life has a band of brownish-red pigment round the inside margin of the velum.	At first colourless, then faint scattered brown pigment forming an irregular border, later on concentrated in four large spots, one at each corner of the velum.
Velum at first bilobed, then four-lobed, but lobes never long.	Velum at first bilobed, gradually becoming four-lobed, the lobes in late stages very long.
Newly hatched larva 0·28 mm. to 3 mm. across shell.	Newly hatched larva 0·18 mm. to 0·2 mm. across shell.
First crawling stage about 0·75 to 0·8 mm.	First crawling stage about 1·2 mm. Probably more than two months from hatching to first crawling stage.
Two months under Laboratory conditions from hatching to first crawling stage.	

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KEY TO FIGURES.

Scale B is six times the scale of A.

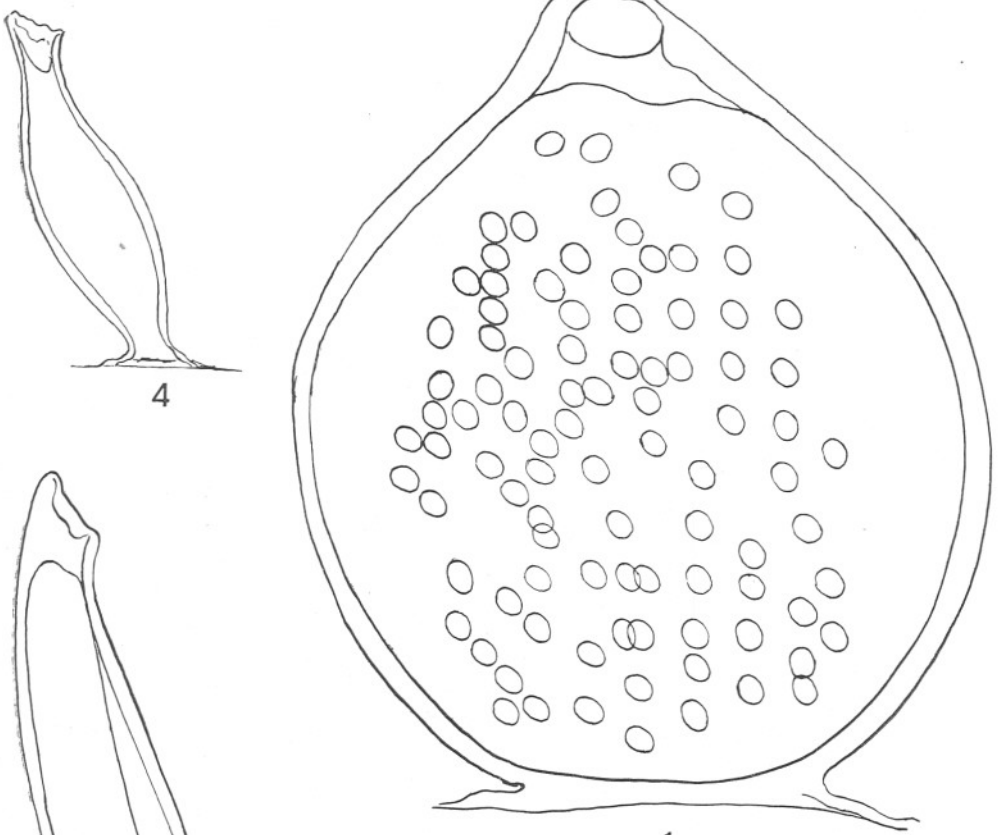
PLATE I.—Egg capsules of *Nassarius reticulatus* and *N. incrassatus*. Scale A.

Fig. 1.—*N. reticulatus*, 0·48 mm. high.

Fig. 2.—The same, side view.

Fig. 3.—*N. incrassatus*, 2 mm. high.

Fig. 4.—The same, side view.



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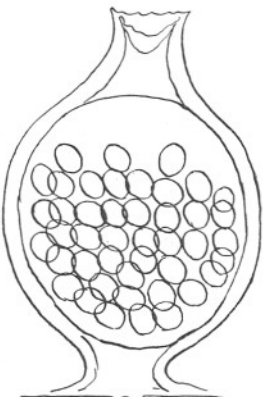

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PLATE II.—Larvæ of *Nassarius reticulatus* reared from egg. Scale A.

FIGS. 1–2.—Newly hatched, shell 0·25 mm. across body whorl.
FIG. 3.—7 days old, 0·32 mm.
FIG. 4.—19 days old, 0·45 mm.
FIG. 5.—25 days old, 0·56 mm.
FIG. 6.—32 days old, 0·64 mm.
FIG. 7.—35 days old, 0·7 mm.
FIG. 8.—40 days old, 0·75 mm.
FIG. 9.—48 days old, 0·75 mm.
FIGS. 10, 11.—The same swimming in different positions.
FIGS. 12–14. Crawling stages, 50 days to two months old.

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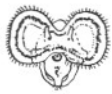

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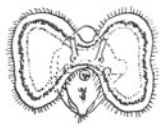

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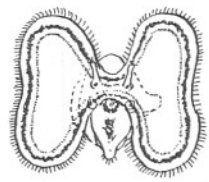

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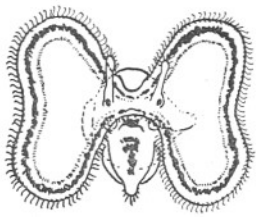

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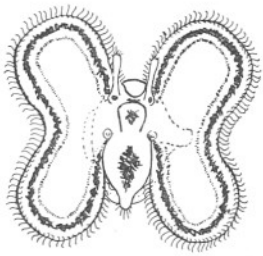

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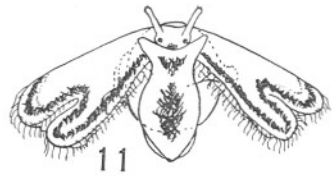

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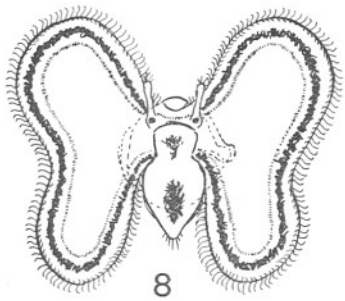

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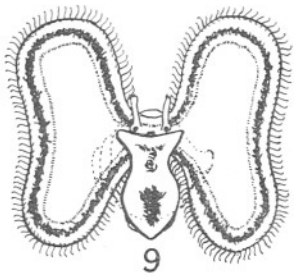

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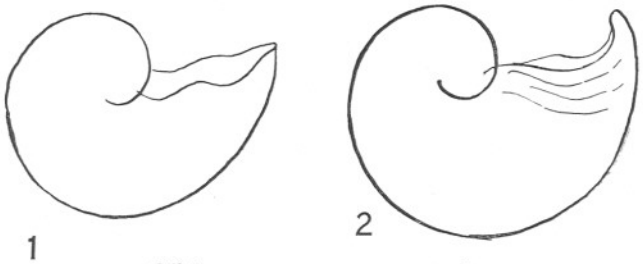
PLATE III.—Larvæ of *N. reticulatus* reared from egg. Scale B.

FIG. 1.—Shell of newly hatched larvæ.
FIG. 2.—Shell of larva 5 days old.
FIG. 3.—Larva 3 days old.
FIGS. 4–5.—Larva 19 days old.



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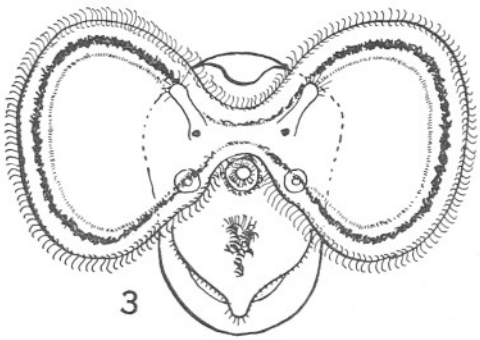

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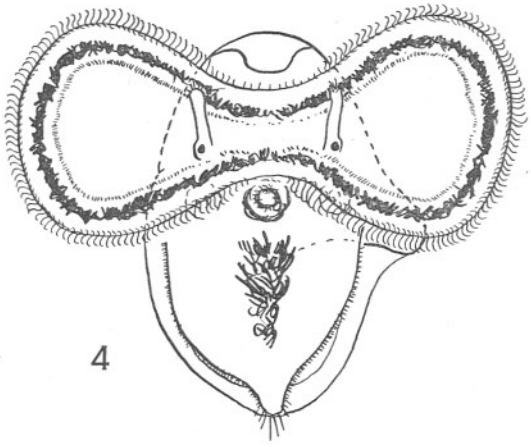

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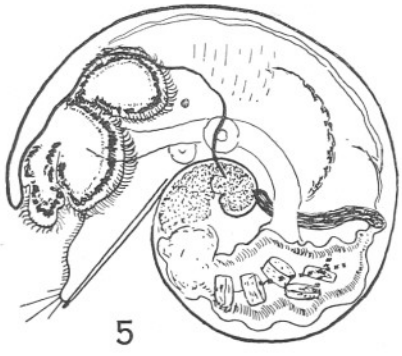

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PLATE IV.—Larvæ of *Nassarius incrassatus*. Scale A.
(1–3 from egg, 4–11 from plankton.)

FIGS. 1–2.—Newly hatched larva, 0·18 mm. across body whorl.

FIG. 3.—14 days old, 0·32 mm.

FIGS. 4–7.—Larvæ from plankton, the ages being probably from 3 weeks to 3 months or more.

FIG. 4.—0·35 mm. across.

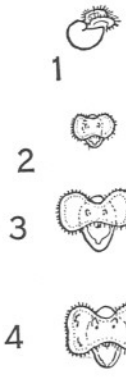
FIG. 5.—0·44 mm.

FIGS. 6–7.—0·55 mm.

FIG. 8.—0·8 mm.

FIG. 9.—Shell of Fig. 7.

FIGS. 10–11.—Shells of crawling stage.



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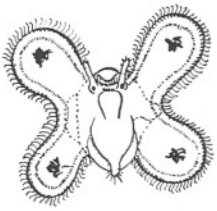

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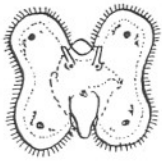

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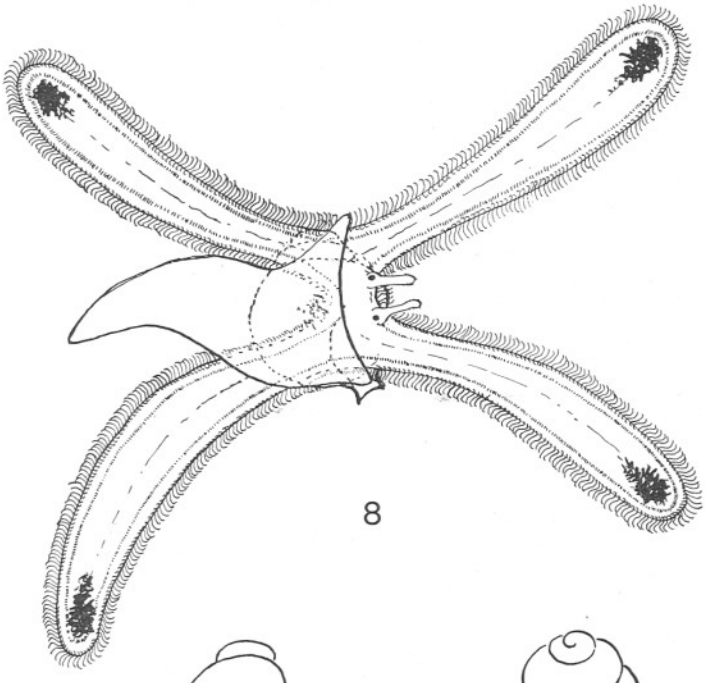

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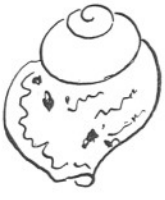

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PLATE V.—Larvæ of *N. incrassatus* (1–6 Scale B, 8 and 9 drawn on a smaller scale).

FIG. 1.—Larva still in egg capsule nearly ready to hatch.

FIG. 2.—3 days old.

FIGS. 3–5.—2 weeks old.

FIGS. 6–7.—Ca. 3 weeks old.

FIG. 8.—Larva crawling; but still retaining velum shell 1·2 mm. long.

FIG. 9.—Larva losing velum, shell 1·5 mm. long.

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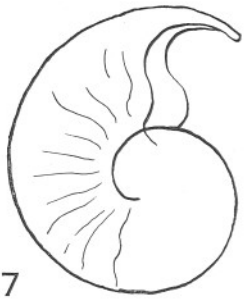

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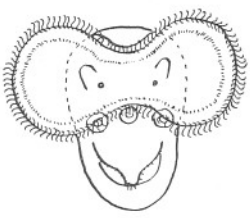

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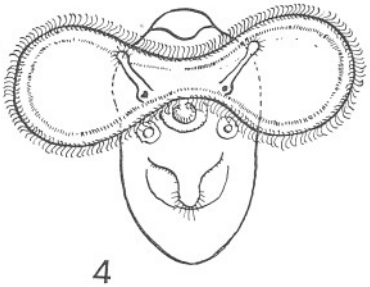

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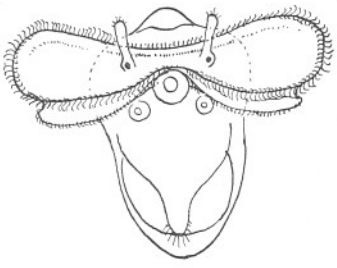

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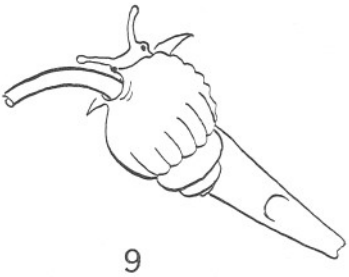

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The Larval Stages of *Trivia europea.*

By

Marie V. Lebour, D.Sc.,

Naturalist at the Plymouth Laboratory.

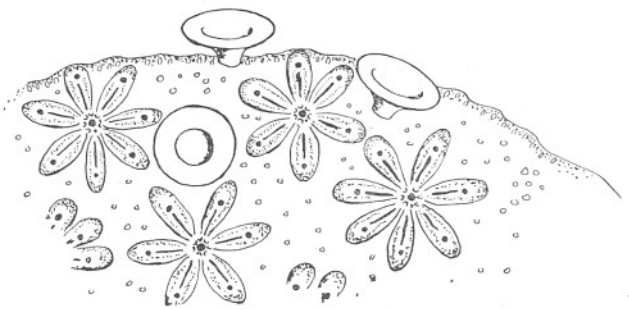
With One Text-figure and Plates I–IV.

In 1926 Pelseneer discovered the eggs of *Trivia europea* on the French coast. These he found were laid in capsules embedded in the compound ascidian *Polyclinum luteum*, the mollusc biting a hole and laying its eggs in a vase-like capsule completely enveloped in the ascidian except for the wide lip of the vase which projects freely and can be easily seen with the naked eye (Pelseneer, 1926, Figs. 11–12). He also hatched some larvæ from these eggs which were very interesting, as they possessed an accessory shell somewhat similar in shape to the Echinospira of *Lamellaria perspicua*. He did not obtain the eggs directly from the Trivia and was not able to keep the larvæ alive more than a few days. In his paper he expresses the hope that some worker will confirm his observations experimentally. This I am now able to do, having procured the eggs actually laid by the Trivia, hatched them out and kept them alive for more than a week, afterwards collecting the larvæ from the plankton from stages which exactly corresponded with those from the egg up to late stages which metamorphosed into young Trivia, and young stages of Trivia feeding on compound ascidians which corresponded with the metamorphosed forms.

Trivia europea is common at Plymouth between tide-marks and in a few fathoms of water; occasionally further out in deeper water. Records are available from the shore to the region beyond the Eddystone.

In order to obtain the eggs several adults were collected and placed in a plunger-jar. They were given various compound ascidians to eat and they ate largely of *Diplosoma listerianum* var. *gelatinosum* (=*Leptoclinum gelatinosum*). This ascidian grows well on the glass sides of the Laboratory tanks and is therefore a very convenient food. The Trivia also ate various forms of Botryllus, Botrylloides, and *Trididemnum tenerum*. Although placed in the plunger-jar in winter and spring and eating well they laid no eggs until June. On June 1st, 1931, several egg capsules were laid in an orange mass of Botryllus placed in the jar the night before (Text-Figure 1). These egg capsules were exactly similar to those found

by Pelseneer. Unfortunately the Botryllus died and also the eggs. On June 5th another capsule was laid in a small aerated glass vessel in which two Trivia and an orange Botryllus had been placed overnight. This Botryllus and eggs also died. During the night of June 14/15th two capsules were laid in a new lot of Botryllus in the plunger-jar. This was pale yellow and only a small piece growing on an old stalk of Eunicella. It was still living on June 16th, and between June 16th and 23rd there were six capsules in this piece of Botryllus. Some of these died, but on June 29th two capsules contained active embryos, probably those laid on the 14/15th. The Botryllus with the two capsules containing active embryos was then placed in a fresh plunger-jar and the young from one



TEXT-FIG. 1.—Egg capsules of Trivia in Botryllus.

capsule hatched on July 6th, those from the other capsule died. On June 29th two egg capsules were laid in *Tridemnum tenerum*, but neither the ascidian nor the eggs lived. Ascidians of an orange or yellow colour were always chosen for the eggs, probably because the eggs were themselves a bright orange and were thus protected. The larvæ from the capsules in Botryllus seemed to have hatched prematurely, for they still retained a large amount of yolk, the accessory shell was not completely formed and the true shell only indicated. The velum was present, however, and the larvæ were swimming about. In a few days they resembled the newly hatched young figured by Pelseneer (*op. cit.*, Fig. 16).

On the whole the Trivia seemed to prefer Diplosoma to eat and Botryllus to lay eggs in. They are usually found in the neighbourhood of Botryllus when collected between tide-marks, or they may be on Diplosoma. It is easy to watch them eating the ascidians with the long proboscis outstretched to its greatest length and the food rapidly entering the mouth (Plate IV, Figs. 5–6).

Although some of the Trivia have been kept for several months no more eggs have been laid since June. They must, however, breed in most months, for in any month of the year the larvæ both young and old may

be found in the plankton, perhaps more plentifully in spring and summer. They are quite common and usually to be found in the tow-nets from inside the Sound or a little way beyond, more rarely from deeper water.

The egg capsules measure about 4·8 mm. in height and contain several hundred eggs, each when newly hatched measuring 0·16 mm. across (Plate I, Fig. 1). The eggs are a bright orange, the capsules colourless and transparent, very thin where they are imbedded in the ascidian, but the lip is thickened where it projects and the eggs are covered over securely. The embryos when hatching break through the mouth-covering and swim away. Those hatched in the plunger-jar had a small bi-lobed velum, eyes on rudimentary tentacles with a projecting lobe in front, conspicuous larval kidneys (so called) just behind the velum, a mouth ventrally, otoliths at the base of the foot which is short and already provided with an operculum, the accessory shell forming and the true shell barely perceptible. Nearly all the body is full of orange yolk (Plate II, Fig. 1). The accessory shell measures about 0·18 mm. across. The unnatural condition may account for them being hatched prematurely. The plunger-jar in which the eggs were laid and hatched were on a Laboratory table under ordinary Laboratory conditions and temperature and the water was not changed at all. A pure culture of Nitzschia was given to the larvæ to eat and those of nearly a week old seemed to be feeding, but they did not live more than ten days.

The yolk disappears when the shell is about 0·24 mm. across, and the stomach, œsophagus, and intestine are developed. The animal is very dark, the liver being dark yellowish brown, the stomach, intestine, and œsophagus a dark purplish brown. These colours are retained throughout the larval life and are very characteristic (Plate I, Figs. 2–20; Plate II, Figs. 2–5). Later the outer margin of the velum has a very thin brown border. At 0·36 mm. across the accessory shell the true shell measures 0·16 mm. across. The velum is about 0·4 mm. across and very slightly indented at the centre of each side. The so called larval kidneys are still recognisable. At this stage the larvæ may be found in the plankton and are exactly like those which were reared from the egg (Plate I, Figs. 3, 4; Plate II, Fig. 4). They agree very well with Pelseneer's newly hatched larvæ. From this stage onwards larvæ of all sizes may be found in the plankton. The so-called larval kidneys now disappear and the true kidneys are formed, but the alimentary canal changes little. The velum grows large, the faint brown border appears in the later stages (Plate I, Figs. 17, 20), the front lobes are rather longer than the hind lobes. The velum has the usual structure, having a ridge with long cilia on the margin and an inner ridge of smaller cilia below, the two forming a groove to the mouth. The foot develops two large lateral lobes which help to support a very large spiral operculum (Plate III, Figs. 1, 2). When the accessory

shell is about 1·25 mm. across there is an anterior lobe to the foot which hides the mouth. The foot in the larvæ usually has scattered brown pigment on the sole. The tentacles are long and the mantle begins to project from the true shell. A gill is beginning to form at this stage (Plate I, Figs. 18–20). The accessory shell is perfectly clear and unsculptured, the only structure being a few lines of growth. The outer lip projects slightly. The true shell lies within the accessory shell and its whorls correspond in those of the accessory shell. This is an important difference which distinguishes it at once from the Echinospira of *Lamellaria perspicua* in which the whorls of the accessory (Echinospira) shell do not correspond with those of the true shell, the latter being placed excentrically. Another Echinospira occurring at Plymouth, probably belonging to Velutina, is like Lamellaria in this respect (Plate III, Figs. 8–9 ; Plate IV, Figs. 1, 2, 3). This unidentified Echinospira in its younger stages is like Trivia in many ways, including the shape of the velum. These facts emphasise the probable relationship of Trivia and the Lamellariidæ which has been suggested by Pelseneer (*op. cit.*).

At about 1·25 to 1·4 mm. across the accessory shell Trivia begins to metamorphose. This is done in quite a different way from Lamellaria, for whereas in Lamellaria the Echinospira shell is cast off as a crumpled skin, the mantle immediately surrounding and covering the true shell, in Trivia the accessory shell remains and the mantle surrounds and covers it (Plate III, Figs. 3–4). It is then probably dissolved. The foot loses its lateral lobes and operculum, a short siphon is formed and the animal crawls (Plate III, Figs. 5–7). As the mantle comes up round the shell, small protuberances with stalks embedded in the mantle are conspicuous. These look like soft nails with yellow heads placed irregularly round the base of the mantle and become the mantle-papillæ of the adult (Plate III, Figs. 5, 7 and 13). The shell soon becomes oval in shape and the body whorl elongated along the main axis. It is pearly white and perfectly smooth (Plate III, Figs. 10 and 11). This young shell is well known. Vayssière (1923) gives a figure of it. The siphon elongates and the mantle gradually covers the shell when the animal is active, but the whole animal may be completely withdrawn into the shell. Young individuals can be found crawling on compound ascidians in the Sound (Plate III, Figs. 12–13). The body and mantle can be variously coloured, the prevailing colours being cream, yellow, orange or brownish purple with small or large spots. Pale yellow with purple spots is a very usual combination, or brownish with orange spots, or the whole may be bright orange with various dark spots. The papillæ which are arranged chiefly on the sides of the lower surface of the mantle are yellow or orange, and there may be yellow or orange spots on the tentacles.

In the plunger-jars the larvæ from the plankton grow quickly and also

grow well after metamorphosis. It seems probably that it takes about a month or five weeks under Laboratory conditions from hatching to metamorphosis, a few weeks sufficing for the animal to obtain the elongated adolescent shell covered by the mantle. The adults live well in a plunger-jar. Some have been in the Laboratory for nine months with only two changes of water and are still alive (September).

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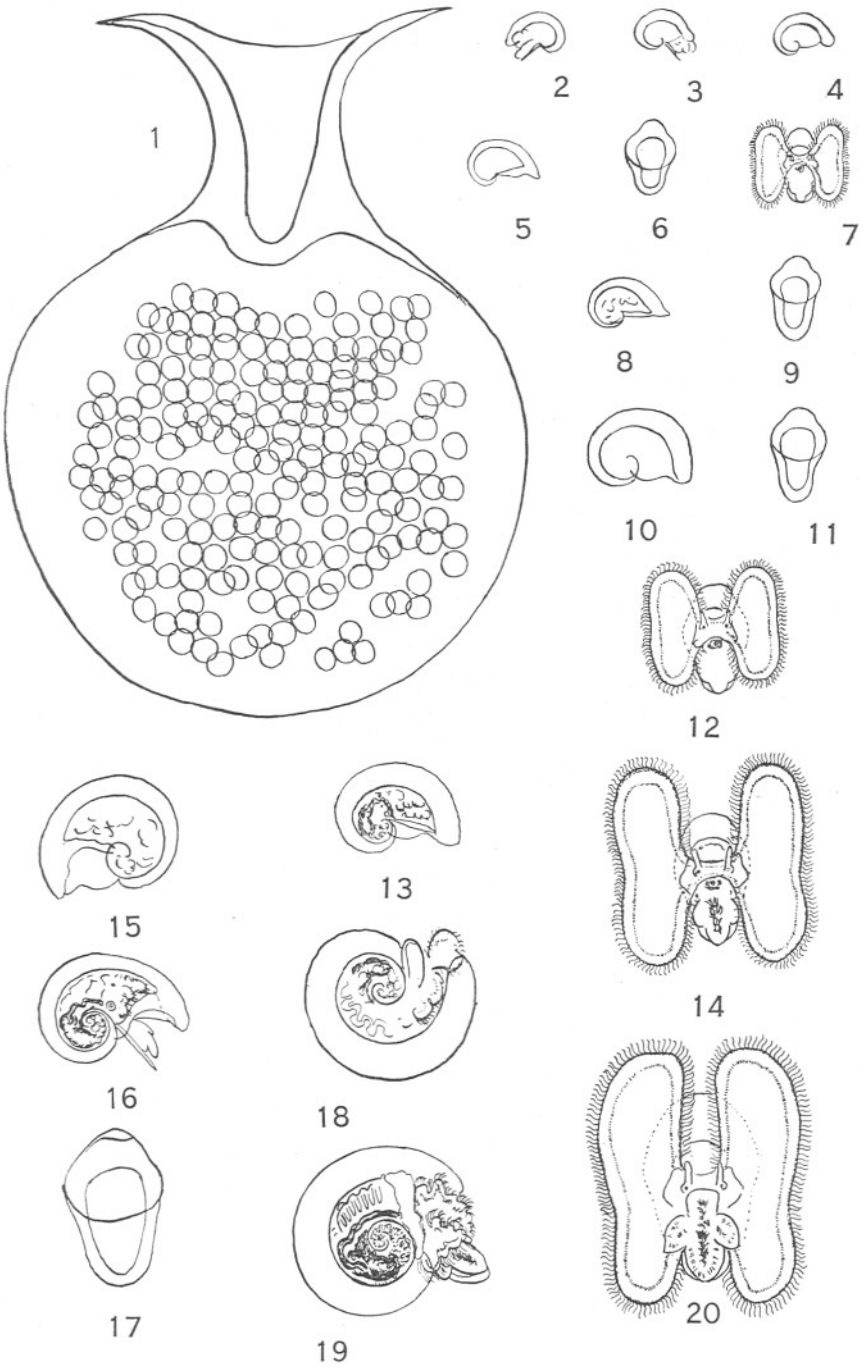
PLATE I. (Scale A.)

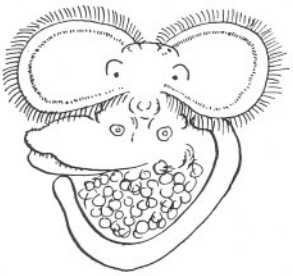
FIG. 1.—Egg capsule from Botryllus, 4·8 mm. high.
FIG. 2.—Young from egg, 5 days old, 0·35 mm. across shell.
FIG. 3.—Young from egg, 7 days old, 0·40 mm. across shell.
FIGS. 4–20.—Young from plankton.
FIG. 4.—0·4 mm. across shell.
FIGS. 5, 6, 7.—0·48 mm. across shell.
FIGS. 8, 9.—0·56 mm. across shell.
FIGS. 10, 11.—0·64 mm. across shell.
FIG. 12.—0·70 mm. across shell.
FIGS. 13, 14.—0·80 mm. across shell.
FIGS. 15, 16, 17.—0·96 mm. across shell.
FIGS. 18, 19, 20.—1·25 mm. across shell.



Eggs and Larvæ of *Trivia europea*.

PLATE II. (Scale B, six times the size of A.)

FIG. 1.—Young newly hatched from egg, 0·18 mm. across shell.
FIG. 2.—Young from egg, 0·24 mm. across shell.
FIG. 3.—Young from egg, 5 days old, 0·35 mm. across shell.
FIG. 4.—Young from egg, 7 days old, 0·36 mm. across shell.
FIG. 5.—Young from plankton, 0·64 mm. across shell.



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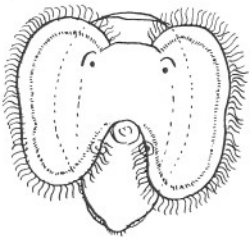

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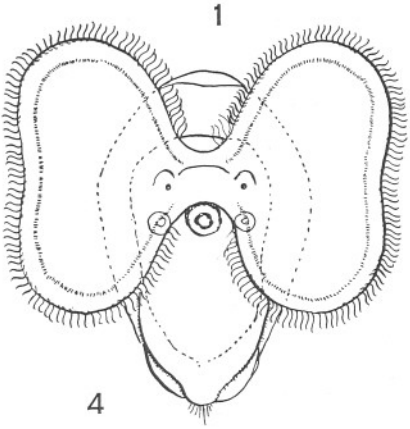

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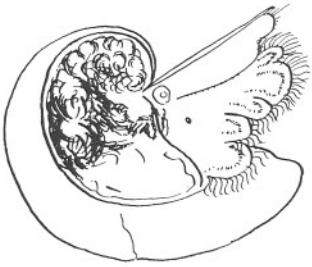

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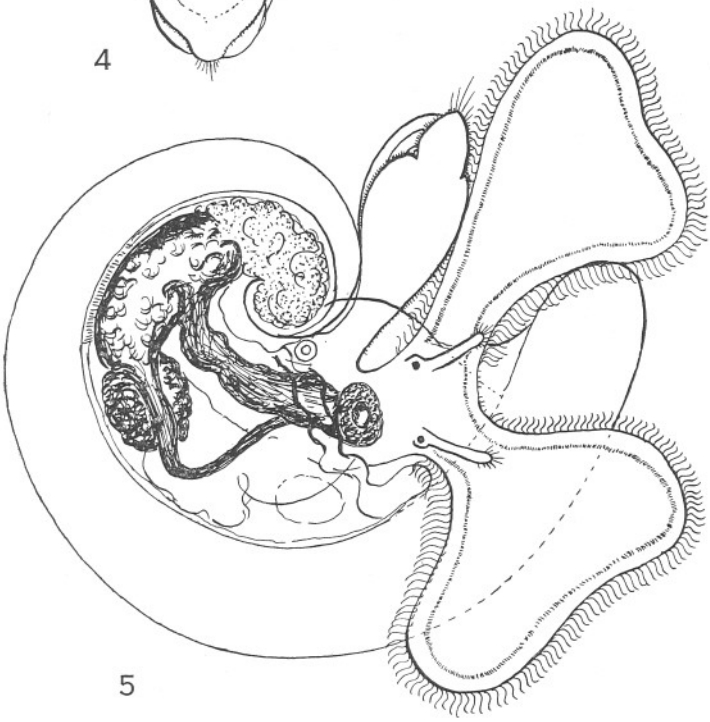

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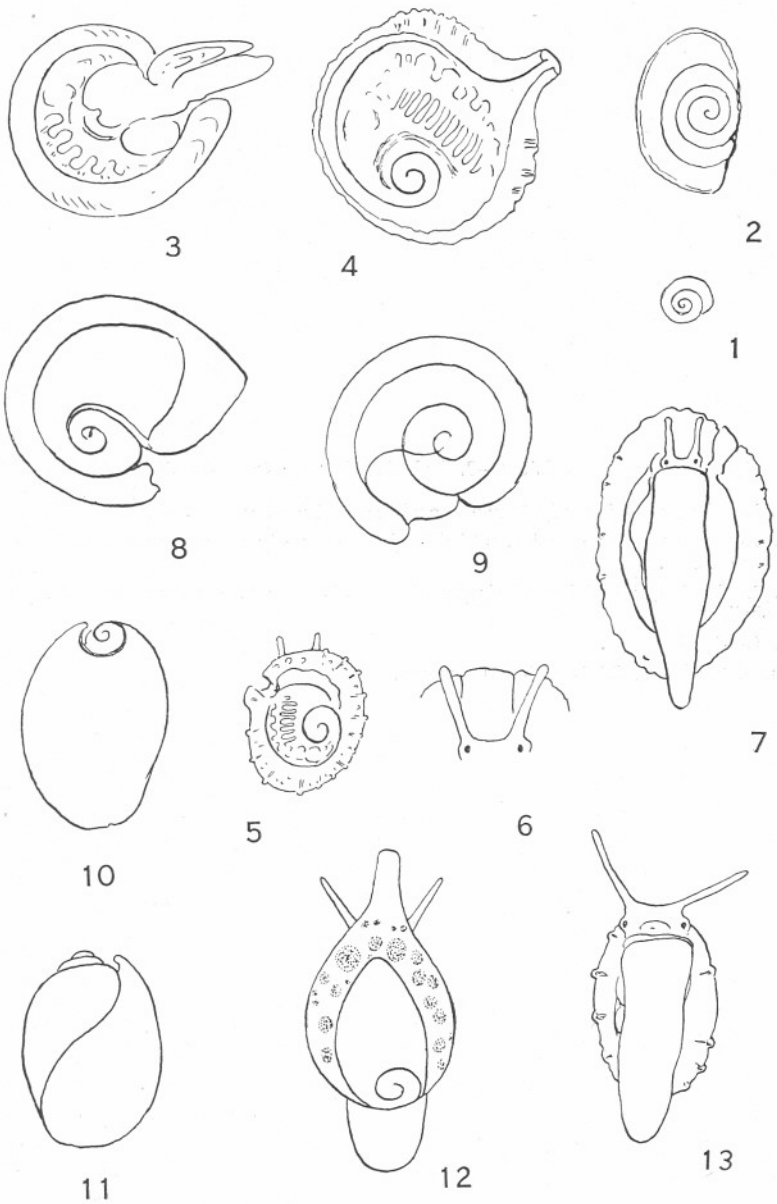
Larvæ of *Trivia europea*.

PLATE III. (1–4 and 8, 9, Scale A, the others on a smaller scale.)

FIG. 1.—Operculum of young, 0·64 mm. across shell.
FIG. 2.—Operculum of young, ready to metamorphose.
FIG. 3.—Young from plankton, 1·44 mm. across shell.
FIG. 4.—The same metamorphosing.
FIGS. 5–7.—The same after metamorphosis.
FIGS. 8, 9.—Empty shell, 1·4 mm. across.
FIGS. 10, 11.—Shell of older individual grown from young in plunger-jar, 4 mm. long.
FIGS. 12, 13.—Young found crawling on Diplosoma, from Sound, shell 3·5 mm. long.



Larvæ and young of *Trivia europea*.

PLATE IV. (1–3, Scale A, others on smaller scale.)

FIG. 1.—Young Trivia ready to metamorphose, 1·44 mm. across shell.

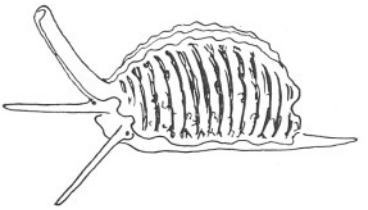
FIG. 2.—Unknown Echinospira, probably Velutina, ready to metamorphose, 1·92 mm. across shell.

FIG. 3.—Echinospira of *Lamellaria perspicua* ready to metamorphose, 2·24 mm. across shell.

FIG. 4.—Adult Trivia.

FIGS. 5, 6.—Adult Trivia eating Diplosoma.

1



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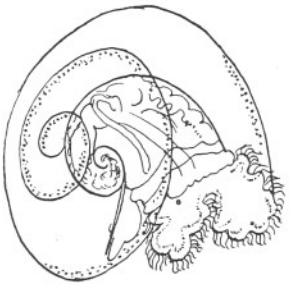

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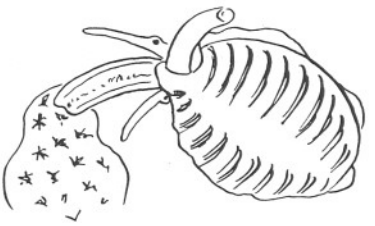

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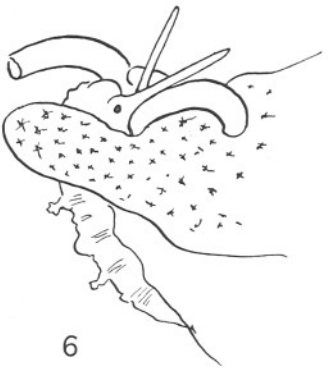

6

Late larvæ of Trivia, Velutina (?) and Lamellaria. Adult Trivia.

Note on a Marine Labyrinthula.

By

Margaret W. Jepps,

Lecturer in Zoology, Glasgow University.

With 6 Figures in the Text.

Plasmodia of Labyrinthula almost invariably appear in the diatom cultures and other small marine aquaria which I have kept during the last several years for a variety of purposes in Glasgow. These aquaria are stocked with material from Millport, I. of Cumbrae, and I think it quite certain that the Labyrinthula is imported thence.

This amazing creature has attracted interest ever since it was first described by Cienkowski in 1867, and good figures of it have been published by Cienkowski (1867), Duboscq (1921), and Valkanov (1929). The following note is to be regarded as a commentary on previous work and a record of my own observations rather than as an exhaustive account of the organism.

Labyrinthula exists, as is well known, in the form of a plasmodium in which small (about 10μ long) more or less spindle-shaped units glide about in a communal ectoplasm. Each spindle has a nucleus at about its centre, and is filled peripherally with oil droplets* which may be colourless or, in some of the specimens I have studied, yellow,† imparting a yellow tinge to the whole plasmodium as seen by the naked eye (cf. Cienkowski's Taf. XV, *loc. cit.*). The number and size of the oil droplets vary considerably—and sometimes spindles are seen in which there are none at all, the cytoplasm appearing quite homogeneous. I have never observed solid food bodies in the spindles, nor contractile vacuoles. The ectoplasm surrounds each spindle with a hyaline layer which is only clearly seen when it is heaped up at some point. Here and there will be a collection of spindles visible to the naked eye as an opaque patch which may be half

* Orange after 10-15 mins. in an alcoholic solution of Sudan III, brown in 2% osmic acid. It is possibly due to the oil droplets that fixation of the spindles is so often not successful. They appear to run together, causing distortion of the cytoplasm. The best results have been obtained with neutral formalin, followed by alcohol; sometimes Bouin's fluid has given good results. Pretty preparations of spindles with the oil drops in situ are obtained by fixing in osmic acid or Flemming (with no acetic acid), staining with picrocarmine, and mounting in glycerine jelly.

† Spindles containing yellow oil may occur in the same colonies as spindles containing colourless oil.

a millimetre or more across. From these there stream out spindles, singly or in small groups, in all directions, along ectoplasmic tracks which branch and anastomose very freely. These tracks in a well established active plasmodium form a widely extended network in which the spindles circulate slowly and intermittently. It is rather rare actually to see a spindle move, but with patience and some luck it is quite possible. On one

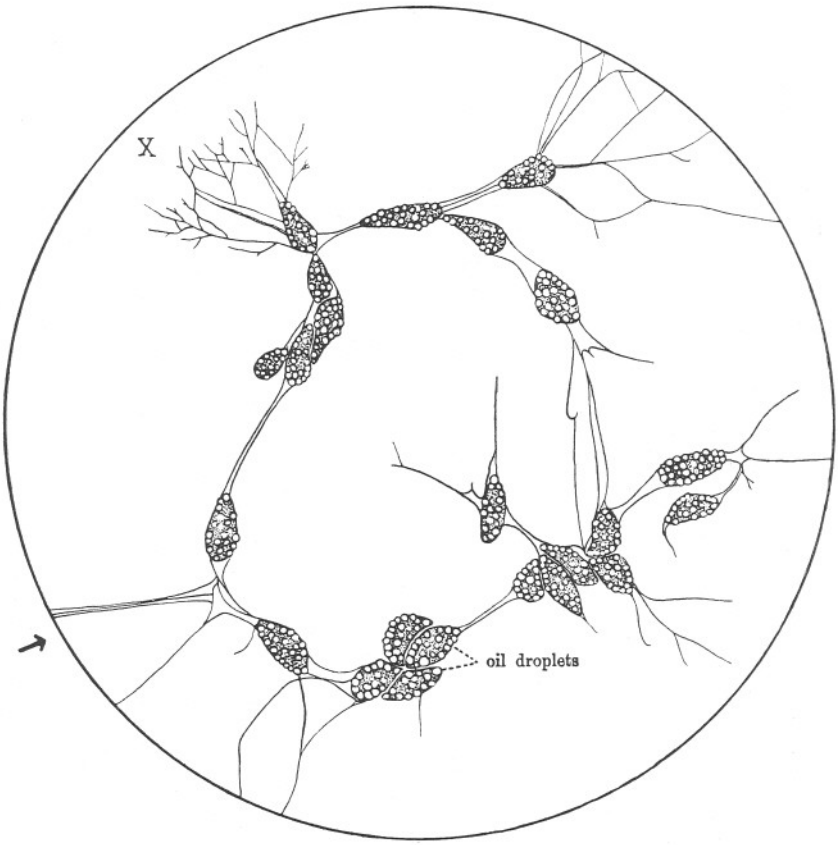

FIG. 1.—Labyrinthula spreading over coverslip in direction of arrow. At X more finely branched pseudopodia (from another specimen): these may extend all round the advancing plasmodium like an edging of fine lace. (From life.)

occasion I watched four spindles pass in succession over a length of 17μ. The times were respectively 1·5, 1·0, 2·25, and 1·25 minutes. The rate of movement is extremely variable however.

If a small portion of a deposit containing living plasmodia of Labyrinthula be removed from an aquarium on to a slide, preferably with a drop of fresh Nitzschia culture, and covered with a coverslip, the plasmodia will

creep out on to the coverslip or on to the slide, and the mode of progression can easily be studied (Fig. 1). The advancing spindles are always preceded by ectoplasmic pseudopodia, and glide along these, looking under the microscope like diminutive trams moving along their rails. There has been some discussion as to the nature of the network in which the spindles circulate (see Valkanov, 1929). Its pseudopodial nature is obvious at the edge of a spreading plasmodium ;* is there any reason for considering the more centrally lying parts as essentially different ?

FIG. 2.—Degenerating pseudopodium.

The exact relation between the ectoplasm and the spindles is obscure. The whole ectoplasm seems to be absolutely common to all the spindles, which are seen to pass one another along the tracks.

Labyrinthula feeds on diatoms and other vegetable cells. An infection

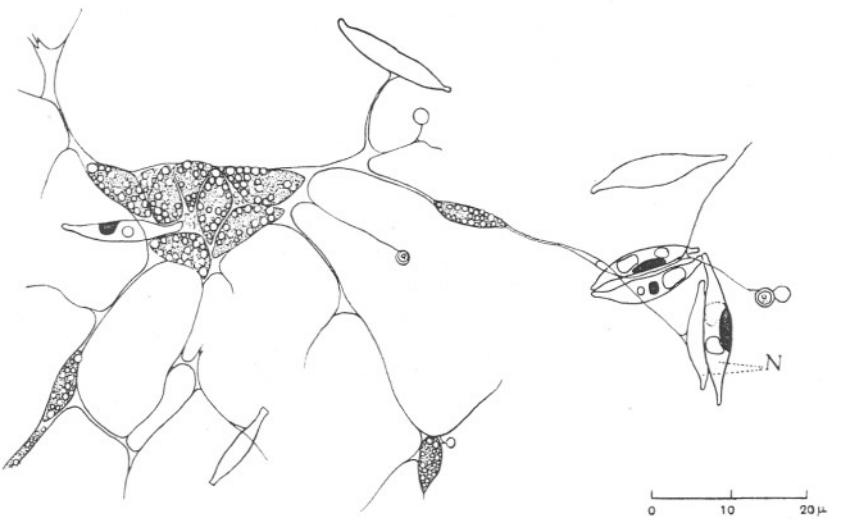

FIG. 3.—Labyrinthula feeding on Nitzschia, N. (From a living specimen.)

is in the end fatal to diatom cultures. One gets the impression that the tips of the pseudopodia gain entrance (? by natural apertures†) to the

* When degeneration sets in, as for example when the organism is observed for a long time, slowly suffocating in a preparation under a coverslip, in the light and warmth of a lamp, the peripheral parts of the reticulum may be seen to behave like other hyaline ectoplasmic structures, running into small droplets as shown in Fig. 2.

† It is well known that shelled organisms may not form their normal tests when grown in artificial culture, and it is possible that in such circumstances diatoms may offer less than the normal resistance to invasion.

cell, which is then completely used up, and the products of digestion passed back into the endoplasm of the spindles. Only very occasionally are isolated granules or droplets to be seen in the ectoplasm. When feeding

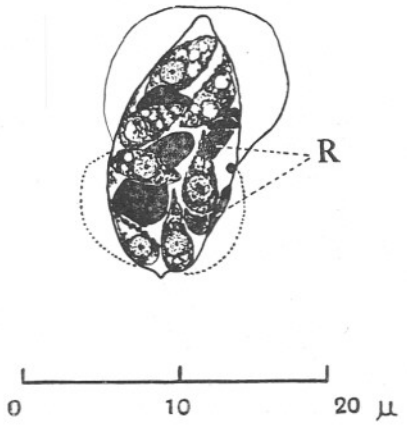

FIG. 4.—Labyrinthula in Amphiprora. From a stained specimen. R, remains of diatom contents.

on Nitzschia the spindles do not enter the diatom (see Fig. 3) ; but I have observed them inside a larger diatom, a species of *Amphiprora* (Ehr.) Cleve. (Peragallo, 1897–1908) as is shown in Figure 4. I was led by the

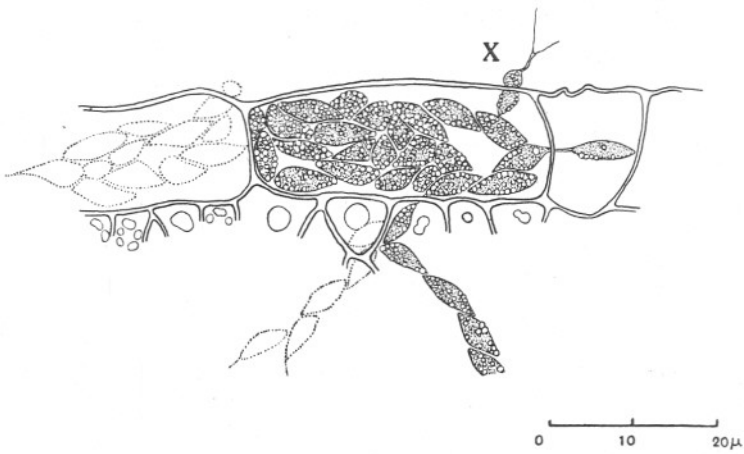

FIG. 5.—Living Labyrinthula in cells of *Laminaria saccharina*. Notice constricted spindle at X. Ectoplasm for the most part not shown.

papers of Professor O. Duboscq (1921) to infect some pieces of Laminaria with Labyrinthula. Pieces of the oarweed were placed in aquaria containing Labyrinthula, and I observed later the living plasmodia moving

through the cells of the alga (see Fig. 5) and presumably feeding on it. In my experiments the Labyrinthula seemed to obtain entrance by a damaged part of the thallus surface. It is not clear that it would otherwise have succeeded in getting in; especially as it was closely followed by ordinarily free-living amœbæ and by ciliates. The constricted spindle at X in Figure 5 suggests, however, an ability to bore a hole in the cell

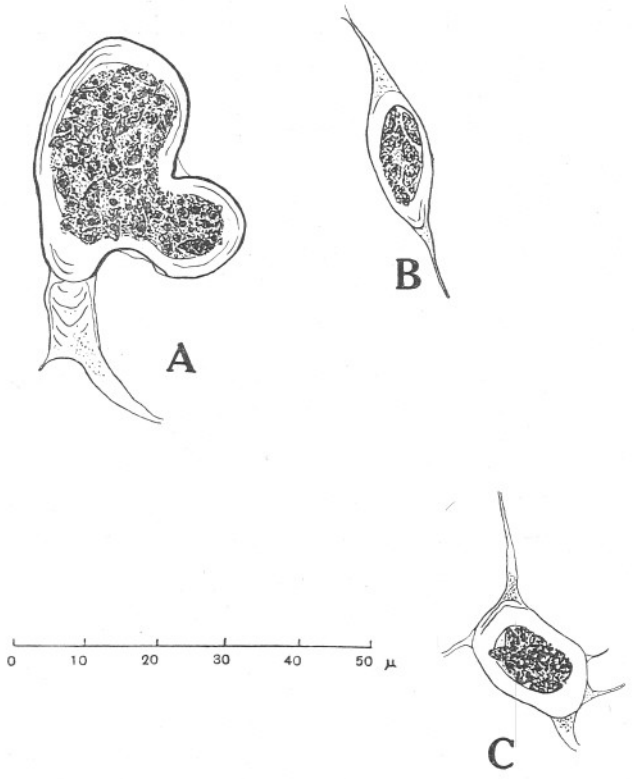

FIG. 6.—Cysts of Labyrinthula on a coverslip, from a stained preparation. Figs. B and C show two cysts evidently formed in the same plasmodium, in their original relative positions.

wall—cf. Duboscq's Figure 10. I may mention here that, though I have seen in my aquaria forms resembling other stages in the life-history of *Labyrinthomyxa* as described by Duboscq, I have not succeeded in connecting them with the Labyrinthula plasmodium. Nevertheless the two organisms appear so closely similar in their plasmodial stage that I venture to suggest that they belong to the same genus, i.e. Cienkowski's *Labyrinthula*.

The spindles multiply by binary fission, first of the nucleus and then of

the cytoplasm. The nuclear division is mitotic, with the formation of a typical division spindle.

Rounded up plasmodia are encountered, each enclosed in a thick hyaline covering of which the exact limits are difficult to see ; nor will it colour with the usual stains.* The separate spindles can be squeezed out by pressure, as indeed they can from an active plasmodium, and they have no special individual protective coats (cf. Cienkowski, 1867). Figure 6, A–C, shows in a permanent preparation what I take to be plasmodia in a similar condition, possibly some little time after their formation. Here the outer covering is brown (in Heidenhain's iron hæmatoxylin) and appears laminated. These structures are very like the cysts described by Valkanov (1929).

It is impossible to decide on a specific name for this organism. Three marine " species " of *Labyrinthula* have been made (Cienkowski, 1867 ; Valkanov, 1929), but not fully described, and it seems that all the forms may in fact belong to the same somewhat variable species. In my cultures the size of the spindles has varied considerably for example. Of the three " species " my organism fits best the description of *L. zopfi* (Valkanov, 1929), but I do not feel convinced that this is its correct name. I do not place it with *L. vitellina* Cienk. as I gather that the colour is not the same ; nor with *L. macrocystis* Cienk. as I have not observed the spore coats described by the author.

It is my pleasure once more to acknowledge my indebtedness to the late Mr. P. Jameson for cutting sections of my Labyrinthula material ; and to Mr. R. Elmhirst for help in supplying me with material both at Millport and at Glasgow.

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3. Peragallo, H. and M. 1897–1908. Diatomées marines de France, p. 183.
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5. Zopf. W. 1887. In Schenk's Handbuch der Botanik. III, 2, p. 24.

* No cellulose reaction was obtained in this covering with iodine and sulphuric acid ; an observation of some interest on account of the similar organisms which have been described as Mycetozoa (Zopf, 1887). It resembles the ordinary ectoplasm in its small staining capacity.

Some Additions to the Sponge Fauna of Plymouth.

By

H. J. H. Borley.

With 2 Figures in the Text.

In a small collection of sponges obtained during the winter of 1930–31 at Plymouth, six specimens were found which are of special interest. Four of these have proved to be new to the locality, the fifth was new to British waters, and the sixth was found to be a new species. Those species new to the Plymouth area are *Gellius angulatus* (Bowerbank), *Pachymatisma johnstoni* Bowerbank, *Eurypon clavatum* (Bowerbank), and *Halichondria firmus* Bowerbank. The latter is the first example of the species to be recorded since it was first described forty years ago. The species new to the British waters is *Reniera aquæductus* Schmidt, and the new species *Pseudaxinella alleni* n.sp.

Unfortunately the interest of the specimens was not fully realised at the time of collection so that only fragments of them were preserved, with the exception of *Eurypon clavatum* which was a thin plate of about 4 square mm. and of which nothing considerable remained after spicule and skeleton preparations had been made.

I must express my deep gratitude to Dr. Allen for his hospitality and very great help to me at Plymouth, and to Mr. Burton, for his invaluable assistance and advice in the writing of the following notes.

LIST OF SPECIES.

Pachymatisma johnstoni Bowerbank.

Occurrence.—Mewstone Ledge, Plymouth.

Reniera aquæductus Schmidt.

R. aquæductus Schmidt, Die Spongien des Adriatischen Meeres, 1862, p. 73, Pl. VII, Fig. 6.

Occurrence.—Mewstone Ledge.

Remarks.—The sponge is made up of 5 upright tubes, 9 cm. high by 1 cm. in diameter, fused together except at the summits. The oscules, 5 mm. in diameter, are apical and are surrounded by a peculiar raised

margin, now somewhat ragged, but probably smooth originally. The cloaca does not run through the whole tube. The surface is rather uneven in places, and minutely hispid, while the porose appearance, due to the numerous subdermal cavities, is marked. The colour in life is grey, strongly tinged with violet, and turns white in spirit. The texture is firm but compressible. The skeleton is subisodictyal, with a triangular mesh and occasional ill-defined trispiculous fibres. These fibres are seldom long and run irregularly towards the surface. The spicules are oxea measuring ·132 by ·006 mm.

The arrangement of the skeleton and dimensions of the spicules agree closely with those of a specimen of *R. aqueductus* from the Adriatic, identified by Schmidt, and now in the British Museum collection. This specimen is dried, while the present specimen is preserved in alcohol, and in this condition certain dissimilarities were observed. When a fragment of the Plymouth sponge was dried, however, the agreement between the two was found to be very close, and in this way the difference was shown to be apparent only. The Adriatic specimen is tubular, about 30 cm. high by 1 cm. in greatest diameter, narrowing slightly towards the summit and markedly towards the base. The spicules measure ·132 by ·006 mm.

The specimen originally described and figured by Schmidt, now unavailable, was an erect tube $3\frac{1}{2}$ cm. by 1 cm., and, in life, violet-blue in colour. Unfortunately, very little is known of this, and our knowledge of the species must depend mainly on the specimens from the same locality, identified by that author.

The main points of difference between the Plymouth sponge and the British Museum specimen are the more massive base and the oscular margin of the former. The presence of the oscular margin is the only considerable difference from the type. Such small differences are, however, hardly sufficient to justify a specific distinction.

Judging by Schmidt's original description the type differs also in the size of the spicules, being ·165 by ·007 mm., but here such a difference has little taxonomic value, especially as the British Museum specimen has spicules identical in size with those of the present specimen. These differences may therefore be regarded simply as evidence of the usual variation in spicule size within the species.

It is probable, judging by several specimens, including some hitherto undescribed, that the arrangement of spicules in the skeleton also shows some variation. In two examples, also in the British Museum, the one from Norway and the other from Cima Island, Madeira, both almost identical with Schmidt's type in external form, and with oxea measuring ·14 by ·004 mm. and ·149 by ·006 mm. respectively, there is a much more regular isodictyal skeleton than in the specimen identified by Schmidt referred to above.

In spite of certain minor differences, which are perhaps indicative of an ecological variation, the Plymouth sponge must undoubtedly be regarded as a representative of *Reniera aquæductus*, in which case the geographical range of the species will now include the British Isles, in addition to the Mediterranean, Madeira, Norway, and (possibly ?) Australia.

Distribution. Adriatic ; Black Sea ; Madeira ; Norway ; British Isles.

GELLIUS ANGULATUS (Bowerbank) Ridley and Dendy.

Halichondria angulata Bowerbank, Mon. Brit. Spong., 1866, II, p. 233 ; *Desmacodes angulatus* Vosmaer, Notes Leyden Mus., 1880, II, p. 107 ; *Gellius angulatus* Ridley and Dendy, Challenger Report Monaxonida, 1887, XX, p. 44 ; Lundbeck Ingolf-Exped. Rep., 1902, VI, 1, p. 62.

Occurrence.—Millbay Channel, Plymouth Sound.

Remarks.—The sponge is massive, globular and sessile, being about 5 cm. high by 10 cm. in diameter, with two oscules 5 mm. in diameter on the upper surface. The surface is very uneven and slightly hispid in places. The dermal membrane is not separable, but is supported by a confusedly subisodictyal skeleton of triangular mesh. The colour, both alive and preserved in spirit, is grey. The texture is friable. Both dermal and choanosomal skeletons are much confused subisodictyal networks with triangular mesh. The spicules are :—oxea ·199 by ·008 mm. ; toxa, ·063 by ·001 mm., with a rather rounded angle ; and minute sigmata, ·009 mm. chord.

The specimen agrees closely in form, colour and texture with the type-specimen in the British Museum. The type differs in having a more open and less confused skeleton, but the only considerable differences are a smoother surface and different spicule measurements. These are as follows :—oxea, ·225 to ·227 mm. by ·008 to ·009 mm. ; toxa, ·063 to ·072 mm. ; and sigmata, ·013 mm.

Although the general surface of the Plymouth sponge is more uneven it does in places approach the condition found in the type. Possibly the complete sponge would have shown different surface characters, but in any case this difference alone is hardly enough to justify a separation of the present specimen from *G. angulatus*.

The differences in the sizes of the spicules are also unimportant in view of the known variation within this species. The oxea vary, according to measurements given by various authors, from ·117 to ·388 mm. ; the toxa, from ·022 to ·095 mm. ; and the sigmata, from 007 to ·021 mm. The extent of the variation of the sigmata would be increased still further by the inclusion of the second set of sigmata, measuring ·078 mm., found by Lundbeck (l.c.), but the fact that this second category is only recorded

for this specimen suggests that it is an abnormal form and must be ignored for the present.

The Plymouth sponge approaches most closely those specimens described by Topsent from Luc, in which the measurements of the spicules are :—oxea, ·160 to ·260 mm. ; toxa, ·023 to ·070 mm. ; and sigmata, ·007 to ·009 mm.

This is the first record of the species from the Plymouth area, though it has been recorded from other points on the British coast.

Distribution.—British Isles ; France ; Spain ; Adriatic ; Azores ; Iceland.

EURYPON CLAVATUM (Bowerbank).

Occurrence.—Eddystone Grounds, Plymouth.

HALICHONDRIA FIRMUS Bowerbank.

Hymeniacidon firmus Bowerbank, Mon. Brit. Spong., 1874, III, p. 186.

Halichondria ambigua Id. t.c., p. 213.

Occurrence.—Winter Shoal, Plymouth Sound.

Remarks.—The sponge consists of thick contorted branches merging into a twisted plate. The branches bear irregular crateriform prominences each with an oscule as a minute opening in the floor of the crater. The surface is markedly glabrous except for deep irregular furrows running up the prominences and converging on the oscules. The dermal membrane is separable and supported by a rather regular network of bundles of spicules with a rhomboidal mesh. The texture is firm and fleshy. The colour in life is yellow, tinged with pink, but the pink disappears in alcohol. The skeleton is typically halichondroid, consisting of oxea, ·193 to ·369 mm. by ·004 to ·009 mm., and occasional styli ·167 by ·006 mm.

This species differs markedly from the two common British species of *Halichondria*, namely *H. panicea* (Pallas) and *H. bowerbanki* Burton, both of which are frequently met with in the Plymouth area. The characteristic features are the external form, the markedly glabrous surface, and the fleshy texture.

Some specimens of *H. panicea* approach *H. firmus* in external form, though not very closely, being distinguished by the greater regularity of the branches when present, and the usually more regular crateriform oscules. *H. bowerbanki*, on the other hand, is markedly different, but neither of these two have so glabrous a surface, and the texture of both is more friable. These two characteristics serve as a ready means of distinction. The furrowing of the surface is also a well-marked characteristic of *H. firmus*. The spicules are of similar size and shape in all three species,

but tend to be stouter in *H. panicea* and *H. bowerbanki* than in the present species.

This specimen agrees very closely with Bowerbank's description of the holotype of *Halichondria* (*Hymeniacidon*) *firmus* in all essential respects, and there can be little doubt as to the identity of the two. In point of fact it approaches more closely the type of *Halichondria ambigua* (Bowerbank), but as there appears to be no considerable difference, judged by the original descriptions, between *Halichondria* (*Hymeniacidon*) *firmus* and *H. ambigua*, there can be little doubt that the two species are synonymous.

Distribution.—British seas.

GENUS **PSEUDAXINELLA** Schmidt.

Genotype.—Pseudaxinella sulcata Schmidt.

(See Schmidt Jahresber. Comm. Unters. d. Meere 1875, V, 2–3, p. 115, and Thiele Arch. Naturg., 1903, I, 3, p. 378.)

Diagnosis.—Axinellidæ with skeleton composed of long curved styli, short bent styli, and oxea ; styli arranged in radial plumose fibres with an axial concentration ; fibres connected by oxea and short styli.

PSEUDAXINELLA ALLENI n. sp. (Figs. 1 and 2).

Occurrence.—Eddystone Grounds.

Diagnosis.—Sponge stipitate, ramose ; branches showing some anastomosis and terminating in palmate anther-like portions ; surface strongly hispid and very minutely conulose ; dermal membrane aspiculous and separable ; colour, living and in spirit, golden-yellow ; texture firm axially and soft extra-axially ; skeleton of radial plumose fibres rendering surface hispid, radiating from longitudinal concentration of fibres at axis of branch ; fibres composed of long curved styli and short bent styli and connected by short styli and few oxea ; spongin plentiful in stalk, sparse in upper branches ; spicules, long styli ·81 by ·02 mm., oxea ·27 by ·008 mm., and short styli ·343 by ·003 mm.

Remarks.—The present species agrees with the genotype in habit and the arrangement of the skeleton. It also agrees in the types and shapes of the spicules present except for the thin styli which are not mentioned for *P. sulcata*. Since these styli appear in the type specimen of the other species of *Pseudaxinella*, namely *P. egregia* (Ridley), this discrepancy is not serious. It seems probably that they are merely developmental forms and cannot therefore affect the identification. It differs further from *P. sulcata* in the comparative scarcity of the oxea and in the measurements of the spicules and from *P. egregia* in a more hispid, but less conulose

surface, a less regular skeleton, as well as in the dimensions of the spicules. The comparative scarcity of oxea may not be a real distinguishing feature in view of the tendency, shown in so many of the Axinellidæ, for the proportions of oxea and styli to vary.

The spicule differences are more striking, however, the measurements

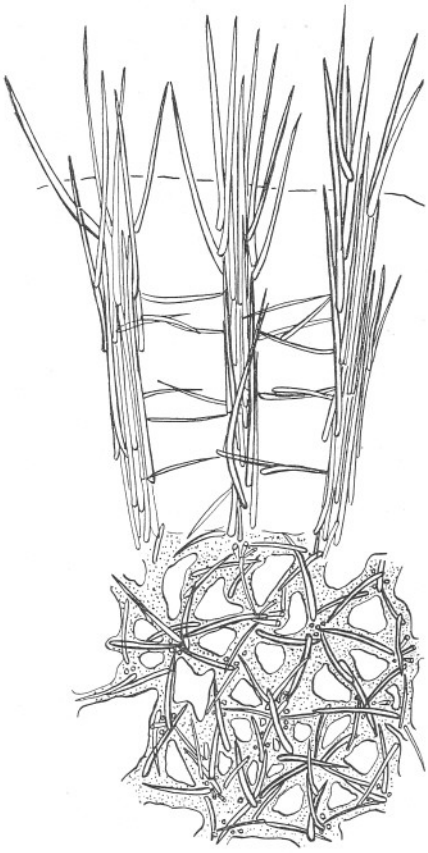

FIG. 1.—*Pseudaxinella alleni* sp. n. Section at right angles to surface.

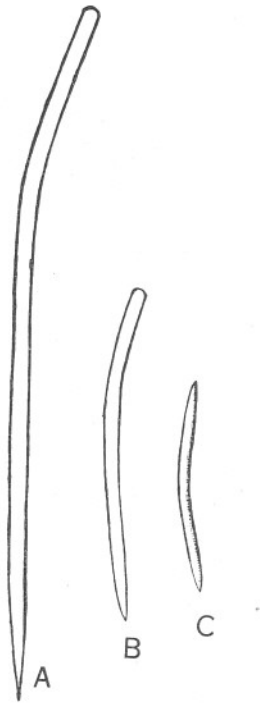

FIG. 2.—*Pseudaxinella alleni* sp. n.; (*a*) long style; (*b*) short style; (*c*) oxeote. × 22.

for *P. sulcata* being :—long styli, 1·45 by ·02 mm.; short styli, ·45 by ·02 mm.; and oxea, ·55 to ·75 mm. by ·02 mm. In *P. egregia* the dimensions are :—long styli, ·88 to 1·207 mm. by ·012 to ·019 mm.; short styli, ·253 by ·009 mm.; and oxea, ·304 by ·012 mm.

Thus the species under consideration does not show a really close agreement with either of the two species so far recorded for the genus. Possibly

a more extensive collection of specimens might show variations in *P. sulcata* wide enough to include the new species, but in the present state of our knowledge of the genus it seems best to consider this specimen as the type of a new species.

I feel myself that I cannot do better than name this species after Dr. Allen in gratitude for his great help to me personally, and as a slight recognition of his help to other workers in the group.

Preliminary Observations on the Early Stages of *Scatella stagnalis* Fal. (Ephydridae, Diptera).

By

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With 4 Figures in the Text.

CONTENTS.

1. Introduction.

The insects, *Scatella stagnalis*,* for the present study were collected from the Marine Biological Laboratory at Plymouth at the kind suggestion of Dr. Allen, F.R.S., the Director of the Laboratory, during my short stay there in the summer of 1929. So far as I can see, no work on the early stages of the genus *Scatella* is available. This led me to put on record the present account of the different pre-imaginal stages of the insect *Scatella stagnalis* in the following pages. I have described here only those stages that are exhibited in my hurried collection which may not be complete. A study of its complete biology would be of considerable interest; this, however, requires a constant watch of the species at the spot for a fairly long period.

2. Material.

The insects were found attached to the growth above the water's edge on the sides of a tank in the laboratory at Plymouth. This growth consists mainly of greenish and brownish algæ which are constantly kept moist by the sea-water from the tank. The algæ, I presume, provide a suitable

* I am grateful to Dr. F. W. Edwards for the identification of the species from the adults.

feeding ground for the Scatella. Various other micro-organisms, such as the protozoa and bacteria, so common in these places, also possibly supply additional nutriment to the species.

The imagines usually lie motionless on the sides of the tanks and generally abound those tanks without rapid currents. They are small blackish flies with spotted wings. For a detailed description of the adults, reference may be made to Fallen (1823) and Berl. Ent. Zeitsch. (1895).

3. Egg.

The egg is 0·1 mm. in length and is nearly twice as long as broad. It is more or less bean-shaped, with a slight depression in the middle of the ventral side, both ends of it being somewhat rounded in the same manner and having an equal width. The micropyle is not distinguishable. The chorion is ridged with a number of transverse ripples, giving it as triated appearance, and is blackish in colour. The eggs are found singly, which suggests that they are perhaps not laid in batches.

4. Larva.

My collections show that there are at least three instars in the larval life such as are generally met with in the Cyclorrhaphous flies. I have differentiated the stages mainly on the basis of the respiratory system and it may be noted here that I have not seen their moultings.

(i) *First Instar* (Fig. 1).

The larva in this stage measures about 1·9 mm. in length with a breadth of 0·4 mm. and is whitish in colour, being more or less transparent. It consists of thirteen segments, the last segment being pushed a little ventralwards. The posterior or the anal end of the larva is truncated and is wider than the anterior end. The caudal branches of the last segment are just visible bearing a pair of spiracles at their blunt ends, one on each side ; the larva is metapneustic, there being no other spiracles. The mouth-parts agree closely with those of Ephydra (Ping, 1921). Anteriorly there is a U-shaped mandibular sclerite which is separated from the remaining parts composed of a pair of H-shaped hypostomal sclerites and a pair of lateral pharyngeal plates posteriorly.

(ii) *Second Instar.*

The second instar larva measures about 2·8 mm. in length and nearly 0·6 mm. in width. It is brownish in colour and somewhat opaque. The larva becomes amphipneustic, there having appeared a pair of thoracic spiracles now, one on each side of the prothorax, in addition to the pair

of caudal spiracles which become more pronounced than in the preceding stage. The cephalo-pharyngeal skeleton becomes highly chitinised.

(iii) *Third Instar* (Fig. 2).

The third instar or the full-grown larva measures from 5·0 mm. to 5·4 mm. in length (from tip of head to extremity of caudal branches) with

FIG. 1.—First instar larva of *Scatella stagnalis*.

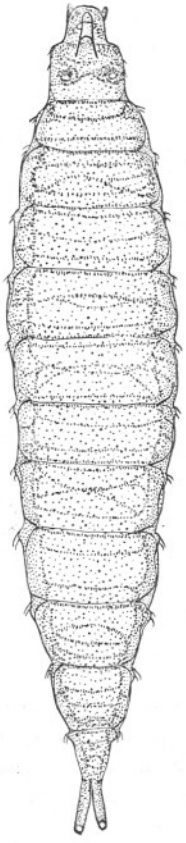

FIG. 2.—Third instar larva of *Scatella stagnalis*.

a breadth of 1·0 mm. to 1·1 mm. in the widest part; the size thus is variable to some extent. The prothoracic spiracles, one on each side, already mentioned in connection with the preceding stage become six-digited and the larva as a whole is more strongly chitinised, having an opaque brownish body surface.

It is cylindrical in shape and consists of a retractile head and twelve

body segments, possessing thirteen segments altogether. The head bears a pair of two-segmented minute antennae, the basal segment of each antenna being much wider than the distal. The body segments, excepting the two or three anteriormost, are not very distinct and are highly wrinkled. The two caudal branches in the last segment are tubular in shape, within which the main tracheæ are extended. At the apex of each of these branches lies a chitinous cap possessing the caudal spiracle in the centre and four fan-shaped membranous structures hanging laterally.

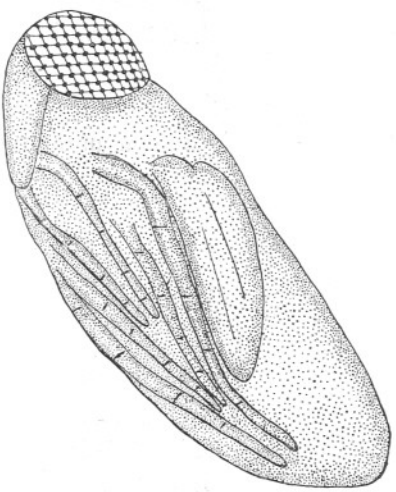

FIG. 3.—Pupa of *Scatella stagnalis*.

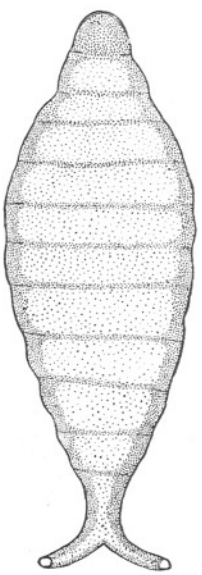

FIG. 4.—Puparium of *Scatella stagnalis*.

The body is thickly beset with spines which are more prominent dorsally. Each of the first eight abdominal segments bears a pair of nipple-like prolegs which are provided with a number of short setæ. The last pair of prolegs are larger than any of the preceding ones.

5. PUPA (Fig. 3).

The pupation takes place within the last larval skin which functions as the puparium (Fig. 4). The anterior three or four segments of the puparium are flattened dorso-ventrally, and posteriorly the puparium is more or less barrel-shaped. The pupæ are attached to the substratum by means of the caudal branches in the puparium and the branches at this stage diverge laterally and are not directed posteriorly as in the larva.

The pupa is much smaller in size than the puparium, being nearly half

the latter, and is enveloped in a thin transparent saccular sheath through which the imaginal appendages can be clearly distinguished. The pupa measures about 2·3 mm. in length with a width of 0·9 mm.

The anterior end of the pupa is broader than the anal end, and the head possesses a pair of prominent eyes. A pair of small antennal tubercles can be seen at the sides of the head in front of the eyes. The proboscis is flattened and firmly pressed to the body in between the coxæ of the legs. The wings and the three pairs of legs are also closely pressed against the ventral surface of the pupal body.

The imago, when ready to emerge, effects a split at the anterior flattened end of the puparium, through which it subsequently escapes. The split runs along the sides of the puparium, dividing this end of the puparium into two almost similar flaps, one dorsal and one ventral.

The species seems to be fairly free from enemies, as most of the parasitic and predaceous insects find the salinity of the water, in which the Scatella abounds, unsuitable for habitation. Certain mites, however, are often found in the beds of *Scatella stagnalis*.

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A New Type of Luminescence in Fishes, III. The Gland in *Cœlorhynchus cœlorhynchus* Risso.

By

C. F. Hickling, M.A.

With 3 Text-Figures and Plates I–IV.

In 1925 I published a paper (**1**) describing a new type of luminescence in fishes, exhibited by the Macrurid fish *Malacocephalus lævis* Lowe, and a further paper (**2**) described experiments made on the luminescent secretion of this fish. In my first paper, I remarked that the Macrurid *Cœlorhynchus cœlorhynchus* Risso also possesses, "between the pelvic fins, a naked, pigmented patch; resembling that of *M. lævis*, and dissection again reveals a flat, pigmented sac lying in the body-wall adjacent to this pigmented patch." "It gives one the impression of a rudimentary organ, yielding no secretion, but connected with the anus by a pigmented, functionless duct." The present paper describes this gland in *C. cœlorhynchus*.*

Farran (**3**) writes, of *C. cœlorhynchus*, "this species is found in the Mediterranean, and in the Atlantic for about 20° to north and south of the Straits of Gibraltar, occurring along the edge of the continental shelf, and descending for a short distance down its upper slopes." I have recorded it (**4**) from the West Coast of Scotland, and Smitt (**5**) includes it among the fishes of Norway. In my first paper, I stated that I had then only seen five specimens on the Hake grounds south-west of Ireland, but, in 1926, I was able to examine many specimens at sea, and to cut out and fix the glands for further examination ashore. Unfortunately, I did not measure these specimens, which, however, were all comparatively large, certainly not less than 30 cm. in length. They will be referred to, in this paper, as "older specimens." Microscopic examination of these glands showed much variation in structure, and I felt that a proper understanding could be attained only after a comparison with younger specimens. I had to wait until August, 1930, and January, 1931, for this material. In August, 1930, the Ministry of Agriculture and Fisheries' research vessel *George Bligh* took two specimens, 14 and 15 cm. in length, on the "West-

* The work has been done in the writer's spare time, with material collected during voyages on hake research.

ward Ground," in about 180 fathoms, latitude about 49° 50′ N., and in January, 1931, the steam trawler *Tenedos*, aboard which I was engaged in hake research, by courtesy of the owner, Mr. H. E. Rees, took many specimens between 18 and 23 cm. in length, and one of 30 cm.

Some specimens were preserved whole, others were dissected, and the ventral gland, with its associated structures, fixed in Bouin's Fluid. The fixed material was cut into sections and stained by Mr. B. G. Clarke, Chief Laboratory Assistant at the Lowestoft Laboratory, to whom I would here acknowledge my thanks for his care and skill.

The stains used were Iron Hæmotoxylin and Eosin. The material was not easy to cut, owing to the abundance of tough connective tissue, and the sections have not always been perfect.

Finally, I would thank Professor Carl L. Hubbs, of the University of Michigan, for the benefit of his expert advice concerning the Macruridæ. In using his correspondence, I wish to avoid casting any responsibility upon him for my own findings.

A. The Anatomical Relations of the Gland.

Farran (**3**) writes, of *C. cœlorhynchus*, "between the ventral fins is a scaleless, oval depression, black in colour." Smitt (**5**) gives a very fine figure of this fish, and describes "a narrow, oblong, bare spot in the median line of the belly between the ventral fins." In his figure, the scaleless, oval spot, or depression, is placed with its centre decidedly anterior to a line joining the bases of the pelvic fins. This was also the usual position in my larger specimens. In my smaller specimens, the depression tended to lie more directly between the bases of the fins.

There is much bluish-black colouring in the skin in the ventral region of the fish, and the scaleless spot occurs in the midst of this, as a distinct, spindle-shaped depression. The margins of the depression project slightly, and the floor of the depression is itself covered with a comparatively thin skin, thickly strewn with melanophores. The posterior half or two-thirds of the depression bulge slightly.

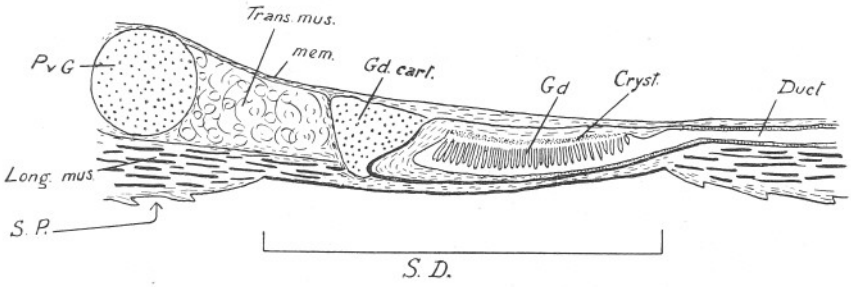
Posteriorly, the depression ends indefinitely, but a well-marked trail of pigment runs backwards from it, between the pelvic fins, to the anus, which is itself surrounded by a slightly swollen area heavily loaded with melanin.

From the dorsal aspect, the body-wall in the region anterior to the anus is seen to be covered by the thin silvery peritoneum, speckled with melanophores, and, when this is stripped off, a gland is revealed, lying in the mid ventral line, appearing as a swelling, well covered with black pigment and silvery guanin, of oval shape, tapering posteriorly into a duct likewise well wrapped in black pigment. Gland and duct are sur-

rounded by the muscles of the body-wall, and are overlaid by a very tough, almost cartilaginous membrane, of stoutly fibrous connective tissue (Text-Fig. 1 : *Mem.*). This membrane runs forward, and is connected to a prominent, curved ridge, which marks the junction of the right and left pelvic bones with the median pelvic cartilage (Text-Fig. 1 : *Pv. g.*). Through this membrane, two small blocks of cartilage may be seen associated with the gland : these cartilages meet in the middle line above the anterior extremity of the gland (Text-Fig. 1 : *Gd. cart.*).

Text-Figure 1 is a drawing of a rough sagittal section of the gland, made with a razor, and viewed through a lens.

The gland (*Gd.*) is a flattened sac overlying the scaleless depression (*S. d.*) ; it is partly filled with a brilliantly white substance, and is surrounded and defined by thick sheaths of black pigment, distinct from the



TEXT-FIG. 1.—Rough sagittal section of the ventral gland and the adjacent structures in a 30-cm. specimen of *C. cœlorhynchus*.

For explanation of the lettering, see text.

black pigment present in the floor of the scaleless depression. Both anterior and posterior to the scaleless depression, the scale-pockets (*S.p.*) are shown.

Posteriorly, the gland tapers away into the duct (Text-Fig. 1 : *Duct*) which runs backward to the anus. Anteriorly, the gland tapers obliquely downwards, to end bluntly, like the toe of a shoe. Text-Figure 1 was made from a specimen of 30 cm. In smaller specimens (for example, of 15 cm., Plate I, Fig. 1) the gland ends roundly, anteriorly, without tapering. This point is dealt with in Section C. In all cases, however, the connective tissue capsule of the gland is strongly bound to the peculiar cartilages (Text-Fig. 1 : *Gd. cart.* ; Plate I, Fig. 1 *et seq.*) mentioned above. Further forward, the section in Figure 1 cuts through the median cartilage of the pelvic girdle (*Pv. g.*) ; between the pelvic girdle and the gland cartilages lie transverse muscles (*Trans. mus.*), and longitudinal muscles lie beneath these (*Long. mus.*).

The gland cartilages are closely associated with the pelvic girdle. In the

first instance, they are bound, and the gland itself with them, to the pelvic girdle, by the overlying membrane of stout connective tissue (Text-Fig. 1 : *Mem.*), but, they are also more directly connected with the posterior processes of the pelvic girdle.

Text-Figure 2 is a reconstruction of the pelvic girdle in *C. cœlorhynchus*. The specimen was of 23 cm., and ossification in the girdle was incomplete.

There is a comparatively large, wedge-shaped median cartilage (*M. c.*) lying in the mid-ventral line, to which the pelvic bones of either side are attached (*P.*). From the posterior region of each pelvic bone, anterior to the point where these expand to form the articulation (*Art.*) of the fin-rays, springs a comparatively stout posterior process (*P. p.*, using the nomenclature of Goodrich, **6**) which inclines in a curve towards the middle

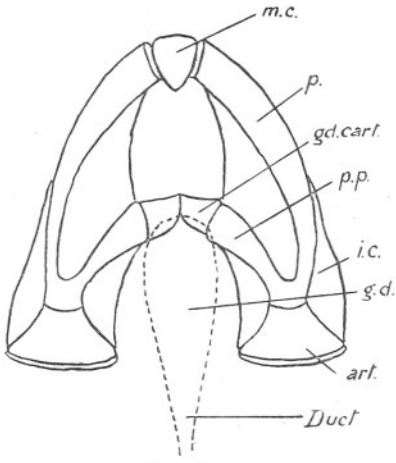


Fig. 2.

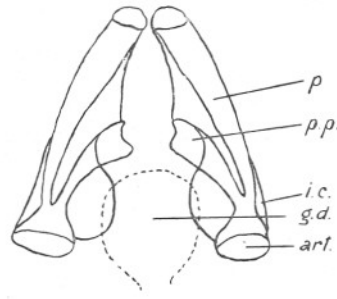


Fig. 3.

Text-Figs. 2 and 3.—Pelvic girdles of *C. cœlorhynchus* of 23 cm. (Fig. 2) and *M. lævis* of 25 cm. (Fig. 3).

line. Each posterior process is bound (but not, apparently, fused) to its corresponding gland-cartilage (*Gd. cart.*). The two gland cartilages curve upwards and towards the middle line, forming a bridge which spans the anterior of the gland. They meet at the middle line, and are bound to each other, and to the connective tissue of the gland, by a strong ligament (Plate II, Fig. 3).

A shallow crest (*I. c.*), which we may call the iliac process, runs dorsally along the pelvic bones of each side, from the angle of the articulation of the fin-rays to a point about half-way along the shaft of the pelvic bone. The posterior process is united, both to the pelvic bones and to the inner (medial) angle of the articulation, by membranes in which ossification was well advanced in the young specimens dissected.

B. The Structure of the Gland in Young Specimens.

Plate I, Figure 1, is a drawing of a sagittal section of the gland and duct in a 15-cm. specimen of *C. cœlorhynchus*. Its general features resemble those of the gland of the 30-cm. specimen in Figure 1. The gland lies in the thickness of the body-wall: above is the body-cavity. The gland is strongly bound with fibrous connective tissue (*C. t.*) which also binds it to the gland cartilage (*Gd. cart.*). In the neighbourhood of the cartilage, the fibres of the connective tissue are very thick, and stain deeply with Iron Hæmotoxylin. Transverse or oblique muscles (*Trans. mus.*) are seen anterior to the gland-cartilage. The scaleless depression can be discerned in the outline of the outer skin of the fish (the lower margin of the section). In this young specimen, the gland overlies the whole of the scaleless depression.

The sheet of stout connective tissue overlying the gland (shown in Text-Fig. 1) is not seen in this section; it has probably become detached, with the peritoneum, during manipulation. The connective tissue in the roof of the gland is thickly impregnated with guanin crystals; these reflect the light strongly, and make this region conspicuous. They constitute the "brilliant white substance" observed in the rough sagittal section of the gland. The walls of the gland also contain a continuous layer of melanophores: these are especially abundant in the floor of the gland (*Mel.*).

From the roof of the gland a system of tubules (*S.t.*) projects downwards; these gradually become confluent into irregular collecting spaces (*C. s.*), which are traversed by trabeculæ of connective tissue with an epithelial lining, and are confluent posteriorly with the duct (*d.*). The tubules are actively secretory; they are lined with a conspicuous epithelium secreting dense masses of minute granules. They seem to resemble, in all respects, those of *M. lævis* (**1**), and the appearance and formation of the secretion is also similar (**2**). A number of small blood-vessels (*B.v.*) are present in the roof of the gland, which branch into very fine vessels passing down into the walls of the tubules.

Plate II, Figures 3, 4, and 5, are drawn from a series of sections cut horizontally through the gland of a 14-cm. specimen of *C. cœlorhynchus*, i.e. parallel to the ventral surface of the fish. Figure 3 is a section just touching the extreme top of the gland, Figure 4 is a section through the upper portion of the gland, and Figure 5 a section near the base of the gland.

The greater part of the space in Figure 3 is occupied by the gland-cartilages (*Gd. cart.*) which almost touch each other at the middle line. They are separated by a few fibres of the stout ligament which binds them together, and to the connective tissue capsule of the gland (*C.t.*). The

fibres of this ligament stain deeply with Iron Hæmotoxylin. The extreme top of the gland is seen posterior to (below in the figure) the gland cartilages. It consists of connective tissue, containing many melanophores (*Mel.*), an area rich in crystals of guanin (*Cryst.*), and numerous much-branched blood vessels (*B. v.*). It is clear that this series of sections is slightly oblique, since the left gland cartilage is cut more longitudinally, the right, more transversely ; this is confirmed by Figure 4, cut at a lower level of the gland, where the left gland cartilage has passed out of the section, while the right, cut more longitudinally as it curves outwards and downwards, is still visible.

In Figure 4, as has just been stated, the right gland cartilage (*G. c*). is seen, attached to the wall of the gland, which contains its usual melanin sheath (*Mel.*) and blood vessels (*B. v.*). The gland itself consists, at this level, almost entirely of the secretory tubules (*S. t.*), here cut transversely. At the anterior end, however, the lumina of these tubules are already running together into collecting spaces (*C. s.*). Longitudinal and transverse muscles surround the gland.

In Plate II, Figure 5, the secretory tubules are no longer present, and the gland consists, at this level, of the collecting spaces (*C.s.*) which are confluent, posteriorly, in the Duct (*D.*). A very complete melanin sheath (*Mel.*) surrounds both gland and duct. There is a constriction at the junction of the gland and duct, and, at first, I suspected some kind of sphincter mechanism : no muscle is apparent, however, and it is probably a fortuitous projection of the wall of the duct.

C. The Structure of the Gland in Older Specimens.

The structure of the gland of *C. cœlorhynchus*, as it is found in small specimens of 14 and 15 cm., may now be compared with that of the gland in larger specimens, whose length, not ascertained, may almost certainly be put at over 30 cm.

In Plate I, Figure 2, is a drawing of a sagittal section through the gland of an older specimen. It is drawn to the same scale as Plate I, Figure 1.

The structure of the gland resembles that of the young fish. The gland cartilage is present, but is out of the field to the right. The gland consists of a connective tissue capsule, bearing melanophores (*Mel.*), and containing secretory tubules (*S. t.*) discharging into collecting spaces (*C. s.*). The tubules are full of secretion.

The striking difference between the larger and the smaller specimens lies in the fact that the gland, in the larger specimen, is about twice the length and depth of that of the smaller, whereas the secreting portion occupies about the same area in both fish. In the larger fish, the connective tissue of the roof has increased greatly in thickness, and the layer

of guanin crystals (*Cryst.*) is separated from the tubular portion of the gland, upon which it abuts in the smaller specimen. The system of collecting spaces occupies a much greater area in the larger fish, and runs far forward, beyond the secretory tubules, as a blind pocket. The melanin sheath is less conspicuous, the pigment is distributed more thinly, almost as if the increase in size of the gland had not been accompanied by an increase in pigmentation.

In Plate III, Figures 6 and 7, are shown, in transverse section, the glands of two older specimens of *C. cœlorhynchus*.

The gland in Figure 6 is, clearly, very similar to that shown in Plate I, Figure 2; there is a well-developed system of secretory tubules (*S. t.*) containing abundant secretion, a well-marked melanophore sheath (*Mel.*), and large collecting spaces (*C. s.*). The tubular portion of the gland, however, is reduced in area as compared with the gland of a smaller fish such as that in Plate I, Figure 1, and appears, in fact, to occupy an even smaller space than that in the gland shown in Plate I, Figure 2, while there is a tendency for the secretory tubules to project obliquely, rather than vertically, towards the collecting spaces.

In Figure 7, the gland has undergone great reduction. The secretory tubules have disappeared, the gland is very much flattened, and contains only collecting spaces (*C. s.*), themselves reduced and flattened. The melanophore sheath is very indistinct (*Mel.*). One of the gland-cartilages (*Gd. cart.*) is visible, bound to the gland by deeply staining fibrous connective tissue.

Three other glands of older specimens were sectioned and examined. In all three there was a relative reduction in the secretory portion of the gland, as compared with a small specimen, and the blind forward prolongation of the collecting spaces, shown in the section in Plate I, Figure 2, is a common feature.

Comparing the structure of the gland in smaller and larger specimens, it appears that, with an increase in the size of the gland, there is no corresponding increase in the amount of the secretory epithelium, and a greater diffusion of the pigmentation of the gland. This points, in my opinion, to disuse and degeneration of the gland as the fish grows larger.

D. The Duct.

It has already been mentioned that the gland narrows posteriorly into a duct, which runs backward to the anus, and is marked by a trail of black pigment. The duct may be seen in Text-Figure 1, in Plate I, Figures 1 and 2, and in Plate II, Figure 5. It is lined with epithelium two or three cells deep, and is, in smaller specimens at least, surrounded with melanophores.

Its length varies with the size of the fish, not only absolutely, as may be expected, but relatively also.

This may be seen in the measurements given below.

Length of Fish.	*Length of Duct.*	$\frac{\textit{Length of Fish.}}{\textit{Length of Duct.}}$
15 cm.	0·5 cm.	30
18 cm.	0·9 cm.	20
19 cm.	0·8 cm.	24
20 cm.	0·8 cm.	25
22 cm.	0·9 cm.	24
22 cm.	0·9 cm.	24
30 cm.	2·0 cm.	15

In the fish of 15 cm., the length of the duct is only one-thirtieth of that of the fish, in one of 20 cm., one-twenty-fifth, and in one of 30 cm., one-fifteenth. This relative lengthening of the duct seems to be associated with a relative forward movement of the pelvic fins, accompanying the growth of the fish.

The duct runs backward to the anus. Its final course there may be traced by examining a series of horizontal longitudinal sections, cut transversely to the rectum, and parallel to the surface of the body in the neighbourhood of the anus.

Drawings are shown, in Plate IV, of sections from such a series in specimens of 21 cm. (Fig. 8), and of 30 cm. (Fig. 9). Both are drawn to the same scale.

In Figure 8, the rectum (*R.*) occupies the centre of the section, lined with its characteristic tall and irregular epithelium. It is surrounded by connective tissue, containing blood vessels (*B. v.*) and melanophores (*Mel.*). The sphincter muscle is not seen in this section. Surrounding the rectum is a system of loose spaces (*P.*) lined with an epithelium closely resembling that of the duct of the ventral gland, but quite distinct from that of the rectum. Surrounding these spaces is a second, and denser ring, of melanophores. Posterior to the anus, there appears, cut in transverse section, the genital duct (*G. d.*), here appearing as a space in the connective tissue, and the kidney duct (*K. d.*) with a well-defined columnar epithelium.

In Figure 9, which is a section cut at a somewhat higher level, in its series, than that shown in Figure 8, the rectum again occupies the centre of the field (*R.*), and the ring of unstriped muscle (*Mus.*) is conspicuous in its wall. Outside this is a dense ring of melanophores (*Mel.*), which surrounds the rectum, and also surrounds a system of spaces (*P.*) lying in the connective tissue surrounding the rectum. Anteriorly (to the right in the figure) the ring of melanophores narrows to a sheath surrounding the

duct of the ventral gland; the latter is shown, cut obliquely, at (*D.*). Posteriorly, the genital duct (*G. d.*) and kidney duct (*K. d.*) are to be seen.

These series of sections show that the duct of the ventral gland widens, at the rectum, into a series of loose spaces, which more or less surround the rectum, and end blindly, dorsally, in irregular pouches. The pouches extend relatively much further up the sides of the rectum in the smaller specimen (21 cm.) than in the larger specimen (30 cm.).

These pouches, with their melanin sheath, are the cause of the " slightly swollen area, heavily pigmented," which may be seen, with the naked eye, surrounding the anus.

E. A Comparison with the Gland and Duct in *M. lævis.*

There can be no doubt but that the ventral glands in *C. cœlorhynchus* and *M. lævis* are homologous. In both, the duct opens to the exterior " about the anus, in such a way as to surround the lower part of the rectum " (**1**). In both, pouches arise from this external opening, which run upwards beside the rectum, and end blindly. In both cases, the secretory part of the gland consists of tubules, which discharge a granular secretion into a system of loose collecting spaces. As pointed out in *M. lævis*, these tubules are best regarded as " an epithelium, which has been thrown into long folds." The tubules and collecting spaces are firmly bound in connective tissue, to form a compact gland, containing a layer of guanin crystals, and insulated from the other tissues of the fish by a screen of melanophores. The gland lies, in both cases, in the thickness of the body-wall, forward of the rectum, and between the pelvic fins.

There are some differences. Firstly, the duct is very short in *M. lævis*, relatively long in *C. cœlorhynchus;* but there is reason to think that this difference becomes less significant in small specimens (Section D). The gland in *C. cœlorhynchus* is notably flatter in shape than that of *M. lævis;* the secretory tubules of *C. cœlorhynchus* project downwards from the roof of the gland, in *M. lævis* they project towards the centre of the gland, mainly from the anterior and lower walls. The gland of *M. lævis* overlies two small scaleless depressions in the skin: one large depression is associated with the gland in *C. cœlorhynchus*. From their respective relations with the gland, the two small depressions in *M. lævis* are probably homologous with the single large depression of *C. cœlorhynchus*. The significance of these depressions might possibly be explained by an embryological study, for which the materials are at present lacking.

These differences are trifling, and might be much less marked in small fish. There are three important differences.

Firstly, the gland in *M. lævis* is furnished with unstriped muscle, which forms a sheet over the top of the gland, " probably closely connected

with the function of compressing the gland to cause emission of the secretion." There is no such muscle even in young specimens of *C. cœlorhynchus*.

Secondly, the gland in *C. cœlorhynchus* is strongly bound, at its anterior end, to two special cartilages, which are connected, in their turn, with the pelvic girdle (Text-Fig. 2). These are present in older specimens of *M. lævis*, but the gland is not closely bound to them, as it is in *C. cœlorhynchus*. The pelvic girdle of a young (25 cm.) specimen of *M. lævis* is shown in Text-Fig. 3. Comparing it with the pelvic girdle of a 23 cm. specimen of *C. cœlorhynchus* it is clear that there are considerable differences. The median cartilage is wanting in *M. lævis*, and the posterior processes, which in *C. cœlorhynchus* are comparatively stout rods, in *M. lævis* are flattened, less definite structures, from which arise sheets of bone, which, arching upwards (dorsally) and towards the middle line, form a shallow cavity in which the gland (of which the outlines are indicated) is contained. In an older specimen of *M. lævis* (43 cm.) the posterior processes are more rod-like, as in *C. cœlorhynchus*, and two very small rounded cartilages are present, which connect the two posterior processes of the pelvic girdle across the middle line. But the luminiferous gland appears to be quite independent of these cartilages.

It seems probable that the " lens-like body " figured and described (**1**) as lying anterior to the gland, in *M. lævis*, is really hyaline connective tissue filling the space between the gland and the enclosing sheets of bone, and in no way " part of an optical apparatus, for casting light from the gland itself," as I doubtfully suggested in my paper on *M. lævis*.

These differences between the relations of the gland and the pelvic girdle are probably associated with a different mode of ejection of the secretion. If ejection is brought about, in *M. lævis*, by the action of the unstriped muscle in the wall of the gland, the sheets of bone, enclosing the anterior portion of the gland, will give the necessary support against which the pressure produced in the gland by the muscle can have effect. In *C. cœlorhynchus*, it seems probable that ejection is accomplished on quite a different plan. The two gland cartilages rise up in an arch, spanning the fore part of the gland, and are united above, at the middle line, by a ligament. This ligament might act as a hinge, so that, if the lower ends of the gland cartilages were pressed towards each other by the posterior processes of the pelvic girdle, to which they are attached, the gland would be squeezed, nutcracker-fashion, and the contained secretion forcibly ejected. Thus ejection could be brought about by the transverse muscles between the two halves of the pelvic girdle, acting on the gland by way of the posterior processes and the gland cartilages.

The third difference is this, that the gland of *M. lævis* remains actively functional, in producing a luminescent secretion, throughout life, whereas,

in *C. cœlorhynchus*, the evidence points to its degeneration with growth. I have not found, among scores of specimens of all sizes, a single *M. lævis* which did not yield abundant brilliantly luminescent secretion on the gentlest pressure applied to the pelvic region. The glands of larger specimens of *C. cœlorhynchus* yield no luminescent secretion, though the gland, newly cut open, may show a very feeble luminescence. In a darkened cabin, I held in one hand a small (20 cm.) specimen of *C. cœlorhynchus*, in the other a 25-cm. specimen of *M. lævis*, and squeezed their ventral glands simultaneously. *M. lævis* instantly yielded a large drop of brilliantly luminescent secretion: *C. cœlorhynchus*, after more vigorous treatment, showed a thin smear, barely visible to the dark-adapted eye.

I have no doubt that the gland on *C. cœlorhynchus* is fully functional in the very small fish, and is probably used in the same way as that of *M. lævis*. But I also have no doubt that, in older specimens, the gland becomes more or less vestigial.

The gland of *M. lævis* is more primitive, or less specialised, than that of *C. cœlorhynchus*, especially in the connection of the gland, in the latter, with the pelvic girdle. If the gland is indeed derived from "a glandular area about the anus, which has become invaginated to form a pouch, and secondarily folded to give an enormous internal area of secretion," the ejecting mechanism in *M. lævis*, consisting of unstriped muscle such as could have been carried in from the rectum, is decidedly more primitive than the association with the pelvic girdle, which we find in *C. cœlorhynchus*, and which must be regarded as a secondary development.

In the adult *Trachyrhynchus trachyrhynchus* Risso, there is no sign of a ventral gland, even in sections of the rectum and its surrounding tissues, and Johnsen (**7**) makes no mention of its presence in young bathypelagic specimens. Had a ventral gland been present, Johnsen could not have failed to mention or investigate it.

F. The Ventral Gland in the Anacanthini.

In my paper on *M. lævis*, I suggested that the gland in *C. cœlorhynchus* was degenerate, and that this might be associated with a stouter armature of scales in the latter species, "which has rendered unnecessary the protective device of a luminous organ." I also suggested that "the organ may be widely spread among Macruridæ, and further work on other species might reveal its presence." The suggestion was ill-informed. The ventral gland is widely spread among the Macruridæ. Gilbert and Hubbs (**8** and **10**) describe its presence in many genera, such as Cœlorhynchus, Abyssicola, Hymenocephalus, Malacocephalus, Ventrifossa, etc. They used it in their classification of these fishes, and suggested that it

might be a phosphorescent organ. Still earlier, Radcliffe (**9**) had suggested that the ventral gland found in *Macrurus lucifer* (= *Ventrifossa lucifer*, Smith and Radcliffe) was phosphorescent.

The macroscopic structure of the ventral gland in the Macruridæ, as described by Gilbert and Hubbs (**8** and **10**), shows great variation. The gland may be sing'e (as I have found it in *M. lævis* and *C. cœlorhynchus*), or double, a second gland being present at the anus. Gilbert and Hubbs (**10**) thus describe the gland in *Cœlorhynchus argentatus*. " The posterior dilatation is bilobed, being divided by the anus. The thick anterior dilatation is roughly triangular in outline . . . it lies within a cavity, and is supported in a strikingly peculiar manner by a cartilaginous rod in close connection with the pelvic girdle. The posterior arm of this bone is a poorly ossified plate, which, by meeting its fellow at the median line, forms a brace directly between the pelvic bases. From the anteromedian angle of each of these posterior limbs, a cylindrical rod of cartilaginous tissue extends forward to the sides of the anterior dilatation, from which it extends dorsad, meeting its fellow in a wide arch, the apex of which is bound to the well-ossified anterior arms of the public (*sic*) bone, where these meet at the middle line." The structure of the gland and cartilages, in their relation to the pelvic girdle, in *C. argentatus* obviously very closely resemble those of *C. cœlorhynchus*. The posterior gland, divided by the anus, described in the former, and in many other species, is plainly to be homologised with the pouches which arise from the duct, about the rectum, in *M. lævis*, and *C. cœlorhynchus*. Hubbs himself, in a letter to me, admits of no doubt that the gland is homologous throughout the group of Macrurids.

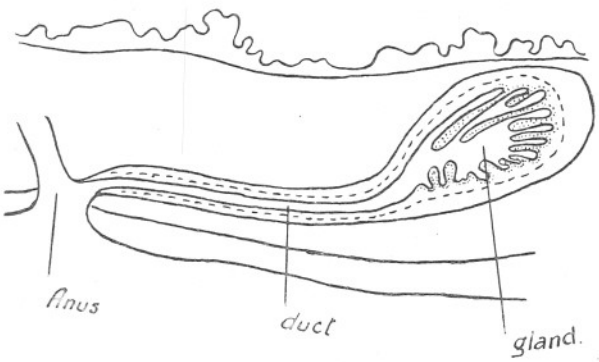
A closely similar gland is present in a genus of the Gadidæ, namely, Physiculus. Franz (**11**) has described briefly the ventral gland in *P. japonicus*. I take the liberty of reproducing his figure below (Text-Fig. 4).

A round, black, scaleless fossa lies in the median line before the anus. " Hierunter eine schöne Drüse im Muskelfleisch eingebettet liegt. Langschnitte . . . zeigten mir ferner, dass der ausfuhrungsgang der Drüse in den After mündet. Die Drüse . . . besteht aus gestrickten, radiär gestellten Drusenschlaüchen, und nicht etwa . . . aus einen gefalteten Drüsenepithel. . . . Das Epithel und überhaupt die Schleimhaut des Ausfuhrungsganges zeigt . . . starke längsfalten." Jordan and Hubbs (**12**) found a similar fossa in three American species of Physiculus, namely, *P. fulvus*, *nematopus*, and *rastelliger*, which makes it probable that a ventral gland is present in these species also.

There can be no doubt that this gland is homologous with that of the Macruridæ : it is present, therefore, in both families of the Anacanthini. As far as I know, it has not been found in any other Gadoids.

Boulenger (**13**) and Regan (**14**) are both of the opinion that the Macruridæ are more primitive than the Gadidæ. I would suggest that the gland arose in the primitive Anacanthini, probably during an invasion of deep water, that it has been retained and elaborated in the Macruridæ, which have persisted in the deeper water, where the gland is presumably of use, but lost in the Gadidæ, with the exception of the genus Physiculus.

Owing to the variation in the structure of the gland among living



TEXT-FIG. 4.—Sagittal section of the ventral gland in *Physiculus japonicus*, after Franz.

Macruridæ, and the fact that it appears to degenerate in some species, it should probably be regarded as essentially a larval or post-larval organ, which may remain functional throughout life in some species. Smitt (**5**) described what is clearly the fossa underlying the ventral gland, in a post-larval Macrurid, but suggested that it might be an adhesive organ.

A comparative study of the structure of the gland in a wide range of Macrurid and Gadoid fishes might throw some light on their mutual relationships.

SUMMARY.

The luminiferous organ of the Macrurid fish *Cœlorhynchus cœlorhynchus* Risso is described in this paper. It consists of a gland, flattened dorso-ventrally, placed in the body-wall, just in front of the pelvic fins. The secretory epithelium is thrown into a series of tubules, projecting downwards from the roof of the gland into a system of collecting spaces : the latter are confluent, posteriorly, with a duct which leads backwards, between the pelvic fins, to the anus. Blind pouches, which run upwards for a short distance beside the rectum, arise from the duct at its external opening at the anus.

The gland itself, which is compactly bound in fibrous connective tissue rich in melanophores, is strongly bound to a pair of cartilages, which rise dorsally to span the anterior end of the gland, are united by a ligament at the middle line, and are connected, lateroventrally, to the posterior processes of the pelvic girdle. It is suggested that contraction of the muscles between the two halves of the pelvic girdle might cause the gland cartilages to squeeze, nutcracker-fashion, the anterior part of the gland, the ligament binding the cartilages together at the middle line acting as a hinge. It is probable that the fish actively expels the luminiferous secretion of the gland by this means.

The gland is apparently functional only in the young fish : it becomes more or less vestigial in larger specimens.

The structure of the gland in *C. cœlorhynchus* is compared with that of the homologous gland in the Macrurid fish *Malacocephalus lævis* Lowe ; the gland of the latter is the more primitive or the less specialised.

Finally, the glands of these fishes are homologised with those in other Macruridæ, and in the Gadoid genus Physiculus. It is suggested that a comparative study of the structure and distribution of these glands might be of help in establishing the relationships of the members of the Anacanthini.

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EXPLANATION OF THE LETTERING USED IN PLATES I–IV.

B. v., Blood vessels. C. s., Collecting space. Cryst., Guanin Crystals. C. t., Connective tissue. D., Duct of gland. Gd. cart., Gland cartilage. G. d., Genital duct. K. d., Kidney duct. L. mus., Longitudinal muscle. Mus., Muscle. Mel., Melanophores. P., Pouches arising from duct of gland. R., Rectum. S. t., Secretory tubules. Trans. Mus., Transverse muscles. The scales accompanying the figures are one millimetre, divided into tenths.

PLATE I.—Sagittal sections through the gland and duct of *C. cœlorhynchus*.

FIG. 1.—In a 15-cm. specimen.

FIG. 2.—In an older specimen.

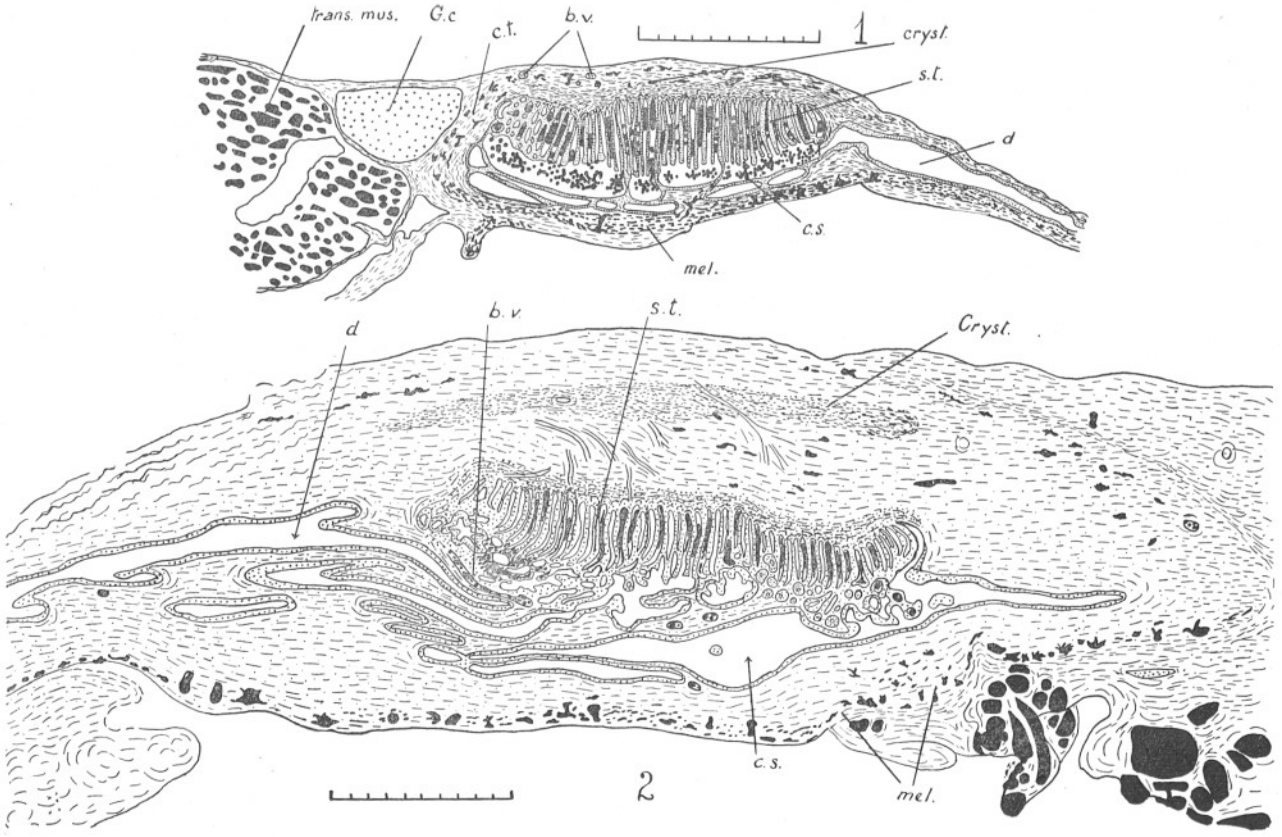


PLATE I.

PLATE II.—Horizontal longitudinal sections through the gland of a 14-cm. specimen of *C. cœlorhynchus*.

FIG. 3.—Through the top of the roof of the gland.

FIG. 4.—Through the tubular portion of the gland.

FIG. 5.—Through the floor of the gland.

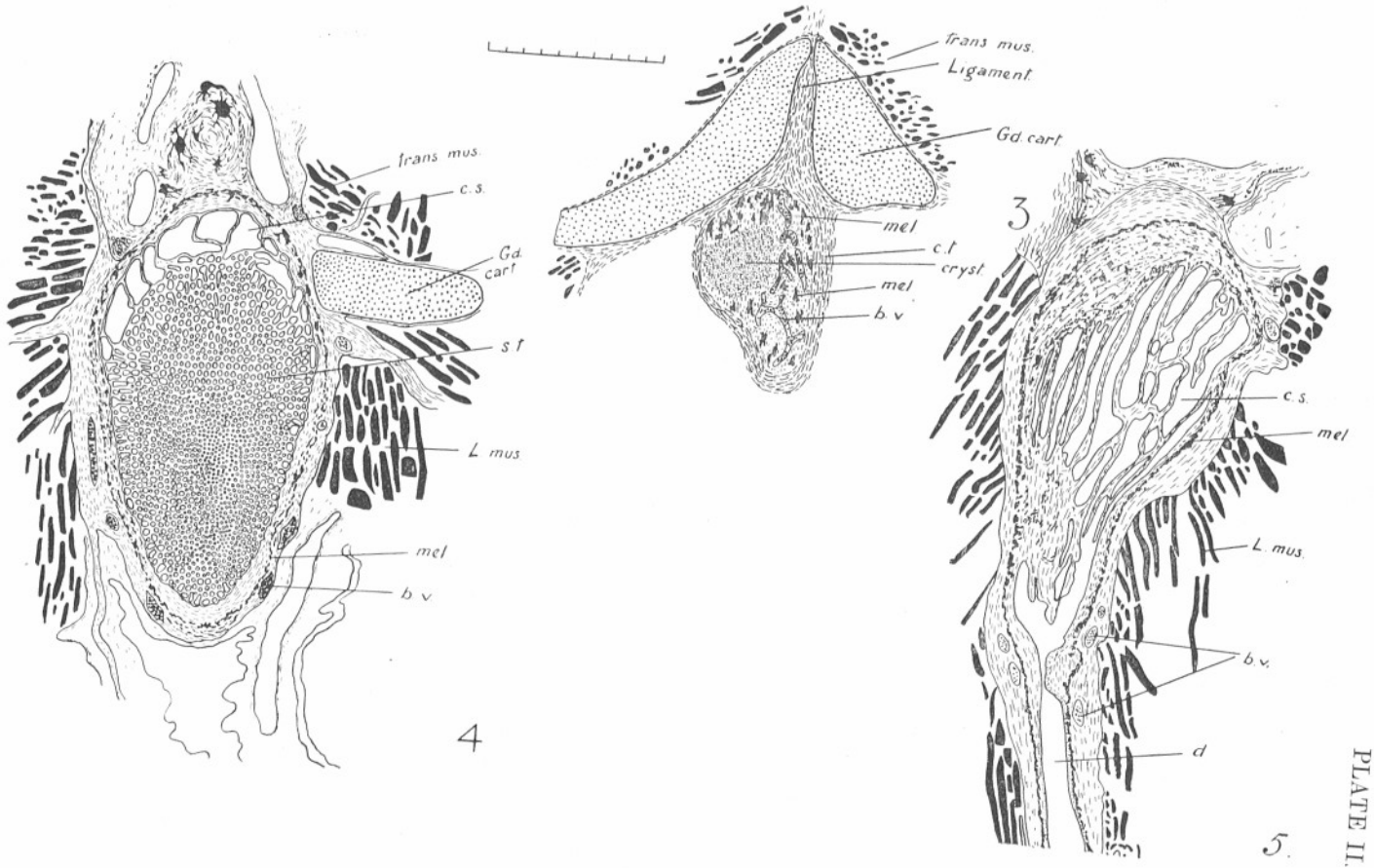

frans mus.
Ligament
Gd cart
mel
c.t
cryst
mel
b.v
3
frans mus.
c.s.
Gd. cart
s.t
L mus
mel
b.v
4
c.s.
mel
L. mus.
b.v.
d
5.

PLATE II.

PLATE III. FIGS. 6 AND 7.—Transverse sections through the gland in two older specimens of *C. cœlorhynchus*.

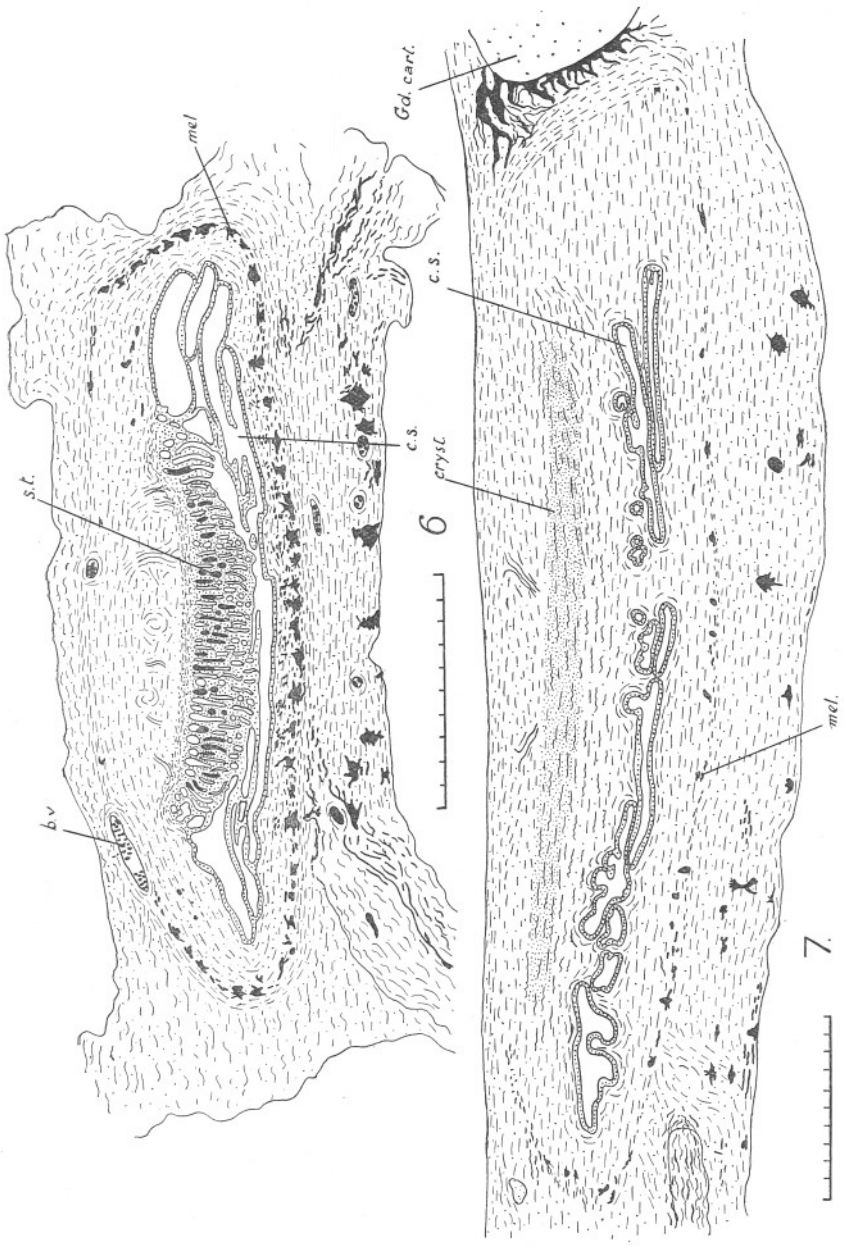
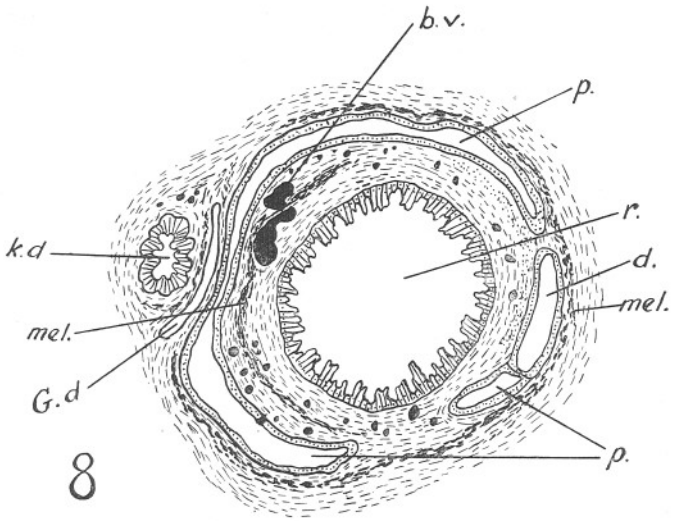

Gd. cart.
mel
c.s.
c.s.
cryst
s.t.
6
b.v
mel.
7.

PLATE IV.—Sections transverse to the rectum in two specimens of *C. cœlorhynchus*.

FIG. 8.—In a 21-cm. specimen.

FIG. 9.—In a 30-cm. specimen.



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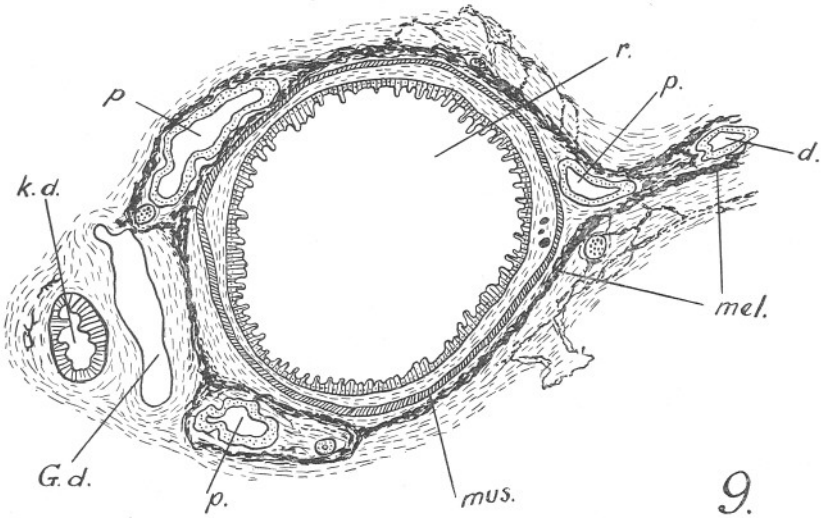

9.

Growth and Maintenance in the Plaice (*P. platessa*, L.) Part II.

By

Ben Dawes, A.R.C.S., D.I.C., F.L.S.

With 11 Figures in the Text.

CONTENTS.

INTRODUCTION AND METHODS.

In a previous paper (Journ. Mar. Biol. Assoc., Vol. XVII, No. 1, Sept., 1930) I described in detail a series of experiments on Growth and Maintenance in the Plaice which were carried out during 1928 and 1929 at Cawsand, near Plymouth, and at Lympstone, near Exmouth. The purpose of the present paper is to present and discuss data collected at the above places during 1930 in continuing the experiments. The conditions under which the last experiments were carried out were identical with those of 1929, i.e. refined with reference to those of 1928. Several additions were made, however, to the series of 1929. Two fish of each sex were supplied with maximum rations while living under the conditions maintained during 1928 and were segregated in a box, which had the original $\frac{1}{2}''$ mesh wire-netting windows but which was divided up into compartments. This experiment was arranged in order that we might ascertain the possibility

of food leakage due to tidal action during the course of the earliest experiments, but it also enables us to compare the results obtained under slightly different conditions of water circulation, which is important in view of the fact that the windows of the modified boxes were of necessity minimal in area.

There is yet another departure from the experiments of 1929. The results of the experiments of 1928 tended to show, if in a rather unsatisfactory manner, that fish taking quantities of food intermediate between maintenance and maximum rations made more efficient use of food for purposes of growth than did maximum-fed fish. Unfortunately, the refinement of the preliminary experiments during 1929 entailed an additional amount of routine work and made it impossible to check these promising results. The question of increased efficiency with intermediate-feeding is a very important one, and it was deemed advisable during 1930 to obtain evidence which would either support or refute the conclusion so tentatively put forward and to impart some finality to our views. Accordingly, two fish of each sex were kept segregated under the refined conditions and in parallel with maximum-fed fish. These fish were supplied with intermediate rations, roughly twice the value of maintenance rations. The number of fish is admittedly small, but it must be emphasised that the inclusion of these four fishes in the experiment distended the routine work to such an extent that it was quite impossible to include more.

Apart from these details, the experiments of 1930 were identical with those of 1929. Feeding operations were performed daily, the food being *Mytilus edulis* as before, and especial care was taken to avoid the inclusion of food fragments likely to be washed out of the boxes by the tides. Each day, before food rations were presented to the fish, the surplus food from the previous meal was meticulously removed and "weighed back." Weighing and measuring operations were performed fortnightly as before, and the time interval between the last meal of the fortnight and the weighing was maintained as constant as was practicable. Temperature records were kept at Cawsand and Lympstone alike, graphs of weekly maxima and minima being prepared finally from them.

Before passing on to a description of results, it must be mentioned that during the first two months the routine work was carried out by Miss Thursby Pelham of the Ministry of Agriculture and Fisheries Laboratory, Lowestoft, and her assistant, under my supervision and direction. Again, during early September I was on leave and in mid-September resigned my position in order to take up an appointment in London. The experiments were therefore directly carried out by me only during the latter part of June and during July and August. When I left the work, Messrs. G. M. Spooner and J. E. Smith of the Marine Biological Association Laboratory, Plymouth, jointly took charge of the experiments, the data

of which were sent to me in London. Before proceeding I wish to record my thanks to the above-mentioned people for their contributions to the work. Mr. H. Lees, Tank Superintendent of the Ministry of Agriculture and Fisheries Mussel Tanks, Lympstone, retained his charge of the Lympstone experiments under the direction of Dr. E. S. Russell and Mr. T. Edser, who kindly sent me the data obtained. Thanks are due to Mr. Lees for his share of the work and especially for the observations which were continued throughout the winter of 1929.

I. RESULTS OF THE CAWSAND EXPERIMENTS OF 1930.

1. Minimum Requirements and Maintenance.

Data concerning the experiments with male fish supplied with minimum rations are shown in Tables 1–6, these fish being referred to as C1–C6. It will be seen from these tables that the initial sizes of the C fish form an ascending series from C1 (13·1 cm. ; 21·5 gm.) to C6 (23·0 cm. ; 115·0 gm.), and it will be realised that the size range thus covered by the series is roughly the size range of growth of maximum-fed, fully-growing plaice during the third season of growth. The aim of these experiments is to obtain data which can be applied to an estimation of the gradually increasing maintenance requirements of plaice which are passing through this season of unrestricted growth. The uniformity displayed in the results of earlier experiments of the same kind with numbers of fish of the same size, justifies this attempt to measure the variation in maintenance requirements with single fish of increasing size, particularly as earlier work had not provided really satisfactory results and as there was no possibility of increasing the number of fish included in the experiments.

The smallest fish, C1 (initial length 13·1 cm. ; initial weight 21·5 gm.),* was maintained fairly constant in weight over a period of 144 days (final weight, 20·8 gm.), slight losses during the early part of the experiment being due to a refusal to take food. The total quantity of food taken during 144 days was 66·9 gm., or roughly 3 times the mid-body-weight. During the various fortnightly periods, less than 0·40 gm. of food per day resulted in slight loss of weight ; more than 0·50 gm. per day in increase in weight except in one instance (Sept. 19th, Table 1). The maintenance requirements of a 21 gm. male plaice thus appear to lie between 0·4 gm. and 0·5 gm. of food per day, i.e. between 0·019 and 0·024 of the mid-body weight for the periods considered (=the maintenance ratio). For 144 days, an average of 0·46 gm. of food per day was required, yielding a maintenance ratio of 0·022.

* In the descriptions to follow, the abbreviations init. lth. (for initial length) and init. wt. (for initial weight) will be used.

C2 (init. lth. 15·3 cm.; init. wt. 31·5 gm.) (Table 2) showed slight periodic fluctuations in weight, but after 176 days had increased its initial weight by only 4·4 gm. Slight losses in weight occurred during three periods when the average daily ration was less than 0·47 gm., slight gains during eight periods when it was more than 0·45 gm. The maintenance ration would therefore appear to be 0·45–0·47 gm. per day, the corresponding ratio 0·013–0·014. Over 176 days the average daily ration was 0·49 gm., the maintenance ratio 0·015.

C3 (init. lth. 16·9 cm.; init. wt. 45·0 gm.) (Table 3) was kept to within 2 gm. of its initial weight over a period of 162 days, despite periodic fluctuations. This fish can be taken to illustrate the difficulty entailed in an attempt to maintain the weight of any plaice constant for a succession of fortnightly periods, although it would be easy to find other suitable examples. For the period ending June 23rd the average daily ration was 0·57 gm. and the body-weight was maintained constant. Consequently, a similar average daily ration was supplied during the next following period to July 7th, which resulted, however, in the relatively great weight increase of 1·9 gm. During the next period to July 21st the ration was lowered by 0·03 gm. per day and the result was good, the weight increase being only 0·1 gm. A further slight reduction of the ration (by 0·03 gm.) during the period ending August 6th resulted in an enormous loss of 2·5 gm. in body-weight, and an increased ration (by 0·02 gm.) during the period ending August 21st also resulted in loss of weight (1·2 gm.). Thereafter, much greater daily rations were required to maintain the weight of the fish constant. This succession of incidents is important and has been dealt with at such length because it shows clearly how maintenance requirements seem to fluctuate, a difficulty which must inevitably be encountered in work of this kind. The difficulty is referred to briefly in my previous paper (p. 119).

During the first 100 days of the experiment, C3 lost weight during fortnightly periods whenever less than 0·53 gm. of food was taken on the average per day, and gained weight whenever more than 0·54 gm. was taken, so that these quantities mark the limits of the maintenance requirements, the maintenance ratio being 0·011–0·012. By comparison with the results for other fish, these values are low and this observation is perhaps not altogether disconnected with the fact that beyond this period and to the end of the experiment, C3 required greatly enlarged daily rations for maintenance. It is suggested that during the early part of the experiment weight was maintained constant on unusually small rations by atypic means (e.g. excessive water imbibition), after which some adjustment was effected causing much greater rations to be necessary. For the whole period of 162 days, the average daily ration was 0·64 gm., providing a maintenance ratio of 0·015.

The results of the experiments with the males C4, C5, and C6 are shown in Tables 4, 5, and 6. Taking C4 (init. lth. 18·9 cm. ; init. wt. 59·0 gm.) first, and noting for the various fortnightly periods loss or gain in weight following upon varying average daily rations, it is found that the maintenance requirements appear to be 0·85–0·86 gm. of food per day (maintenance ratio=0·014). During the whole course of the experiment (178 days), an average daily ration of 0·89 gm. was taken and at the end of this period the initial weight had been increased by 3·5 gm., so that the maintenance ratio of 0·015, which is indicated, is slightly high. C5 (init. lth. 21·2 cm. ; init. wt. 86·7 gm.) appeared to require daily rations of from 0·87 gm. to 0·99 gm. for maintenance from one period to another (Table 5), this giving a maintenance ratio of 0·010–0·011. For the whole period of 164 days an average daily ration of 0·95 gm. was taken and the total loss in weight was 1·3 gm., so that for the whole experiment the maintenance ratio was 0·011, which closely follows the figures indicated by study of the fortnightly periods. The largest fish, C6 (init. lth. 23·0 cm. ; init. wt. 115·0 gm.), seemed to require 1·27–1·40 gm. of food per day for maintenance (Table 6), which suggests a maintenance ratio of 0·011–0·012. During 147 days it took an average daily ration of 1·42 gm. and lost a total of 3·9 gm. in weight, so that for this period a maintenance ratio of 0·013 is indicated.

The results of these maintenance experiments with male plaice are summarised for the whole course of the experiments in Table 7. It is seen that the average daily ration required for purposes of maintenance by males of from 13·1 cm. to 23·0 cm. and from 21·5 gm. to 115·0 gm. gradually increased from 0·46 to 1·42 gm., neglecting slight losses in body-weight. The corresponding maintenance ratios gradually decreased from 0·022 to 0·012. The difference between these quantities and values represents the difference between the maintenance requirements of different male plaice of various sizes, but by analogy it can be interpreted as representing the difference between the maintenance requirements of a single male plaice at various times during its third season of unrestricted growth, since the limiting sizes are approximately those which mark the two extremes of this season, having been chosen to serve this purpose. In Figure 1 the decrease in value of the maintenance ratio with increase in size of fish, and therefore by analogy also with increasing age, is shown graphically.

The female plaice used in maintenance experiments, like the corresponding males, were arranged so as to form a series having a total size range comparable with that passed through by a freely-growing female plaice during its third season. The results of these experiments are shown in Tables 8–13, the fish being referred to as A5, A6 (a and b), A2, A4, A3, and A1, and being taken in this order, which is that of increasing size.

In the descriptions to follow the maintenance requirements suggested by the study of fortnightly data will be found, as in the case of males, by noting the periods when loss or gain in weight occurred on average daily rations below or above a certain value. This will render unnecessary much of what would otherwise prove to be tedious and almost endless repetition.

The smallest female A5 (init. lth. 12·2 cm.; init. wt. 17·3 gm) appeared able to maintain itself on average daily rations of 0·39–0·47 gm. for six consecutive fortnightly periods (July 7th–Oct. 6th; Table 8), the

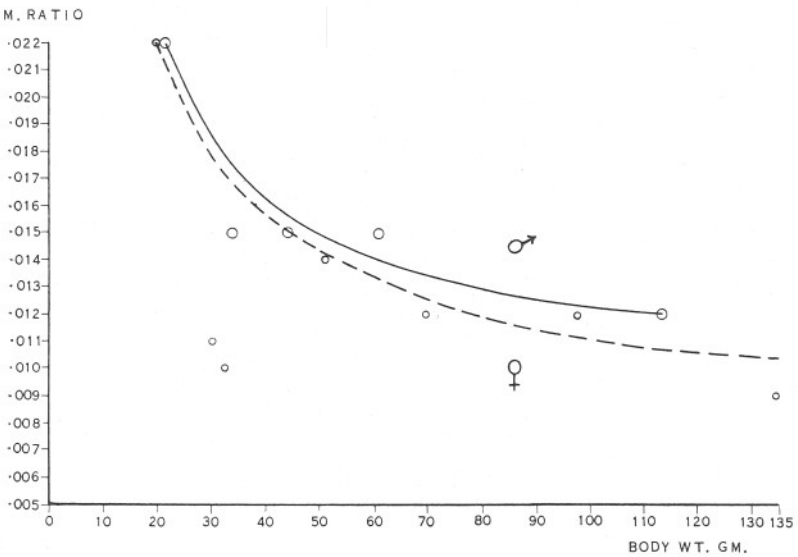

FIG. 1.—Graphs showing, for male and female plaice between 2 and 3 years old, the relationship between the maintenance ratio and the body-weight. Based upon the results of the Cawsand experiments, 1930.

corresponding maintenance ratio ranging from 0·018 to 0·025. During 143 days, an average daily ration of 0·43 gm. enabled the fish to maintain itself and to increase its initial weight by 4·7 gm., so that the maintenance ratio of 0·022 which is thus indicated is slightly high. Both the fish referred to as A6 steadily declined to take food in sufficient quantities to satisfy their maintenance requirements, with the result that they consistently and steadily lost weight. The data for these fish are shown in Table 9 but we must decline to make use of them since they would scarcely assist our purpose. A glance at the two points widely separated from the curve on the left of Figure 1, which represent the maintenance ratios for these fish, will convince one that these data are best disregarded.

The data for A2 (init. lth. 17·3 cm.; init. wt. 49·0 gm.), which are shown in Table 10, indicate that from one fortnightly period to another between July 7th and September 5th, this fish was able to maintain itself on daily rations of 0·64 gm.–0·67 gm., the corresponding range in the maintenance ratio being 0·012–0·013. During 148 days an average daily ration of 0·69 gm. allowed of an increase in weight of 4·0 gm., so that the maintenance ratio of 0·014 thus indicated is slightly high. A4 (init. lth. 19·8 cm.; init wt. 71·0 gm.) required a daily ration of from 0·83 gm. to 0·94 gm. for purposes of maintenance (Table 11), showing a maintenance ratio of 0·012–0·014. Over a period of 178 days there was a slight loss of weight (2·7 gm.) after an average daily ration of 0·87 gm. had been taken, this figure indicating a maintenance ratio of 0·012.

A3 and A1 were both initially over 100 gm. in weight. The daily ration required for maintenance by A3 (init. lth. 22·0 cm.; init. wt. 101·5 gm.) was 1·21–1·29 gm. from period to period (Table 12), the corresponding ratio being 0·012–0·013. During 147 days, an average daily ration of 1·21 gm. resulted in 6·3 gm. loss in weight, so that the maintenance ratio is slightly greater than 0·012. A1 (init. lth. 24·5 cm.; init. wt. 132·0 gm.) required 1·23 gm.–1·36 gm. of food per day for purposes of maintenance from one period to another, the maintenance ratio being 0·009–0·010. During 178 days an average daily ration of 1·24 gm. allowed this fish to increase its initial weight by 4·9 gm., which indicates that the maintenance ratio was slightly less than 0·009.

Summarised data concerning the females used in these maintenance experiments are shown in Table 14, which is set out parallel with Table 7 for males. It is seen that the average daily ration required over long periods for purposes of maintenance by female plaice ranging in length from 12·2 cm. to 24·5 cm. and in weight from 17·3 gm. to 132·0 gm., increases from 0·43 gm. to 1·24 gm., the corresponding maintenance ratio diminishing from 0·022 to 0·009. This then is approximately the order of the changes which would occur in the maintenance requirements of a female plaice during its third season of growth since, as in the case of males, the sizes of these maintained fish were arranged in a series, the size limits of which are also the limits for this season of growth.

Thus for male and female plaice alike, the maintenance ratio at the end of the third season of growth is only approximately one-half its value at the commencement of the season. And this is strikingly shown in another way. The following table shows the multiple of the mid-body-weight taken by male and female plaice during the whole period of experiment indicated in days.

♂Fish No.	No. of Days.	Multiple of Body-wt. of Food (gm.).	♀Fish No.	No. of Days.	Multiple of Body-wt. of Food (gm.).
C1	144	3·2	A5	143	3·2
C2	176	2·5	A6	—	—
C3	162	2·4	A2	148	2·0
C4	178	2·6	A4	178	2·2
C5	164	1·8	A3	147	1·8
C6	147	1·8	A1	178	1·6

The smallest fish is shown at the top of the table, the largest at the bottom, and it is clearly indicated that for the smallest plaice the ratio of food-weight to body-weight is double that for the largest plaice. This is in accordance with the suggestion tentatively put forward in my previous paper, although the method then employed of combining Cawsand and Lympstone data was not altogether legitimate.

2. Maximum Requirements and Growth.

The growth experiments were marked out into two sets, the first consisting of six fish of each sex housed in the modified boxes with fine mesh windows, the second of two fish of each sex confined in boxes with $\frac{1}{2}''$ mesh windows similar to those used in the preliminary experiments. All fish were segregated, however, and were tended separately. The fish kept under the refined conditions will be referred to as D (♂) and B (♀) fish respectively, those kept in boxes with $\frac{1}{2}''$ mesh windows as M (♂ & ♀) fish.

The results of the experiments with D and B fish are summarised in Table 15, where it is seen that considerable variation in rate of growth characterised both groups. Amongst males, the greatest total increases in length and weight were shown by D1 (4·2 cm. ; 41·3 gm.), the least being shown by D6. The rate of growth was generally very slow as compared with that shown during previous years, D1 and D2 succeeding in doubling their initial weights over long periods (162–178 days), other males failing to achieve this result during periods up to 116 days in extent. The relatively slow rate of growth is best shown by comparison of these results with that for D3 during 1929 which, during 175 days, multiplied its initial weight by 6·8. This feature of rate of growth was shown also by females during 1930, none of which achieved much more than a mere doubling of the initial weight, B6 failing to do this, even over a period of 131 days. For the whole range of the experiments the average daily ration varied, among males from 1·6 to 3·0 gm., among females from 1·8 to 3·5 gm., so that appetite was rather smaller than during the previous year, when for corresponding periods it ranged among males from 2·2 to

3·3 gm. and among females from 2·3–4·1 gm., neglecting obviously unhappy fish. Efficiency, i.e. the relation between food taken and growth ensuing, also varied in different fish, but to a slighter degree than during the previous year and it was generally much lower, i.e. the indices were greater. Among males 9·1–11·9 gm. of food was required to produce 1·0 gm. increase in body-weight, among females 8·5–12·9 gm. From the above it will be seen that at Cawsand the growth performances of 1930 were distinctly inferior to those of 1929.

Data concerning the experiment with D1 are shown in Table 16, where it is seen that the increments of length and weight added from period to period were most irregular, especially the latter, which varied from −0·3 gm. to 10·2 gm. per fortnightly period. The average quantity of food taken daily varied similarly during different periods, but only slightly, from 2·15 gm. to 4·08 gm. Variation also occurred in respect to efficiency, as measured by the quantity of food required to produce 1·0 gm. of fish irrespective of time, and was very strongly marked, as will be seen by inspection of col. 6 of the table. The maximum efficiency shown during the whole course of the experiments is represented by the index 4·2 for the period ending June 9th.

Similar results were shown by the other male plaice, D2–D6 (Tables 17–21). In the case of D2, growth in weight per period varied from −0·9 gm. to 7·0 gm., the average daily ration taken from 1·00 gm. to 2·64 gm., and efficiency between tremendously wide limits (Table 17). Efficiency was greatest (index 4·3) during the period of maximum growth (June 9th ; 7·0 gm.). D3 showed maximum appetite (3·20 gm. per day), maximum growth (10·6 gm.), and maximum efficiency (index 4·2) for the whole experiment during the period ending July 21st when the ratio W/L^3 attained its maximum value (0·011), (Table 18). D4 shows the maximum increase in weight for any period (6·2 gm.) when the appetite was a maximum (2·2 gm. per day) during the period ending August 6th, when efficiency was high (index 5·7) but not a maximum (period ending June 9th ; index 4·4). At the same time W/L^3 reached its maximum value of 0·010 (Table 19). D5 and D6 did not show such high degrees of efficiency at any time, the maxima for these fishes being represented by the indices 6·5 and 7·1 (Tables 20 and 21).

The results of the experiments with males thus lend support to the conclusion previously put forward that there is no simple relationship between the quantity of food taken and the degree of growth ensuing. They also show that such relatively high efficiency as is indicated by the indices 4·2–4·4, which neglect maintenance allowances, may be attained at certain indeterminate times during the growth season. In Figure 2 the results of these experiments are shown graphically as regards growth increments of weight. It will be seen that the slopes of the curves shown

are much less steep than that of the typical sigmoid curve shown for D3 (1929) in my previous paper (Fig. 5, p. 123).

Data concerning the female B1 are shown in Table 22. Growth in length per period varied from —0·1 cm. to 0·9 cm., growth in weight from —5·9 gm. to 8·6 gm. Growth per period was a maximum during the period ending July 21st, when efficiency was also a maximum (index 4·7) and when the ratio W/L^3 attained its maximum value of 0·011. When

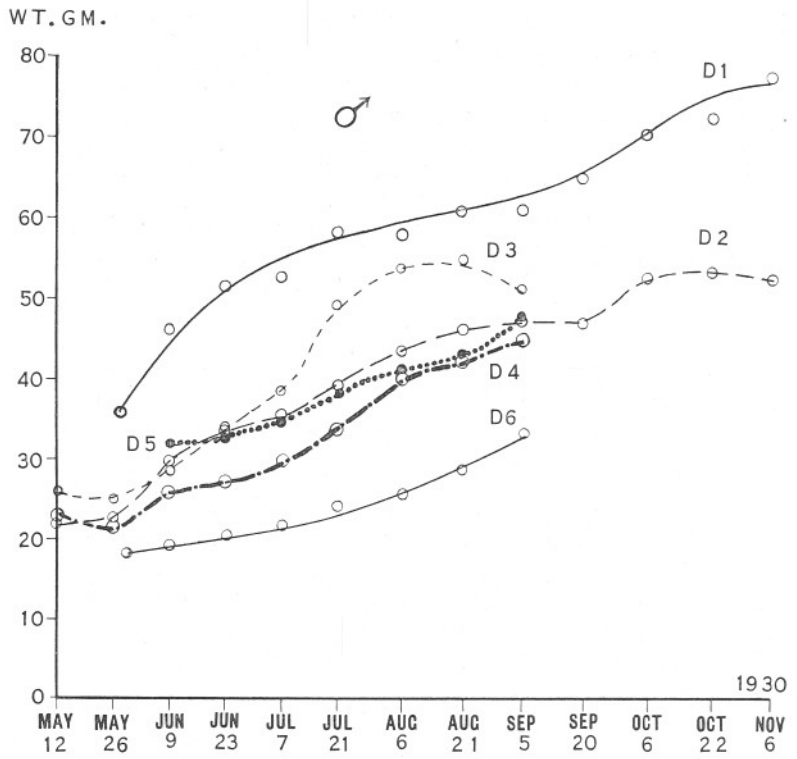

FIG. 2.—Growth curves of weight for the male plaice D1–D6 (Cawsand, 1930).

appetite was greatest (3·48 gm. per day, Aug. 21st), growth and efficiency were both high in degree (7·5 gm. per period; index 7·0). This fish showed consistently high efficiency from June 17th to August 21st, the index 4·7 occurring during two periods, yet as in the case of the males, considerable variation was shown from time to time.

The remaining females showed similar variations in rate of growth, in efficiency and in appetite from period to period, as will readily be seen if Tables 23–27 be scrutinised. B2 took daily rations ranging from 1·32 gm. to 3·56 gm. (neglecting the first week of mere maintenance), increased

in weight by quantities varying from 0·2 gm. to 10·3 gm. per period and showed efficiency indices as widely separated as 4·8 and 30·8 from June to September (Table 23). It is interesting to note that growth, appetite, and efficiency were all maxima during the period ending July 21st. B3 showed maximum growth and efficiency (5·9 gm. ; index 5·4) during the period ending June 23rd (Table 24). B5 was the most promising fish in the experiments until September 5th when it was lost. From Table 25 it will be seen that the periodic increases in length and weight were consistently great, maxima at 1·0 cm. and 11·0 gm. respectively, and that for the whole experiment the efficiency indices lay between the limits 5·5 and 9·2. B4 also showed high efficiency, the index remaining between such narrow limits as 5·1–5·7 for three consecutive periods (Table 26). B6 was the least efficient of the Cawsand fish, the maximum being represented by the index 6·0 (Table 27).

The results of the experiments with females thus confirm completely the conclusions mentioned above regarding the variation in rate of growth, in appetite and in efficiency from period to period during the growth season. The results show also that the maximum values of these three sets of growth characteristics may or may not coincide in time. The greatest efficiencies shown by the females read as follows : 4·7 (B1), 4·8 (B2), 5·1 (B4), 5·4 (B3), 5·5 (B5), and 6·0 (B6), so that the females are slightly inferior to the males in this respect, the efficiencies of these latter reading 4·2 (D1 and D3), 4·3 (D2), 4·4 (D4), 6·5 (D5), and 7·1 (D6). That such efficiency is not sustained will readily be seen by examination of the tables mentioned above.

The growth curves of weight for the females (Fig. 3) are seen to compare fairly closely with those shown in Fig. 2 for the males. The slopes of the curves are much less steep than those of the curves for B1 and B4 (1929) as shown in Fig. 7 of my previous paper (p. 125).

Turning now to the results of the experiments with M fish (maximum-fed fish housed in boxes with $\frac{1}{2}''$ mesh windows), we see in Table 28, where these results are summarised, that growth has proceeded at much the same rate as in the case of the D and B fishes, excepting M1, which surpassed the rest in performance and succeeded in tripling its initial weight, M2, M3, and M4 failing to achieve this result. The quantities of food taken by this fish greatly exceeded those taken by the D and B fish, but efficiency was not as high. These values, however, are affected by certain incidents to be mentioned below, where it is shown that these results do not have the same degree of accuracy that the other results have.

During the preliminary experiments of 1928, fish supplied with intermediate rations appeared to show a greater efficiency in utilising food for purposes of growth than fully-feeding fish. But intermediate-fed fish invariably take the whole of the ration supplied to them whereas in the

case of maximum-fed fish there is a distinct possibility of food remaining over from a meal. If during 1928, small quantities of food remained in the boxes containing the latter fish and were washed out of the boxes by ebbing or running tides, then the observed efficiency of the maximum-fed fish would be lower than the true efficiency. By comparison, the efficiencies of intermediate-fed fish would appear higher. During the earliest experiments there was no sign of appreciable quantities of food

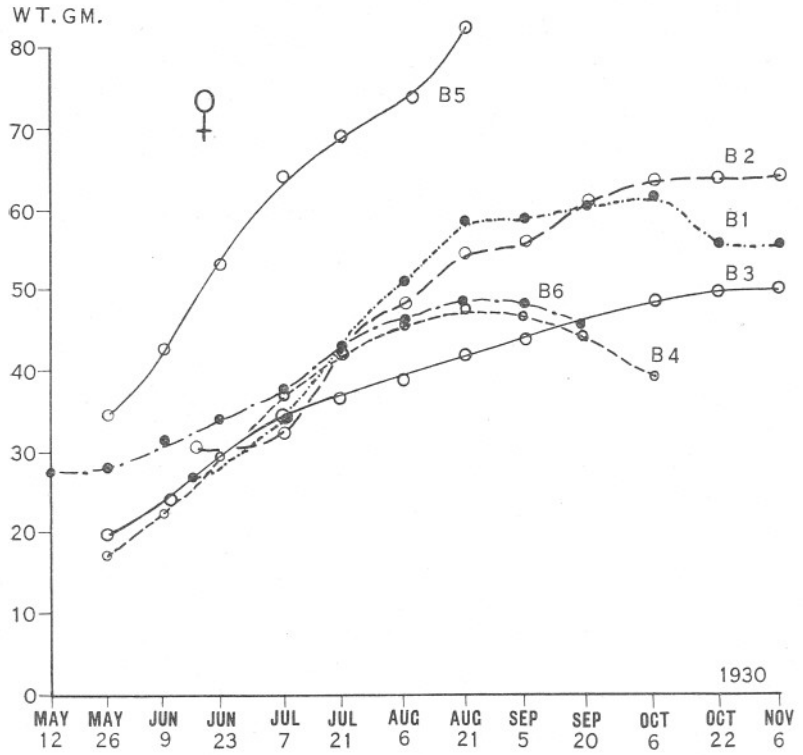

FIG. 3.—Growth curves of weight for the female plaice B1-B6 (Cawsand, 1930).

left over from meals. That fact in itself is strange, since later experiments have shown conclusively that in fish as in other animals, appetite is by no means constant. Thousands of observations made since 1928 have proved this point. Hence it was considered essential to apply a series of tests in order to ascertain the possibility of food having been swept out of the boxes during the earliest experiments. The matter concerns not only food loss but also efficiency of maximum-fed fish, and more importantly of intermediate-fed fish.

To test this possibility of food leakage, Miss Thursby Pelham was asked

to place into the boxes containing M fish quantities of food greatly in excess of the normal ration for such fish and to weigh back the quantities remaining on the next day. This was done during the period ending July 7th and by myself during that ending July 21st. More than this, the wire-netting windows were alternately cleared of epifauna and epiflora (as they were regularly during 1928) and allowed to foul (which may happen in one to a few days).

That the data from these tests were conclusive is seen in the single case of M1. During the last seven days of the period ending June 23rd, this fish was taking a ration of less than 6·0 gm. per day when the box windows were slightly fouled. During the period ending July 7th, it was supplied with 15·0 gm. of food on each of eight days, when the windows were cleared, and no food was found to remain. In some of the tests when this quantity of food was presented, varying quantities were left over, but the essential point is that on many days, often consecutively, no food remained although much more than a normal ration had been presented and despite the fact that sea conditions were calm. In the tests I applied myself this was similarly the case. Consequently, henceforth I used my own judgment as to the constitution of maximum rations and for the rest of the experiment provided what was considered to be an adequate but not overadequate ration, thus ensuring that loss should be minimal if and when it did occur. This applies only to the M fish of course.

In view of the above-mentioned facts it appears reasonably certain that during 1928 there was some loss of food, yet it must be emphasised that the quantities supplied during this year were not unduly large. Moreover, the fish were active and showed a rapid growth-rate. They took food avidly and it is likely that the losses were small. But loss undoubtedly must have occurred. Hence the suggestion of increased efficiency on the part of intermediate-fed fish is open to doubt, or at least objection. This question, however, has been set quite independently during 1930 and data of greater reliability have been forthcoming. These will be presented when the results of the experiments with M fish have been described.

Data concerning the M males are shown in Tables 29 and 30 and growth-curves of weight are presented in Figure 4. M1 was the most rapidly growing fish in the experiments, but, like other fish, it showed great variation in rate from one fortnightly period to another. Periods of rapid growth-rate, July 7th, 10·3 gm.; August 21st, 11·0 gm.; October 6th, 12·6 gm., and November 6th, 15·7 gm., alternated with periods of slow rate, June 23rd, 0·9 gm.; July 21st, 4·0 gm., and October 23rd, −0·2 gm., growth in length paralleling growth in weight (Table 29). Food rations were much more regular than weight increases, so that efficiency must have varied widely from time to time. Similar general results hold good for the male

M2, which, however, showed increasing degrees of growth, appetite and efficiency as the experiment proceeded (Table 30).

The results for the females M3 and M4 are very similar to those for the

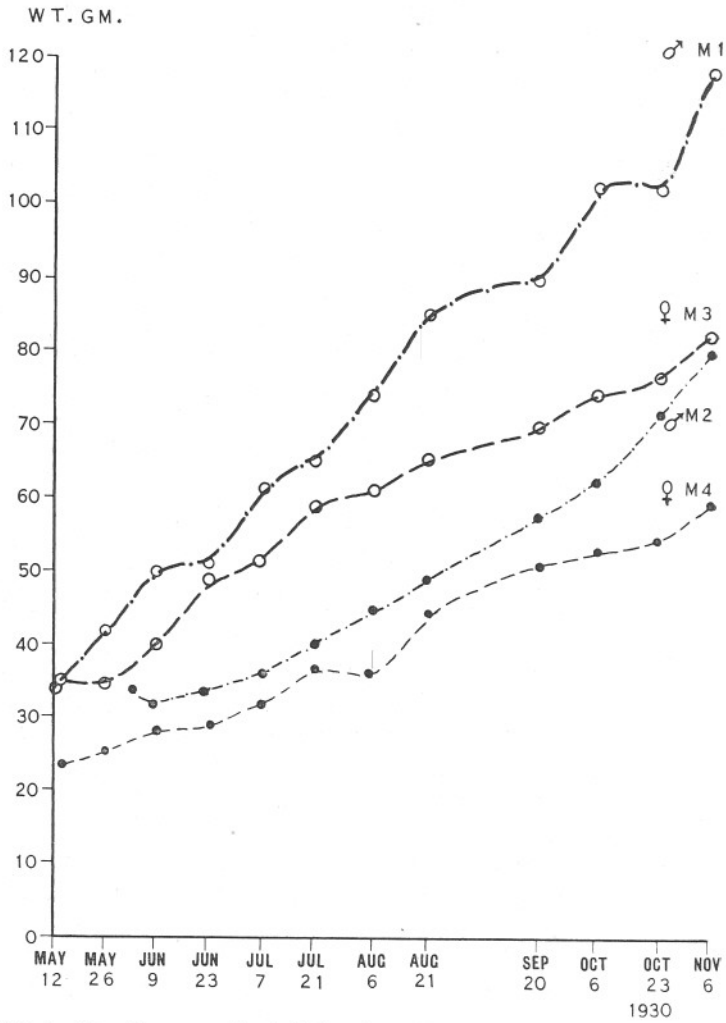

FIG. 4.—Growth curves of weight for the male plaice M1 and M2 and for the female plaice M3 and M4 (Cawsand, 1930).

males. Considerable differences are shown in the degree of growth, appetite, and efficiency occurring during different periods. These results are shown in detail in Tables 31 and 32.

It is evident from the foregoing description that the M fish do not display a rate of growth markedly different from that of the D and B fish, so

that we are able to assert that the conditions of life in the boxes containing the former fish are not markedly superior to those containing the latter, which are the modified boxes with reduced windows of minimum-sized mesh. In maximum-fed fish generally, the growth-rate during 1930 was slower than during 1929, no matter whether we consider the experiments with D and B fish, or those with M fish of the latter year. This was doubtless due to factors other than those arising out of the methods of experimenting and the type of accommodation afforded the fish.

3. Growth and Intermediate Food Supplies.

The results of the experiments with M fish indicate the necessity for looking beyond the experiments of 1928 for a satisfactory answer to the question as to whether intermediate-fed fish utilise food more efficiently than do maximum-fed fish. Fortunately, this question was investigated as a separate concern during 1930. Two fish of each sex were kept segregated in one of the modified boxes and were supplied with rations intermediate in quantity between maintenance and maximum rations, and roughly twice the value of the former. Apart from the size of rations, these fishes were treated in exactly the same manner as maximum-fed fish and lived under similar conditions, so that it is perfectly legitimate to compare the rate of growth and degree of efficiency with the corresponding characteristics in the case of D and B fish. In the description which is to follow, these fish will be referred to as I fish, I1 and I2 being males, I3 and I4 females.

The summarised results of these experiments are shown in Table 33, where it is seen that for periods of 141–178 days, an average daily ration of not more than 1·5 gm. was provided. In the cases of the D and B fish as much as 3·5 gm. per day was taken. It is seen also that for the whole range of the experiments the I fish showed an unmistakably higher degree of efficiency than was shown by the D and B fish. No fish of the latter categories approached an efficiency such as is indicated by the indices 6·8, 6·3, and 5·9 for I1, I3, and I4 respectively. I2 showed relatively high efficiency (index 10·5), which was surpassed, however, by that of D4, B3, and B5 (indices 9·1, 9·7, and 8·5 respectively).

The detailed results of the experiments are presented in Tables 34–37. In the first of these, it is seen that I1 showed consistently high efficiency from June 13th to October 6th, the greatest index during this period of 98 days being 8·6, while during each of four periods the index was less than 5·0. By way of contrast it might be pointed out that during the whole series of experiments with six D fish, the index of efficiency was smaller than 5·0 during a total of only four periods. I1 also showed a rapid growth-rate, and almost doubled its initial weight of 33·7 gm. over a period of 146 days. I2, the remaining male, was not a particularly

efficiently growing fish, but it showed an efficiency index smaller than 9·0 on four occasions, neglecting the index for the period ending June 23rd. This last index is extraordinarily small and perhaps of doubtful accuracy, there being the possibility of weighing error during the previous period, although length records suggest that this view is not fully justified (Table 35). Fusing the two periods between May 26th and June 23rd yields an index of 5·4 for the month, showing that in any case this fish showed a very high degree of efficiency about this time.

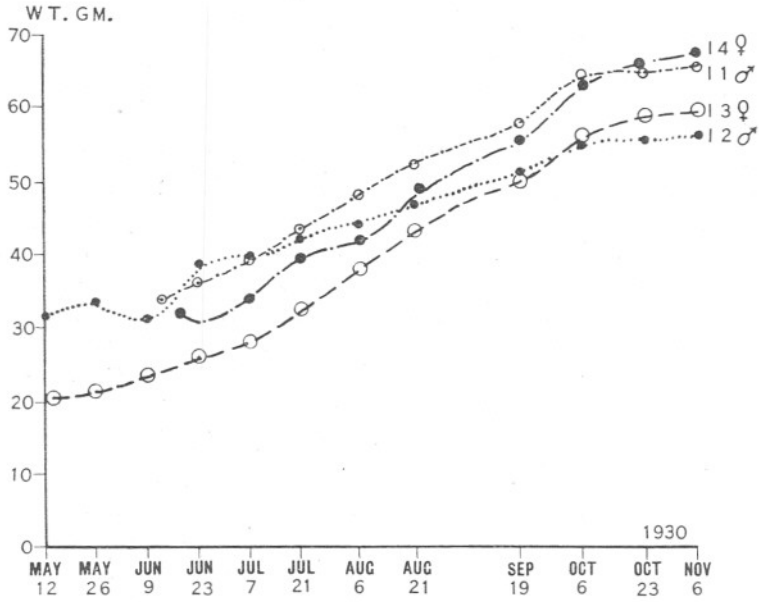

FIG. 5.—Growth curves of weight for the male plaice I1 and I2 and for the female plaice I3 and I4, fish supplied with intermediate rations (Cawsand, 1930).

Turning to the females we find in I3 a most surprisingly efficient fish. In Table 36 it is seen that during one period only 3·8 gm. of food were required to produce 1·0 gm. increase in weight (July 21st). During three other periods, the efficiency index was smaller than 5·0 and during three others it was less than 6·0. It is readily seen to be far more efficient than any one of the B fish. During 176 days the initial weight of this fish was almost tripled (Tables 33 and 36). I4 showed more variable efficiency, which however was generally distinctly high. Table 37 shows that the efficiency index was 3·1 during one period, 4·5 or smaller during three others, and the largest index for the whole experiment was 10·8. This fish easily doubled its initial weight over a period of 141 days (Table 33).

Examination of the data of these experiments on intermediate feeding shows that whether we consider efficiency over periods of 141–178 days or for much shorter periods, there is considerable justification for the conclusion that male and female plaice alike make relatively much more efficient use of food for purposes of growth when supplied with rations intermediate between their maintenance requirements and maximum demands and roughly twice the value of the former than when maximum quantities of food are supplied to them. Among such intermediate-fed fish, not only are efficiency indices of 4·0–5·0 more common, but there is also less variation in efficiency, the larger figures met with among the

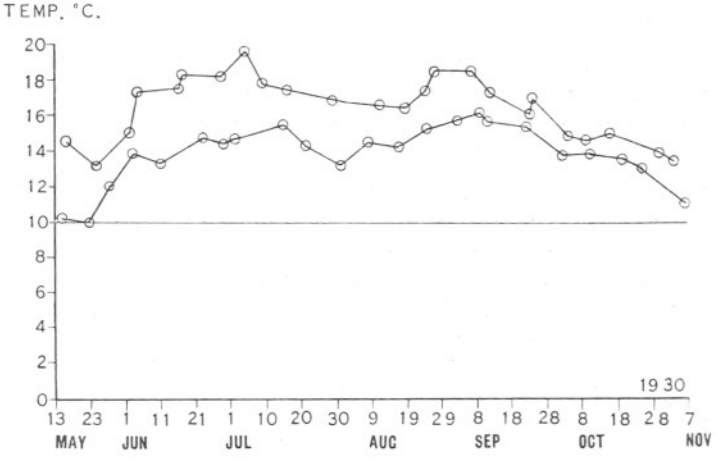

FIG. 6.—Graph of maximum and minimum temperatures at Cawsand, 1930.

indices for maximum-fed fish being absent. In the case of the four plaice we have considered, only during 12 periods out of a total of 40 was the efficiency index greater than 10·0, which fact in itself is much more than merely a suggestion of consistently high efficiency. The growth curves of weight for these fishes are presented in Figure 5.

Figure 6 shows graphically the temperature range at Cawsand during 1930, minimum and maximum temperatures being plotted against time.

4. Conclusions Drawn from the Experiments of 1930 (Cawsand).

(1) A male plaice 13·1 cm. in length and 21·5 gm. in weight was able to maintain its weight to within 0·7 gm. of constancy over a period of 144 days from May 14th, 1930, on an average daily ration of 0·46 gm. of Mytilus flesh, which gives a maintenance ratio, i.e. the ratio food consumed per day/mid-body weight, of 0·022. These values would hold good for a fish just commencing its third season of growth.

(2) Increasingly large fish require larger daily rations for purposes of maintenance, but increase in size of these rations is not directly proportional to increase in body-weight. Experiments with a graded series of fish of various sizes characterising the third season of growth show that the maintenance ratio decreases with increase in size of fish. Thus, passing to the upper limit of the series, a male plaice 23·0 cm. in length and 115·0 gm. in weight was able to maintain its weight to within 4·0 gm. of constancy over a period of 147 days from June 12th, 1930, on an average daily ration of 1·42 gm. of similar food, thus showing a maintenance ratio of 0·012. These values would hold good for a male fish just ending its third season of growth.

(3) The values given above vary from one fortnightly period to another throughout the year, but it is suggested that a reasonably accurate estimate of the increasing maintenance requirements of a freely-growing, two-year-old male plaice would be afforded by accepting the averages for long periods such as the above, excluding the winter months of low temperatures. Thus the maintenance requirements of such a fish would vary between 0·46 gm. and 1·42 gm. of Mytilus flesh per day, the maintenance ratio decreasing from 0·022 to 0·012, approximately. Intermediate values are presented in the text and, graphically, in Figure 1.

(4) A female plaice 12·2 cm. in length and 17·3 gm. in weight was able to maintain its weight to within 4·7 gm. of constancy over a period of 143 days from June 16th, 1930, on an average daily ration of 0·43 gm. of similar food, thus showing a maintenance ratio of 0·022. Thus the maintenance requirements of male and female plaice just commencing the third season of growth appear to be almost if not quite identical.

(5) Among females, as among males, the maintenance ratio decreases with increase in size of fish. Thus, passing to the upper limit of a graded series of fish chosen to represent stages in the third season of growth, a female plaice, 24·5 cm. in length and 132·0 gm. in weight, was able to maintain its weight to within 4·9 gm. of constancy over a period of 178 days from May 12th, 1930, on an average daily ration of 1·24 gm. This value would hold good, approximately, for a fish just ending its third year of growth.

(6) From (4) and (5) it may reasonably be assumed that the maintenance requirements of a freely-growing female plaice would vary, during the third season of growth, between approximately 0·43 gm. and 1·24 gm. of Mytilus flesh per day, if growth were as unrestricted as for example at Cawsand during 1928. The main-

tenance ratio would vary between 0·022 and 0·009 approximately, steadily falling to the latter value. Intermediate values are presented in the text and, graphically, in Figure 1.

(7) Growth of maximum-feeding plaice at Cawsand was poor during 1930 and the rate of growth was much more irregular than it was during 1929. But the results of the experiments with such fish lend support to the conclusions put forward earlier, that growth and efficiency (as indicated by the quantity of food required to produce 1·0 gm. increase in fish weight) vary very considerably in both males and females, from one fortnight to another throughout the growth season. During certain fortnightly periods, but rarely, such high efficiency as is shown by the indices 4·7 (B1), 4·8 (B2), 4·2 (D1 and D3), 4·3 (D2), and 4·4 (D4) was indicated, but during many periods the efficiency shown was very much lower. Thus among males, during 30 periods out of a total of 52, more than 10·0 gm. of food was required to bring about an increase in weight of 1·0 gm., and during 13 of these, more than 15·0 gm. was required. Among females more than 10·0 gm. was required during 26 periods out of a total of 54 ; during 18 of these, more than 15·0 gm. was required.

(8) It has been shown that during the experiments of 1928, there was possibly some leakage of food materials through the coarse meshwork of the box windows, and it is concluded that the efficiency of maximum-feeding fish was higher during this year than the experimental results indicate. This finding also affects the conclusion previously ventured that intermediate-feeding fish show a greater efficiency in the utilisation of food for purposes of growth than maximum-feeding fish. But this matter was investigated independently during 1930, the conclusions formed being shown below (9).

(9) Evidences have been presented which support the conclusion that male and female plaice alike, when supplied with rations intermediate in value between maintenance and maximum rations and about twice the value of the former, utilise food more efficiently for purposes of growth than fish which receive maximum rations. For periods of 141–176 days, the efficiency indices of three fish fed in this way were 6·8 (I1, ♂), 6·3 (I3, ♀), and 5·9 (I4, ♀). No maximum feeding plaice show such consistently high efficiency as this, the smallest indices for a corresponding period during 1930 in the case of such fish were 9·1 (D4, ♂) and 8·5 (B5, ♀). Moreover, indices, for fortnightly periods, of less than 5·0 were much more common among intermediate-feeding fish, 13 out of a possible total of 40 as against 7 out of a possible 106 for maximum-feeding fish. Similarly

for indices less than 10·0, 28 out of a possible 40 as against 48 out of a possible 106. Stated slightly differently, intermediate-feeding plaice required more than 10·0 gm. of food for the production of 1·0 gm. of fish doing only 12 periods out of 40, maximum-feeding plaice during 58 periods out of 106. In the light of this evidence the conclusion of consistently higher efficiency seems perfectly justified.

II. RESULTS OF THE LYMPSTONE EXPERIMENTS OF 1930.

1. Experiments of January to April.

These experiments were really a direct continuation of the experiments of 1929, and thanks are due to Mr. Lees for facing the unpleasantness of winter in continuing the routine observations. As a glance at my previous paper will show, the experiments of 1929 concerned four maintained fish of each sex and four fully-growing fish of each sex. Of these, two of each sex in each group were retained for the work to be described presently, namely, L1 and L4 (♂), and L5 and L7 (♀) of the maintained groups, L10 and L12 (♂) and L13 and L15 (♀) of the freely-growing groups. All these fish were supplied with maintenance rations until summer feeding commenced, when the four latter fish were supplied with full rations. But as long as they declined food, only very small rations were offered so as to reduce the possibility of error, these rations being steadily increased according to appetite as soon as the fish showed signs of taking food readily. The results of these experiments will be described as briefly as possible, but they may be readily grasped by reference to the tables cited.

Maintenance requirements will be indicated by noting rations which result in loss of weight or allow of increase in weight and by considering that these quantities mark the experimental limits of maintenance.

L1w (init. lth. 17·6 cm.; init. wt. 52·8 gm.) during January and February required 0·44–0·61 gm. of food per day for maintenance (Table 38), the maintenance ratio corresponding to these figures being 0·009–0·012. During later months the value of the ratio rose to 0·014–0·015. L4w (init. lth. 21·1 cm.; init. wt. 78·8 gm.) during the first 42 days required a daily ration of 0·77–0·78 gm., the maintenance ratio being 0·010. During the latter part of the experiment these quantities had risen to 1·10 gm. and 0·014 (Table 39). The female L5w (init. lth. 18·9 cm.; init. wt. 69·8 gm.) took rather more food than was required for pure maintenance and consequently it is more difficult to fix maintenance requirements. But during the early stages of the experiment 0·43–0·64 gm. seemed to be the daily ration required, giving a ratio of 0·006–0·009 (Table 40). L7w (init. lth. 22·7 cm.; init. wt. 103·4 gm.) took rather less food than it needed for maintenance and declined

in weight. During the colder months the maintenance requirements were 0·64–0·96 gm. of food daily, which gives a ratio of 0·006–0·009 (Table 41).

In Table 42, the above results are summarised for the whole period of 112 days and included in the table are data from my previous paper showing the maintenance requirements of the same fishes during 1929 to November 25th, so that the decrease in value of the maintenance rations can readily be seen. In the first example, that of L1, the daily ration required for purposes of maintenance fell from 0·90 gm. to 0·58 gm. during the colder months, the maintenance ratio from 0·017–0·011. Other examples will be found in the table.

The plaice which had been maximum-feeding and freely-growing previously, ceased to feed during early November, as is shown in my previous paper, and immediately commenced to lose weight. Having ceased to take maximum rations, these fish characteristically refused even mere maintenance rations. Thus during 56 days from January 6th, it is doubtful if L10w–L15w took food at all (Table 43). On the other hand, minimum-feeding fish continued to take food throughout the colder months, during 56 days from January 6th, the average daily rations taken by L1w–L7w ranging from 0·61–0·91 gm. (Table 43). It is interesting to note also that the losses in weight shown by these non-feeding fishes were not very much greater than those of imperfectly maintained fish (see table). This is the most striking feature of the winter experiments.

The data of the experiments with previously maximum-feeding fish are presented in Tables 44–47. In all cases, it will be seen, feeding has been resumed completely before the end of March. In every case, little more than a maintenance ration was taken daily from February 17th to March 3rd. During the next fortnight the daily ration accepted increased until by March 17th the fish were almost fully-feeding. These findings present no new knowledge, but they do tend to show that the experimental fish behaved in very much the same way as do fish living under natural conditions, which speaks well for the experimental conditions.

When feeding was resumed, the fish at once showed increases in weight and corresponding to these, remarkably high degrees of efficiency, especially during the first fortnight of partially-resumed feeding. [Note : the efficiency index of L15 (Table 47) is misleading, since weight increases are undoubtedly due to ripening of the gonads.]

2. Minimum Requirements and Maintenance.

The results of the experiments on maintenance in male plaice are shown in Tables 48–51, the fish being referred to as L1–L4 respectively. These fish were much larger than the corresponding ones at Cawsand and their maintenance requirements would appear to be those of a fully-growing

plaice at about the middle of its third season, in the larger ones towards the end of this season.

The maintenance requirements of L1 (init. lth. 17·9 cm.; init. wt. 62·2 gm.) lay between 0·71 gm. and 0·98 gm. of food per day from one fortnightly period to another, giving a maintenance ratio of 0·012–0·017 (Table 48). For the whole experiment (182 days) an average daily ration of 0·86 gm. was slightly too small to maintain the weight constant, the corresponding ratio, 0·015, being slightly low (Table 52). For L2 (init. lth. 20·0 cm.; init. wt. 65·0 gm.) the daily maintenance ration lay between 0·83 gm. and 1–14 gm., the ratio between 0·012 and 0·019 (Table 49). Over a period of 182 days an average daily ration of 1·03 gm. allowed of a slight increase in weight, so that the ratio 0·015 is a trifle high (Table 52). L3 (init. lth. 21·5 cm.; init. wt. 90·3 gm.) consistently lost weight to a great extent although the average daily ration taken over a period of 182 days was 1·09 gm., the maintenance ratio 0·013, both of which figures are high by comparison with those for C5 (cp. Tables 50 and 5). L4a (init, lth. 18·5 cm.; init. wt. 65·5 gm.) required 0·82 gm. of food per day for maintenance, the corresponding ratio being 0·013 (Table 51, July 7th and 21st). L4b (init. lth. 24·4 cm.; init. wt. 149·6 gm.) was undoubtedly a three-year-old fish. It required a daily ration of 0·87 gm. for maintenance during the fortnight ending November 10th, a very low value indeed, giving a ratio of 0·006 (Table 51). These results are summarised to November 10th in Table 52, where it is seen that the requirements of L1 alone compare closely with those of Cawsand males (Table 7).

Data concerning the experiments with the females L5–L8 are shown in Tables 53–56. L5 (init. lth. 14·7 cm.; init. wt. 28·9 gm.) showed exceptionally high maintenance requirements (0·80–0·82 gm. per day) (Table 53). Over a period of 182 days an average daily ration of 0·78 gm. was required to maintain the weight constant, the maintenance ratio being as great as 0·027 (Table 57). The data for the remaining females are not of particular interest, and examination of the tables cited will show that the Lympstone results are far less satisfactory and useful than the results of the corresponding experiments at Cawsand. In fact, this statement might be extended to the Lympstone results in general as regards the maintenance experiments. The variations in quantity of the maintenance requirements of the Lympstone plaice are exceptionally wide and the results when examined closely are decidedly discordant. Losses in weight of rather serious proportions were more common than at Cawsand and these detract from the value of the results. Yet it must be remembered that it is not invariably as easy as one might assume to maintain the weights of segregated fish constant since they often decline to take food.

3. Maximum Requirements and Growth.

Summarised data derived from the results of the Lympstone experiments with maximum-feeding plaice are presented in Table 58. The fish, it will be noticed, are generally much larger than those used at Cawsand and most of them are, in all probability, three and not two years old at the

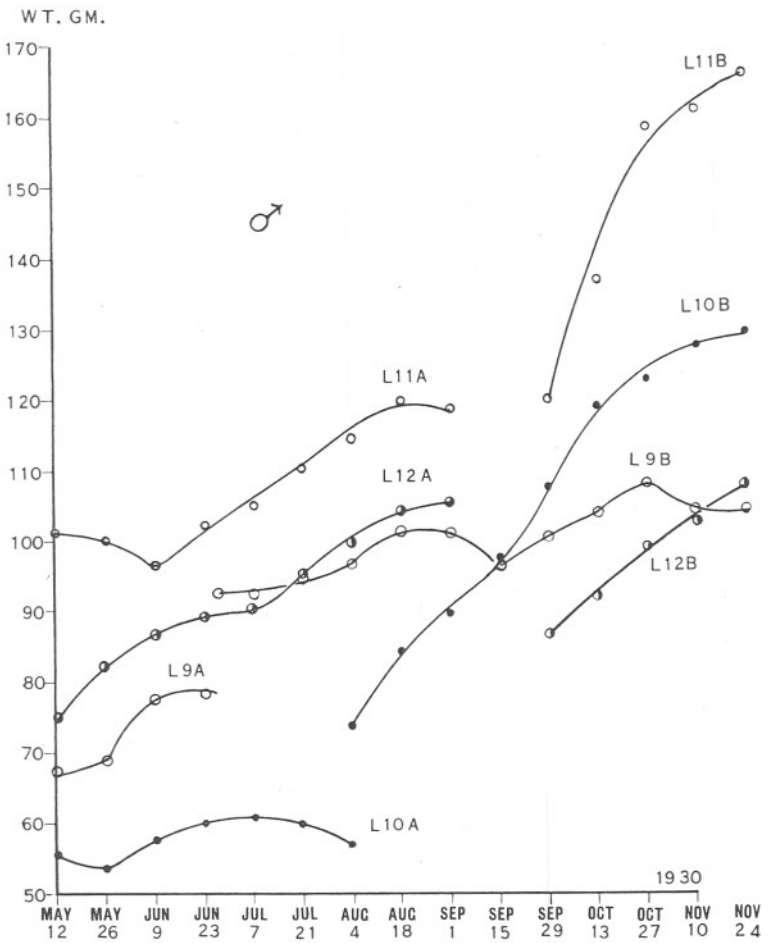

Fig. 7.—Growth curves of weight for the male plaice L9–L12 (Lympstone, 1930).

outset. Such data should provide a useful supplement to those of Cawsand. Unfortunately, in all cases save two the continuity of the experiments was broken, and it was necessary to employ two fishes instead of a single one. The growth-curves of weight for these fishes are shown in Fig. 7.

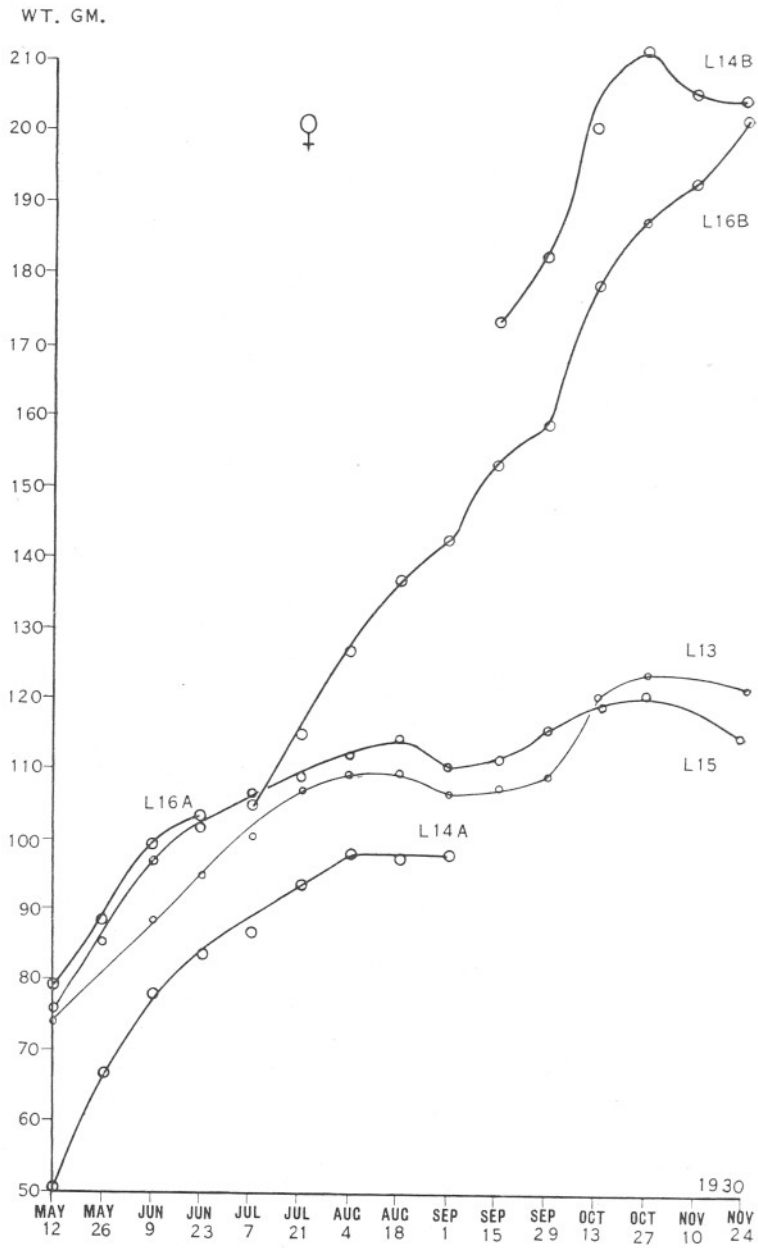

FIG. 8.—Growth curves of weight for the female plaice L13–L16 (Lympstone, 1930).

It is seen from Table 58 that the growth rates of certain fishes were abnormally slow, e.g. those of L9b, L10a, and L11a. In these cases the efficiency indices were tremendously high, 45·4, 186·1, and 26·6 for periods of 84 or more days. Certain females also showed high indices, e.g. L13 (20·0) and L15 (22·4). A glance at these results shows conclusively that tremendous variation occurred in growth-rate and in efficiency in different individuals. As at Cawsand, the growth-rate was much slower than during 1929. Not a single fish rivalled the performances of L11, L15, and L16 of that year, which fish showed weight increases for a period of 154 days of 157·4, 140·7, and 175·0 gm. respectively (see Table 41 of my previous paper). This statement might also be applied to efficiency, with slight

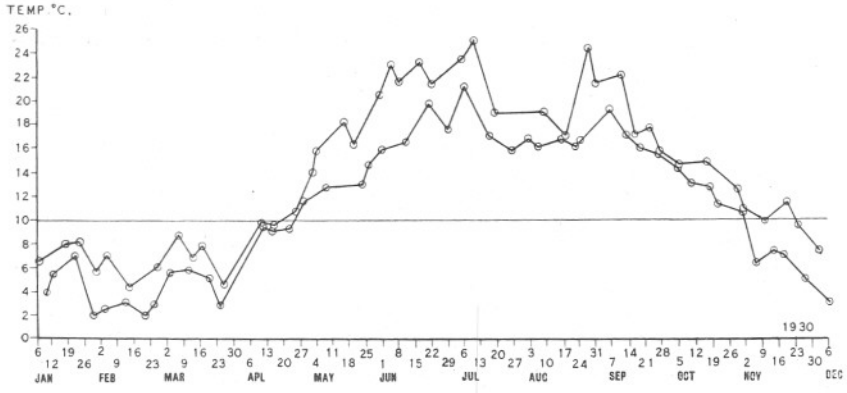

FIG. 9.—Graph of maximum and minimum temperatures at Lympstone, 1930.

reservation, since the fish mentioned showed indices of 7·1, 8·1, and 8·5. During 1930, L10b and L11b among males showed indices of 9·6 and 6·5 for periods of 98 and 42 days respectivly, L16a and b indices of 8·8 and 9·4 for periods of 42 and 126 days respectively, but no other fish showed such high efficiency as this over long periods (Table 58).

L10b showed a rapid growth-rate from one fortnightly period to another, with increments of 10·4, 7·7, 10·2, and 11·4 gm. and corresponding efficiency indices of 5·7, 8·7, 8·0, and 8·5 (Table 60). But it had not doubled its initial weight at the end of 112 days. L11b showed the remarkable fortnightly weight increases of 16·8 and 21·6 gm., with such high efficiency as indices of 4·4 and 4·8 indicate, yet this phenomenal growth-rate rapidly declined and during the next period only 2·3 gm. was added to the weight of the fish at a cost of 38·5 gm. of food per 1·0 gm. increase. These examples illustrate the slow rate of growth, variation in efficiency and irregularity of growth characterising the results of the Lympstone experiments with males. Other examples may be found readily in Tables 59–62. And these generalisations may well be applied to the

females also, where great variation occurs as characteristically as among males. The results for the females are shown in Tables 63–66, where details may be inspected readily. The growth-curves of weight for these females are presented in Figure 8.

Figure 9 shows graphically the maximum and minimum temperatures recorded for weekly periods from January 6th to December 6th, 1930, the data employed having been kindly sent to me by Mr. H. Lees.

4. Conclusions Drawn from the Experiments of 1930 (Lympstone).

(1) The results of the experiments of January to April indicate the fall in value of the maintenance requirements of both male and female plaice during the coldest months of the year. By comparing these results with those obtained for the same fishes during 1929, we see that in the case of a male fish approximately 50 gm. in weight (e.g. L1) the average ration required daily for maintenance falls from 0·9 gm. to 0·6 gm., i.e. by about one-third of its former value. The maintenance ratio diminishes from 0·017 to 0·011. In the case of a female approximately 100 gm. in weight, the daily ration falls from 1·3 gm. to 0·7 gm., the maintenance ratio from 0·013 to 0·007. The degree of reduction of these quantities varies considerably in different fish, but the results warrant the conclusion that during the colder months of the year, a plaice requires for purposes of maintenance only a fraction ($\frac{1}{2}$ to $\frac{2}{3}$) of the daily ration which is required to maintain the weight constant during warmer months.

(2) These early experiments also serve to show that maximum-fed plaice of one summer refuse even mere maintenance rations during the following winter months, whereas previously minimum-fed fish continue to take maintenance rations. Moreover, the former fish appear to require much smaller quantities of food for purposes of maintenance during the winter than do the latter fish.

(3) It is shown that at Lympstone, maximum feeding was completely resumed before the end of March and that it was attained in little more than a fortnight. Growth commenced at once and strikingly high efficiency was shown during the first few weeks.

(4) At Lympstone during the summer of 1930, maintenance requirements were in some cases much higher than at Cawsand, which might be expected in view of the fact that water temperatures were higher. The results of maintenance experiments are inconsistent in their variability, however, although they tend to support the Cawsand results in showing the order of the fall in value of the maintenance ratio with increase in size of fish.

(5) The growth-rate of maximum-feeding fish at Lympstone, as at Cawsand, was slow and the efficiency correspondingly low. These results similarly show the tremendous variation in rate of growth, and efficiency from one fortnightly period to another in the case of all fishes and from one fish to another at the same time. High efficiencies, e.g. 4·4 and 4·8 for L11b ; 4·5 and 6·8 for L13, were shown from time to time, but rarely. Lower efficiencies were common, and among both males and females for at least one half the total number of fortnightly periods, more than 15·0 gm. of food was required to produce 1·0 gm. increase in weight of the fish. Among males the efficiency index was less than 10·0 during only 10 periods out of a total of 52, among females during only 18 periods out of a total of 54, clearly very low degrees of efficiency.

III. GENERAL DISCUSSION OF RESULTS.

The experiments on maintenance in the plaice, which have extended over three years, have on the whole rendered fairly uniform and very conclusive results. We may lay claim to a considerable body of facts, which shows with some precision the order of the maintenance requirements of a two years' old plaice, not only at the commencement of, but also during and towards the end of the third season of growth. The results of these experiments directly apply to different fish of various sizes, but by a process of analogy, to which objection can scarcely be raised, they can be applied to the same fish at different times during the growth season with which we are concerned. Thus we arrive at an approximate evaluation of the maintenance requirements of fully-feeding, freely-growing plaice, using methods which are more in keeping with growth experiments than others which might have been selected, e.g. determination of maintenance requirements by study of respiratory exchanges. Data are available also to show how maintenance requirements diminish during the months when water temperatures are lowest, when plaice which have been fully-feeding have ceased to take food to any considerable extent and consequently have ceased to grow.

In a previous paper (Journ. Mar. Biol. Soc., Vol. XVII, No. 1, Sept. 1930, pp. 103–174) it was shown that the maintenance requirements of a 44 gm. male plaice are satisfied when an average daily ration of 0·6–0·7 gm. of Mytilus flesh is injested, but reasons were given for supposing that this ration value is low and that a more accurate value would be 0·7–0·8 gm., or 0·018 of the body weight (=maintenance ratio). During 1929, this statement was substantiated, for it was found that a 42 gm. male fish, C6a, maintained its weight constant over a period of 131 days when it took an average daily ration of 0·7 gm., which yields a maintenance ratio

of 0·017. It was shown further that C5a, a 30-gm. male, required a daily ration of 0·6 gm. for purposes of maintenance (ratio=0·019) and that the mean C fish, 17·6 gm. in weight, required 0·4 gm. per day (ratio=0·024). This was the closest approach that could be made to a determination of the increase in value of maintenance requirements with increase in size of the fish when the results of the Cawsand experiments of 1929 alone were employed. But it was seen that the increase in value of these requirements is not directly proportional to the increase in size, the maintenance ratio decreasing in value. By combining these results with the Lympstone results of the same year, it was possible to proceed a little way further. The male L1, a 52-gm. fish, required a daily ration of 0·9 gm. (maintenance ratio=0·017), while L2, a 130-gm. male, required 1·4 gm. per day (ratio=0·011). Indicating that objections might be raised to a combination of the two sets of results, the conclusion was nevertheless put forward that an increase in weight from 18 gm. to 130 gm. among male plaice entailed an increase in the daily ration required for maintenance from 0·4 gm. to 1·4 gm., which implies a decrease in the value of the maintenance ratio from 0·024 towards 0·011.

It is obviously both important and interesting to observe how far the results of 1930 conform to or depart from the conclusions ventured. Fortunately, at Cawsand during 1930, a far greater measure of success was met with in the experimental determination of maintenance requirements than had been met with during the previous two years, due to the arrangement of a graded series of individuals of various sizes representing stages passed through by a plaice during its third season of growth. And the results of this last year both strengthen and broaden the conclusions previously formed. In the text of this paper it has been shown that during 1930, the maintenance requirements of a male plaice 21·5 gm. in weight were approximately 0·46 gm. of Mytilus flesh daily, those of a similar fish 115·0 gm. in weight approximately 1·42 gm. of such food per day. The maintenance ratios corresponding to these quantities are 0·022 and 0·011. The close conformity between these results and those of the previous year is clearly seen and is also noteworthy.

It was suggested further, that the size difference indicated above is a close measure of the difference shown by a two-year-old plaice at the commencement of and towards the end of its third season of growth. We have thus reached the point at which it is possible to conclude, and with much faith in the accuracy of the conclusion, that about the commencement of the third season of growth a male plaice requires approximately 0·022 body-weight, or the first 0·4 gm. of its daily ration, to satisfy basal requirements and maintain its weight constant, and that towards the end of this season 0·011 body-weight, or the first 1·4 gm. of the daily ration for this purpose. The food is understood to be Mytilus flesh. The

variation in basal need with increase in size is presumably a steady one, so that it is possible to infer, with some experimental evidence to support the inference, that the maintenance ratio is a variable quantity which, during the season with which we are concerned, ranges from 0·022 towards 0·011. This is shown graphically from experimental results in Figure 1 (♂).

For females, corresponding success was met with during the final years' work, the results substantiating and amplifying the conclusions previously ventured. In my previous paper it is seen that at Cawsand during 1929 a female 22 gm. in weight required 0·4 gm. of food per day for maintenance, a similar fish 42 gm. in weight required 0·6 gm., or expressed in the form of maintenance ratios 0·019 and 0·015 of the body-weight respectively. A Lympstone female 103 gm. in weight required 1·3 gm. per day or 0·013 body-weight. The results of 1930 correspond more closely with those presented above for males. A female 17·3 gm. in weight required 0·43 gm. of food per day, a similar fish of 132·0 gm. required 1·24 gm. per day, the corresponding ratios being 0·022 and 0·009. The latter value appears to be subnormal in that the female A3, 101·5 gm. in weight, required 1·21 per day, yielding a maintenance ratio of 0·012, and it is distinctly possible that the maintenance requirements of females parallel those of males. It is unlikely that serious error would arise if the maintenance ratio of a female 130 gm. in weight was taken as being 0·011. In Figure 1 the results of these experiments are shown graphically for females as well as for males. These results can be extended in the way indicated above for fully-growing males.

The growth-rate shown at Cawsand during 1928 was rapid, the mean male increasing its initial weight of 38·8 gm. by 86·0 gm., the mean female increasing its initial weight of 43·3 gm. by 107·9 gm. during a period of 176 days. But the efficiency of these fish, as measured by the quantity of food required to produce an increase of 1·0 gm. in weight, was low, the mean male requiring 12·7 gm. and the mean female 10·5 gm. In the present paper it has been shown that during these preliminary experiments it is likely that there was a slight leakage of food materials through the coarse mesh of the box windows during the ebb and flow of tides. If this was the case, the efficiency indices shown are slightly greater than the true values. When the conditions and apparatus were refined, the efficiency shown was much higher, i.e. the indices were smaller. Thus during 1929 the average efficiency of D3, the most rapidly-growing male, for a period of 175 days was represented by the index 6·5, the average efficiencies of B1 and B4, the most rapidly-growing females, by the indices 7·6 and 7·2 respectively, over a corresponding period. Moreover, examination of the data for fortnightly periods showed that among Cawsand males, the efficiency was so high during certain periods as to yield an index of 4·8 and among the corresponding females an index of 5·2 was shown.

At Lympstone the efficiencies over long periods were lower, that of the male L11 being 7·1, those of the females L15, and L16 being 8·1 and 8·5 respectively. As at Cawsand, and to an even greater extent, higher efficiencies were shown during certain fortnightly periods, and generally there was much more variation in efficiency from period to period than at Cawsand.

At Cawsand during 1930, the highest efficiency over long periods was shown by the male D4, with an index of 9·1 for 116 days and the females B3 and B5, with indices of 9·7 and 8·5 for 165 and 87 days respectively. If these values are compared with those given for D3, B1, and B4 of 1929 above, it is seen that they are slightly greater, i.e. the efficiencies during 1930 were slightly lower. But the efficiencies shown during 1930 were higher than those shown during 1928, and we can safely infer, on the evidences of the results of two consecutive years, that the maximum average efficiency for periods approaching whole growth seasons in extent lies between efficiencies corresponding to the indices 6·5 and 9·1 for males, and 7·2 and 8·5 for females. In view of the fact that the higher efficiencies went side by side with more rapid, and perhaps more nearly typical, growth-rates, it would probably be safe to infer that they are more accurate from the viewpoint of normality.

Growth proceeded at a rapid rate at Cawsand during 1928, as is mentioned above. Such rapid rates and degrees of growth have not been shown since 1928, either at Cawsand or at Lympstone. This applies with additional force if we consider individual performances at Cawsand during the first year, when the male C3 increased its weight from 36·0 gm. to 158·0 gm., and the female D5 from 50·0 gm. to 203·0 gm., both performances taking 176 days. Such weight increase has not been equalled although the percentage growth has been exceeded. As has been shown, the above plaice increased their initial weights by over 300 per cent, while the later experiments yielded smaller actual weight increases but higher percentages of growth. Thus the Cawsand male D3 of 1929 increased in weight from 15·5 gm. to 105·0 gm., the corresponding females B1 and B4 from 24·0 gm. to 105·5 gm. and from 18·5 gm. to 103·5 gm. respectively, during 175 days, percentage increases of 580, 340, and 460 respectively. Actual weight increase is our chief concern however. It is obvious that any figures for percentage growth call for uniform initial weights and periods. The experiments of 1929 were started earlier than those of 1928, and with smaller fish. This fact causes percentage growth of 1929 to appear greater than that of 1928 despite the actually smaller weight increases. At Lympstone during 1929, slightly larger fish were used and, over a period of 154 days, the male L11 increased in weight from 23·2 gm. to 157·4 gm., the females L15 and L16 from 31·9 gm. to 140·7 gm. and from 50·5 gm. to 175·0 gm. respectively. Only L11 equalled

the performance of the Cawsand (1929) male C3 as regards actual weight increase.

For some reason which remains unknown, the rate of growth shown at both Cawsand and Lympstone during 1930 was much slower than that shown during 1929, degrees of growth being smaller also. The most actively-growing male, D1, increased in weight merely from 35·8 gm. to 77·1 gm. during 162 days, the most actively-growing female, B5, from 34·5 gm. to 82·5 gm. during 87 days. At Lympstone, L10b showed weight increase from 73·9 gm. to 127·7 gm. during 98 days, the female L16b, a three years' old fish presumably, from 104·9 gm. to 192·8 gm. during 126 days. These fishes were the most actively-growing individuals at Lympstone.

From the point of view of typical growth then, the results of 1930 are of much less value than those of the previous year. The experiments of 1929 are of most use in this respect, since they were commenced earlier in the year. But perhaps the best indication of maximum growth during the third season of the plaice is afforded when the results of 1929 are combined with those of 1928, i.e. when an hypothetical fish is built up of two individuals of consecutive years, taking care, of course, that the two periods do not overlap. Thus, if we take D3 (1928) and B4 (1929) as characteristic of females, it is seen that from May 22nd to July 19th, 1929, B4 increased its weight from 18·5 gm. to 43·0 gm., its length from 13·2 cm. to 16·1 cm. On July 16th, 1928, i.e. at the commencement of the experiment, D3 was 16·6 cm. in length and 43·0 gm. in weight. And it is reasonable to assume, bearing the performance of B4 in mind, that had the experiments of 1928 been commenced some 48 days earlier, they might have been commenced with a D3 fish of approximately 13 cm. in length and 18 gm. in weight, this being the size of B4 on May 22nd, 1929. Even when two sets of results are combined in this way, the whole growth season is not completely covered since, according to the Lympstone results of 1930, plaice are fully-feeding and freely-growing by the end of March, but a closer approximation is afforded for total growth during the third season.

By this means we can infer that the theoretical D3 fish of May 22nd, 1928, increased in size until by the end of December growth had taken place from 13 cm. and 18 gm. to 23·5 cm. and 155 gm. It might be considered objectionable to estimate growth to the end of December since during 1929 growth ceased before the end of November, but it should be realised that the degree of growth during December was slight. Moreover, as the duration of this theoretical growth season (221 days) has not been extended beyond the normal span (see below), no serious error is involved.

It is possible to repeat the above in the case of males, and by thus combining the results for C3 (1928) and D3 (1929) we can infer that growth

in weight from 15·5 gm. to 151 gm. takes place, theoretically, during the corresponding period. This approximation would hold as an index of maximum growth shown during the third season by a typical female. The method employed is open to objection, but the aim in view is an estimate of growth for the whole of the season with which we are concerned. Such methods will be discarded when it comes to attempting to estimate food requirements and food fractions going to satisfy maintenance requirements and to promote growth respectively. In attempting to do this the data of one particular year will be adhered to closely. Before leaving this question of total growth it might be mentioned that the Lympstone male, L11, increased in weight from 23·2 gm. to 147·2 gm. during 182 days ending December 23rd, 1929. This shows the estimates made above to be reasonable ones.

We might consider briefly Lympstone data which indicate the duration of the growth season. The results of the experiments of January to April show that the winter fast ceases quite abruptly during early March and that before the end of this month appetite is completely restored. About March 1st, 1930, the four Lympstone plaice L10–L15 were taking mere maintenance rations of approximately 2 gm. per day. On March 4th they commenced to take 4–5 gm. per day, and by March 6th were taking 5–6 gm. per day. The daily rations by the end of the month were 6–7 gm. It is clear that during the first week in March these plaice increased their daily rations from maintenance ones to almost maximum ones. We may consider that the feeding and growth season commences about the end of this week, say March 6th. At Lympstone during 1929, feeding ceased abruptly about November 11th, when maximum water temperatures approached 10°C., as the following data show. During the fortnight ending November 11th, L12, L13, and L15 took 50·0, 36·3, and 65·4 gm. of food respectively, while during the next fortnight only 8·4, 7·2, and 24·8 gm. respectively was taken. L15 continued partial feeding until December, but it is generally true that full feeding was discontinued about November 11th. And in each case this discontinuance marks the onset of a period when loss in weight occurs. The period of winter fasting thus extends over 16 weeks and includes the whole of December, January, and February. For about 36 weeks full feeding and unrestricted growth ensue. The growth period is seen to be about 30 days longer in extent than that corresponding to the total growth estimate provided above. Doubtless, some variation in duration of the growth period occurs, and at Lympstone during 1930, feeding and growth proceeded longer than during 1929, but after November 10th, when maximum water temperatures reached 10° C., feeding was partial, so that the above conclusions are not materially affected.

In my previous paper it was suggested that plaice which take food

rations intermediate in quantity between maintenance and maximum rations utilise food more efficiently for purposes of growth than do maximum-feeding plaice. It has been shown in the present paper that the evidence upon which this conclusion was based proved to be of doubtful accuracy. There is a possibility that slight quantities of food were washed out of the boxes during the early experiments and, if this actually occurred, the efficiency of the maximum-feeding fish was higher than the data indicate. The efficiency of these fish was used as a basis of comparison for intermediate-feeding fish and hence the higher efficiencies were possibly more apparent than real. But during 1930, this question was investigated under refined conditions, and more reliable data have been obtained.

Two fish of each sex were housed, in a segregated condition, in the modified fish boxes and were supplied with rations about twice the value of the maintenance rations. It is seen in Table 33 that these fish took an average daily ration of not more than 1·5 gm. over periods from 141–178 days, whereas the maximum-feeding fish took as much as 3·5 gm. per day. For the whole range of the experiments the I fish (intermediate-feeding) showed an unmistakably high degree of efficiency in the utilisation of food for growth purposes. No D or B fish (maximum-feeding) showed such low efficiency indices, i.e. high efficiency, as was shown by these fish for long periods, e.g. 6·8 (I1), 6·3 (I3), or 5·9 (I4). The indices for the two most efficient D fish are 9·1 (D4) and 10·2 (D3), those for the most efficient B fish, 8·5 (B5) and 9·7 (B3). Thus the male I1 required 2·3 gm. of food less than the male D4 did in order to increase its weight by 1·0 gm., the female I4 2·6 gm. less than the female B5 for corresponding weight increase. The conclusion that intermediate-feeding plaice are more efficient than maximum-feeding plaice seems perfectly justified. The evidences are presented in greater detail in the text of this paper.

Finally, it is intended to attempt to fulfil the principal aim of these experiments, which is to determine what portion of the maximum ration taken by a freely-growing plaice is used in satisfying basal requirements, i.e. supporting life by supplying the energy necessary for its maintenance, for tissue repair and replacement, and what portion remains for the promotion of growth. The results of the preliminary experiments of 1928 are of little or no use in this attempt since within 14 days of the commencement the maximum-feeding male fish were larger than the minimum-feeding fish. As the latter were retained for the whole course of the experiments it is not possible to compare the two sets fairly. In the case of females there was no fair basis of comparison from the very outset, on account of size differences existing then. In my previous paper an attempt was made to estimate the maintenance requirements of the fully-growing males, but it was based upon the assumption that the maintenance ratio

is constant throughout the third season of growth. Subsequent work has shown that such is not the case, the ratio decreasing with increase in size of the fish. But the estimate that approximately one-fifth of the total food ration was used in satisfying maintenance requirements compares as closely with the more refined estimate presented below as could be expected from the facts then available.

TABLE 67.

DATA CONCERNING THE MALE PLAICE D3 (1929).

Showing growth in weight, food taken, and variation in maintenance ratio with increasing size. Also food quantities estimated as having been used for purpose of maintenance, fraction of total food and efficiency as regards food available for growth.

Date (1929).	Weight. (gm.)	Food per period. (gm.)	Maintenance ratio (from Graph Fig. 1).	Days in period.	Estimated food required for maintenance per period. (gm.)	Fraction of total food used for maintenance.	Growth in weight per period. (gm.)	Efficiency (gm. of food required to produce 1·0 gm. increase in wt. of fish allowing for maintenance.)
June 6	15·5	—	—	—	—	—	—	—
,, 20	18·0	22·0	0·024	14	6·0	0·27	2·5	6·4
July 5	22·5	26·0	0·024	15	7·3	0·28	4·5	4·2
,, 19	30·0	36·0	0·020	14	7·4	0·21	7·5	3·8
Aug. 2	37·0	41·4	0·018	14	8·4	0·20	7·0	4·7
,, 16	41·5	44·2	0·0165	14	9·0	0·20	4·5	7·8
,, 30	51·5	53·2	0·015	14	9·8	0·18	10·0	4·3
Sept. 16	65·5	68·5	0·014	17	13·9	0·20	14·0	3·9
Oct. 1	79·0	65·2	0·0135	15	14·6	0·22	13·5	3·7
,, 15	90·0	76·5	0·013	14	15·4	0·20	11·0	5·6
,, 29	95·0	63·0	0·0125	14	16·2	0·26	5·0	9·4
Nov. 13	103·0	50·0	0·012	15	17·8	0·36	8·0	4·0
,, 28	105·0	39·0	0·012	15	18·7	0·48	2·0	10·1

During 1929 an attempt was made to remedy the defects of the early experiments by determining the maintenance requirements of fish of different sizes, but the attempt was not completely successful. It was intended to commence the experiments with minimum and maximum-feeding plaice of about the same size and to change the former periodically so as to be able to keep the sizes comparable throughout, but difficulty

was met with in the substitution of freshly-trawled fish for settled fish. The fish appear to require a period of time in which to settle down and segregation is not conducive to rapid settling down. However, the results of these experiments provided the valuable conclusions which have been mentioned above. Considerable advance was made during 1930 at

TABLE 68.

DATA CONCERNING THE FEMALE PLAICE B1 (1929).

Showing growth in weight, food taken, and variation in maintenance ratio with increasing size. Also food quantities estimated as having been used for purpose of maintenance, fraction of total food and efficiency as regards food available for growth.

Date (1929).	Weight. (gm.)	Food per period. (gm.)	Maintenance ratio (from Graph Fig. 1).	Days in period.	Estimated food required for maintenance per period. (gm.)	Fraction of total food used for maintenance.	Growth in weight per period. (gm.)	Efficiency (gm. of food required to produce 1·0 gm. increase in wt. of fish allowing for maintenance.)
May 22	24·0	—	—	—	—	—	—	—
June 6	31·0	40·0	0·019	15	7·8	0·20	7·0	4·6
,, 20	35·0	22·0	0·017	14	7·9	0·36	4·0	3·5
July 5	40·0	26·0	0·016	15	9·0	0·35	5·0	3·4
,, 19	47·0	38·0	0·015	14	9·1	0·24	7·0	4·1
Aug. 2	53·5	44·3	0·014	14	9·8	0·22	6·5	5·3
,, 16	61·0	46·2	0·0135	14	10·6	0·23	7·5	4·7
,, 30	69·0	57·0	0·0125	14	12·0	0·21	8·0	5·6
Sept. 16	79·5	69·0	0·012	17	15·1	0·22	10·5	5·1
Oct. 1	89·5	66·9	0·0115	15	14·6	0·22	10·0	5·2
,, 15	96·0	63·0	0·011	14	14·2	0·23	6·5	7·5
,, 29	98·5	49·0	0·011	14	15·0	0·31	2·5	13·6
Nov. 13	104·0	54·0	0·011	15	16·7	0·31	5·5	6·8
,, 27	105·5	43—	0·011	14	16·1	0·37+	1·5	18·0+

Cawsand, what is perhaps the best method of experimenting being employed, the arrangement at the outset of a graded series of fish such as has been described previously. It remains only to apply the results obtained to the estimation it is intended to make. By the use of the graphs shown in Figure 1 it is possible to read off the maintenance ratios of steadily-growing plaice from one fortnightly period to another, using the

mid-body weights for the periods concerned, and thus estimate approximately the quantity of food required for maintenance, which can then be expressed as a fraction of the total quantity of food taken.

Probably, the most useful estimate will be provided if the performances of plaice showing typical sigmoid growth-curves are made use of. The

TABLE 69.

DATA CONCERNING THE FEMALE PLAICE B4 (1929).

Showing growth in weight, food taken, and variation in maintenance ratio with increasing size. Also food quantities estimated as having been used for purpose of maintenance, fraction of total food and efficiency as regards food available for growth.

Date (1929).	Weight. (gm.)	Food per period. (gm.)	Maintenance ratio (from Graph Fig. 1).	Days in period.	Estimated food required for maintenance per period. (gm.)	Fraction of total food used for maintenance.	Growth in weight per period. (gm.)	Efficiency (gm. of food required to produce 1·0 gm. increase in wt. of fish allowing for maintenance.)
May 22	18·5	—	—	—	—	—	—	—
June 6	26·0	40·0	0·0215	15	7·2	0·18	7·5	4·4
,, 20	32·0	22·0	0·0185	14	7·5	0·34	6·0	2·4
July 5	36·5	26·0	0·017	15	8·7	0·33	4·5	3·8
,, 19	43·0	36·5	0·016	14	8·9	0·24	6·5	4·2
Aug. 2	50·5	48·7	0·015	14	9·8	0·20	7·5	5·2
,, 16	60·5	51·4	0·0135	14	10·5	0·20	10·0	4·1
,, 30	66·0	54·3	0·013	14	10·9	0·20	5·5	7·9
Sept. 16	76·0	65·5	0·0125	17	15·1	0·23	10·0	5·0
Oct. 1	83·5	55·2	0·012	15	14·4	0·26	7·5	5·3
,, 15	90·0	59·0	0·0115	14	14·0	0·24	6·5	6·9
,, 29	102·0	63·0	0·011	14	14·8	0·23	12·0	4·0
Nov. 13	108·0	52·5	0·011	15	17·2	0·34	6·0	5·9
,, 27	103·5	38·5	0·011	14	16·3	0·42	4·5	—

growth performances during 1930 are apparently subnormal, those of 1928 are marred by the possibility of food leakages. Undoubtedly the results obtained in the experiments with the male D3 and the females B1 and B4 are likely to be of most use in this respect. Accordingly these will be employed.

In Table 67, which is partly derived from data shown in Table 20 of

my previous paper, are shown the weights of D3 on a succession of weighing days from June 6th to November 28th, 1929. The maintenance ratios, obtained from the graph in Figure 1, are shown in col. 4, while in col. 6 is shown the estimated maintenance requirements for the periods, these being given as fractions of the total food in col. 7. It is seen that for the period ending June 20th, 6·0 gm., or 0·27 of the total food taken, was required for maintenance and that for the period ending October 29th, 16·2 gm., or 0·26 of the total, was required. From June 6th to October

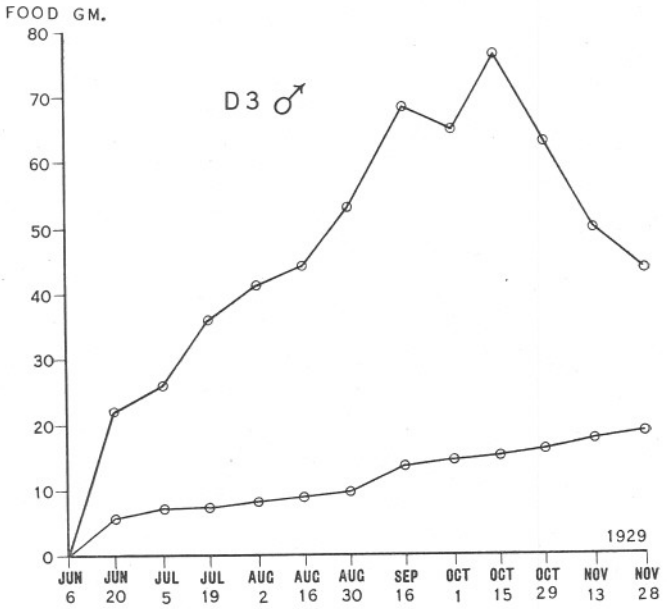

FIG. 10.—Acceleration curves showing the relationship between the total quantity of food taken by D3 (♂) during 1929 and the quantities estimated as having been used for purposes of maintenance. Above, total food ; below, food for maintenance.

29th the fraction for the various fortnightly periods varied between 0·18 and 0·28. These results are shown graphically in Figure 10. During November, when feeding was becoming inhibited, the fraction was increased, but the figures quoted do not take into consideration the slight fall in value of the maintenance ratio which would undoubtedly occur here. For the whole of the experiment, 177 days, the total food taken was 585 gm. of which, according to this estimate, 145 gm. have been required to satisfy basal requirements, i.e. approximately 25 per cent of the total. In the last column of Table 67 are shown indices of efficiency relating to food available for the promotion of growth, and it is seen that these vary

from period to period up till the end of October between 3·7 and 9·4. Thus, no matter whether efficiency is estimated in terms of total food or in terms of food available for growth, the efficiency index is not constant for successive short periods during the growth season. But the table indicates that the index is, in round numbers, 4 during each of six periods and greater than 4 during six others. It appears that of food available for growth purposes every 4 gm. generally produces 1·0 gm. of fish.

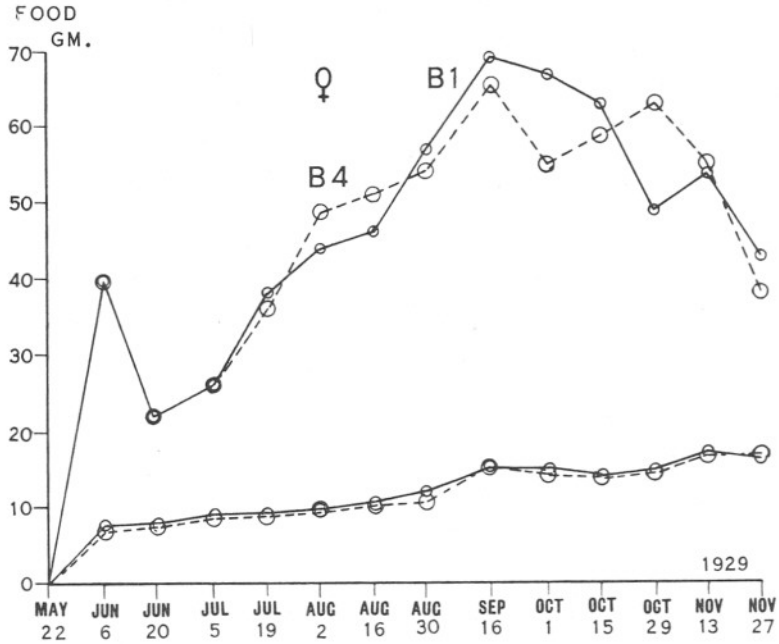

FIG. 11.—Acceleration curves showing the relationship between the total quantities of food taken by B1 and B4 (♀) during 1929 and the quantities estimated as having been used for purposes of maintenance. Above, total food: below, food for maintenance.

Tables 68 and 69 present data for the females B1 and B4, the method of obtaining them being precisely the same as that used for D3. For the period of 15 days ending June 6th, B1 required 7·8 gm. of food for maintenance, 0·20 of the total quantity taken, while for the period of 14 days ending October 29th it required 15·0 gm. or 0·31 of the total quantity taken (Table 68). For the whole experiment, 189 days, 618 gm. of food was taken, of which 158 gm. is estimated as having been required for maintenance, i.e. approximately 25 per cent of the total. These results are shown graphically in Figure 11. In the case of B4 7·2 gm. of food or 0·18 of the total quantity taken was required for maintenance during 15 days to June 6th, 14·8 gm. or 0·23 of the total during 14 days to October

29th. During 187 days a total of 613 gm. of food was taken, of which 155 gm. was used for purposes of maintenance, again approximately 25 per cent of the total (Table 69). It is seen that the efficiency as regards food available for growth was just as inconstant as in the cases of B1 and D3. But for five periods the efficiency index was, in round numbers, 4, and for three periods 5, from which it can be inferred that generally between 4 and 5 gm. of food available for growth produce 1·0 gm. of fish. For B1 it appears that 5 gm. was required to produce this weight of fish, the efficiency shown being slightly less than that shown by B4. For the whole experiment the average efficiencies read as follows : B1—5·4, B4—4·9, and D3—4·8, the male thus showing the greatest degree of efficiency.

The general conclusions afforded by these estimates are uniform for males and females alike. Of the total food taken during the growth season, approximately 25 per cent is used for maintenance. Of the remainder which is available for the promotion of growth, on the average for the season and expressed in round numbers each 5 gm. produces 1·0 gm. increase in weight of the fish, although for shorter periods 4 gm., or even slightly less, may produce such an increase.

The discussion part of this paper must serve as a summary of results, since to summarise further would scarcely serve a useful purpose. In many respects it is considered that the treatment of the available data by the methods adopted is scarcely adequate, and it is hoped to be able to treat these data by strictly statistical methods in the near future. When the methods of correlation are applied to the data, it is likely that reliable generalised results will be forthcoming which might possibly have a greater practical application in fishery research.

IV. Acknowledgement.

I wish to record my cordial thanks to Dr. E. J. Allen who in very many ways has helped to meet the difficulties that have arisen during the course of this work and who by consistent kindness has caused very tedious work to seem much less tedious, for which I am very grateful. Dr. E. S. Russell and Mr. T. Edser have been ever ready to help with suggestions and criticism and to them also is recorded a mark of my appreciation. Thanks are also due to Mr. H. Lees for the care he has shown in his charge of the Lympstone experiments under the direction of Dr. Russell and Mr. Edser, and to all members of the staff of the Marine Biological Association who have assisted in the work. Mr. Seale and the captain and crew of the *Salpa* have also rendered valuable service and to them also my thanks are tendered.

TABLES 1–6.

Data Obtained from the Experiments on the Maintenance Requirements of Male Plaice.

Table 1 : C1.

Date (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 14	13·1	21·5	—	—	—	—	—	—	—	—	—	—
,, 26	13·0	20·5	− 0·1	− 1·0	4·2	12	0·35	0·017	4·5	12	− 0·1	− 1·0
June 9	13·0	19·3	nil	− 1·2	3·4	14	0·24	0·012	7·9	26	− 0·1	− 2·2
,, 23	13·0	17·8	nil	− 1·5	3·4	14	0·24	0·013	11·3	40	− 0·1	− 3·7
July 7	13·0	19·3	nil	1·5	8·5	14	0·61	0·031	19·8	54	− 0·1	− 2·2
,, 21	13·1	20·0	0·1	0·7	7·1	14	0·51	0·026	26·9	68	nil	− 1·5
Aug. 6	13·3	21·0	0·2	1·0	8·0	16	0·50	0·024	34·9	84	0·2	− 0·5
,, 21	13·3	21·5	nil	0·5	7·5	15	0·50	0·024	42·4	99	0·2	nil
Sept. 5	13·3	20·7	nil	− 0·8	6·0	15	0·40	0·019	48·4	114	0·2	− 0·8
,, 19	13·3	20·7	nil	nil	8·5	14	0·61	0·030	56·9	128	0·2	− 0·8
Oct. 5	13·4	20·8	0·1	0·1	10·0	16	0·62	0·030	66·9	144	0·3	− 0·7

Table 2 : C2.

May 14	15·3	31·5	—	—	—	—	—	—	—	—	—	—
,, 26	15·3	31·6	nil	0·1	7·8	12	0·65	0·021	7·8	12	nil	0·1
June 9	15·4	32·5	0·1	0·9	6·9	14	0·49	0·015	14·7	26	0·1	1·0
,, 23	15·5	32·3	0·1	− 0·2	6·4	14	0·46	0·014	21·1	40	0·2	0·8
July 7	15·6	33·2	0·1	0·9	7·0	14	0·50	0·015	28·1	54	0·3	1·7
,, 21	15·8	34·0	0·2	0·8	6·6	14	0·47	0·014	34·7	68	0·5	2·5
Aug. 6	15·9	35·0	0·1	1·0	7·5	16	0·47	0·014	42·2	84	0·6	3·5
,, 21	15·9	35·2	nil	0·2	7·4	15	0·49	0·014	49·6	99	0·6	3·7
Sept. 5	16·0	35·0	0·1	−0·2	7·0	15	0·47	0·013	56·6	114	0·7	3·5
,, 19	16·0	35·4	nil	0·4	7·0	14	0·45	0·013	63·6	128	0·7	3·9
Oct. 6	16·1	36·5	0·1	1·1	8·5	17	0·50	0·014	72·1	145	0·8	5·0
,, 22	16·1	36·8	nil	0·3	5·8	16	0·41	0·011	77·9	161	0·8	5·3
Nov. 6	16·2	35·9	0·1	− 0·9	6·0	15	0·40	0·011	83·9	176	0·9	4·4

Table 3 : C3.

May 28	16·9	45·0	—	—	—	—	—	—	—	—	—	—
June 9	17·0	46·5	0·1	1·5	9·3	12	0·77	0·016	9·3	12	0·1	1·5
,, 23	17·2	46·5	0·2	nil	8·0	14	0·57	0·012	17·3	26	0·3	1·5
July 7	17·3	48·4	0·1	1·9	8·0	14	0·57	0·012	25·3	40	0·4	3·4
,, 21	17·4	48·5	0·1	0·1	7·6	14	0·54	0·011	32·9	54	0·5	3·5
Aug. 6	17·4	46·0	nil	− 2·5	8·2	16	0·51	0·011	41·1	70	0·5	1·0
,, 21	17·3	44·8	− 0·1	− 1·2	8·0	15	0·53	0·012	49·1	85	0·4	− 0·2
Sept. 5	17·2	42·9	− 0·1	− 1·9	8·0	15	0·53	0·012	57·1	100	0·3	− 2·1
,, 19	17·4	42·7	0·2	− 0·2	11·5	14	0·82	0·019	68·6	114	0·5	− 2·3
Oct. 6	17·4	44·1	nil	1·4	14·0	17	0·81	0·019	82·6	131	0·5	− 0·9
,, 22	17·4	44·1	nil	nil	10·8	16	0·67	0·015	93·4	147	0·5	− 0·9
Nov. 6	17·4	43·0	nil	− 1·1	10·3	15	0·70	0·016	103·7	162	0·5	− 2·0

TABLE 4 : C4.

Date (1930)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth.	
	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)							Lth. (cm.)	Wt. (gm.)
May 12	18·9	59·0	—	—	—	—	—	—	—	—	—	—
,, 26	18·9	61·0	nil	2·0	11·3	14	0·81	0·013	11·3	14	nil	2·0
June 9	19·0	59·6	0·1	− 1·4	11·9	14	0·85	0·014	23·2	28	0·1	0·6
,, 23	19·0	61·0	nil	1·4	14·0	14	1·00	0·017	37·2	42	0·1	2·0
July 7	19·0	61·2	nil	0·2	13·0	14	0·93	0·015	50·2	56	0·1	2·2
,, 21	19·1	63·0	0·1	1·8	12·1	14	0·86	0·014	62·3	70	0·2	4·0
Aug. 6	19·2	62·2	0·1	− 0·8	12·4	16	0·77	0·012	74·7	86	0·3	3·2
,, 21	19·2	61·0	nil	− 1·2	12·5	15	0·83	0·013	87·2	101	0·3	2·0
Sept. 5	19·2	60·1	nil	− 0·9	12·0	15	0·80	0·013	99·2	116	0·3	1·1
,, 19	19·2	61·8	nil	1·7	17·5	14	1·25	0·020	116·7	130	0·3	2·8
Oct. 6	19·3	62·8	0·1	1·0	18·5	17	1·09	0·016	135·2	147	0·4	3·8
,, 22	19·4	62·8	0·1	nil	15·0	16	0·94	0·015	150·2	163	0·5	3·8
Nov. 6	19·3	62·5	− 0·1	− 0·3	7·5	15	0·50	0·008	157·7	178	0·4	3·5

TABLE 5 : C5.

May 26	21·2	86·7	—	—	—	—	—	—	—	—	—	—
June 9	21·3	86·5	0·1	− 0·2	13·8	14	0·99	0·011	13·8	14	0·1	− 0·2
,, 23	21·4	87·5	0·1	1·0	13·8	14	0·99	0·011	27·6	28	0·2	0·8
July 7	21·4	88·2	nil	0·7	13·0	14	0·93	0·011	40·6	42	0·2	1·5
,, 21	21·4	89·0	nil	0·8	12·3	14	0·88	0·010	52·9	56	0·2	2·3
Aug. 6	21·4	86·5	nil	− 2·5	13·4	16	0·84	0·010	66·3	72	0·2	− 0·2
,, 21	21·4	87·2	nil	0·7	13·5	15	0·90	0·010	79·8	87	0·2	0·5
Sept. 5	21·5	85·2	0·1	− 2·0	13·0	15	0·87	0·010	92·8	102	0·3	− 1·5
,, 19	21·4	84·3	− 0·1	− 0·9	15·5	14	1·11	0·013	108·3	116	0·2	− 2·4
Oct. 6	21·5	85·6	0·1	1·3	19·0	17	1·12	0·013	127·3	133	0·3	− 1·1
,, 22	21·5	85·6	nil	nil	16·0	16	1·00	0·012	143·3	149	0·3	− 1·1
Nov. 6	21·5	85·4	nil	− 0·2	13·0	15	0·87	0·010	156·3	164	0·3	− 1·3

TABLE 6 : C6.

June 12	23·0	115·0	—	—	—	—	—	—	—	—	—	—
,, 23	23·0	113·0	nil	− 2·0	14·7	11	1·34	0·012	14·7	11	nil	− 2·0
July 7	23·0	112·8	nil	− 0·2	19·5	14	1·39	0·012	34·2	25	nil	− 2·2
,, 21	22·8	115·0	− 0·2	2·2	19·8	14	1·41	0·012	54·0	39	− 0·2	nil
Aug. 6	22·7	113·2	− 0·1	− 1·8	19·8	16	1·24	0·011	73·8	55	− 0·3	− 1·8
,, 21	22·8	113·2	0·1	nil	19·0	15	1·27	0·011	92·8	70	− 0·2	− 1·8
Sept. 5	22·7	110·0	− 0·1	− 3·2	18·5	15	1·23	0·011	111·3	85	− 0·3	− 5·0
,, 19	22·8	109·5	0·1	− 0·5	25·0	14	1·79	0·016	136·3	99	− 0·2	− 5·5
Oct. 6	22·7	109·8	− 0·1	0·3	27·7	17	1·63	0·015	164·0	116	− 0·3	− 5·2
,, 22	22·8	112·5	0·1	2·7	25·2	16	1·57	0·014	189·2	132	− 0·2	− 2·5
Nov. 6	22·8	111·1	nil	− 1·4	19·3	15	1·29	0·012	208·5	147	− 0·2	− 3·9

TABLE 7.

SUMMARISED DATA CONCERNING THE MAINTENANCE REQUIREMENTS OF THE MALE PLAICE, C1–C6.

Fish No.	Initial size. Lth. cm.	Initial size. Wt. gm.	Final size. Lth. cm.	Final size. Wt. gm.	Growth. Lth. cm.	Growth. Wt. gm.	Days in period.	Average weight of food per day. (gm.)	Ratio Food per day/ /mid body-weight per period.
C1	13·1	21·5	13·4	20·8	0·3	—0·7	144	0·46	0·022
C2	15·3	31·5	16·2	35·9	0·9	4·4	176	0·49	0·015
C3	16·9	45·0	17·4	43·0	0·5	—2·0	162	0·64	0·015
C4	18·9	59·0	19·3	62·5	0·4	3·5	178	0·89	0·015
C5	21·2	86·7	21·5	85·4	0·3	—1·3	164	0·95	0·011
C6	23·0	115·0	22·8	111·1	—0·2	—3·9	147	1·42	0·013

TABLES 8–13.

Data Obtained from the Experiments on the Maintenance Requirements of Female Plaice.

Table 8 : A5.

Date (1930)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth.	
	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)							Lth. (cm.)	Wt. (gm.)
June 16	12·2	17·3	—	—	—	—	—	—	—	—	—	—
,, 23	12·4	17·8	0·2	0·5	3·5	7	0·50	0·029	3·5	7	0·2	0·5
July 7	12·6	19·0	0·2	1·2	8·0	14	0·57	0·031	11·5	21	0·4	1·7
,, 21	12·8	20·0	0·2	1·0	6·6	14	0·47	0·025	18·1	35	0·6	2·7
Aug. 6	12·9	20·5	0·1	0·5	7·5	16	0·47	0·023	25·6	51	0·7	3·2
,, 21	13·0	21·2	0·1	0·7	6·6	15	0·44	0·021	32·2	66	0·8	3·9
Sept. 5	13·2	20·6	0·2	− 0·6	6·0	15	0·40	0·019	38·2	81	1·0	3·3
,, 19	13·2	21·8	nil	1·2	5·5	14	0·39	0·018	43·7	95	1·0	4·5
Oct. 6	13·3	22·3	0·1	0·5	8·0	17	0·47	0·021	51·7	112	1·1	5·0
,, 22	13·3	22·3	nil	nil	5·5	16	0·34	0·015	57·2	128	1·1	5·0
Nov. 6	13·3	22·0	nil	− 0·3	5·0	15	0·33	0·015	62·2	143	1·1	4·7

Table 9 : A6 (a and b).

May 14	15·6	33·0	—	—	—	—	—	—	—	—	—	—
,, 26	15·5	31·8	− 0·1	− 1·2	6·3	12	0·52	0·016	6·3	12	− 0·1	− 1·2
June 9	15·5	30·8	nil	− 1·0	6·3	14	0·45	0·014	12·6	26	− 0·1	− 2·2
,, 23	15·5	30·1	nil	− 0·7	3·9	14	0·28	0·009	16·5	40	− 0·1	− 2·9
July 7	15·5	29·1	nil	− 1·0	6·2	14	0·44	0·015	22·7	54	− 0·1	− 3·9
,, 21	15·3	28·0	− 0·2	− 1·1	1·0	14	0·04	—	23·7	68	− 0·3	− 5·0
Aug. 6	15·3	27·0	nil	− 1·0	5·2	16	0·32	0·012	28·9	84	− 0·3	− 6·0
Aug. 22	15·2	35·0	—	—	—	—	—	—	—	—	—	—
Sept. 5	15·2	34·2	nil	− 0·8	3·5	15	0·24	0·007	3·5	15	nil	− 0·8
,, 19	15·2	32·3	nil	− 1·9	4·6	14	0·33	0·010	8·1	29	nil	− 2·7
Oct. 6	15·2	31·5	nil	− 0·8	5·6	17	0·33	0·010	13·7	46	nil	− 3·5
,, 22	15·2	30·2	nil	− 1·3	4·9	16	0·31	0·010	18·6	62	nil	− 4·8
Nov. 6	15·2	30·1	nil	− 0·1	7·6	15	0·51	0·017	26·2	77	nil	− 4·9

Table 10 : A2.

June 11	17·3	49·0	—	—	—	—	—	—	—	—	—	—
,, 23	17·3	46·8	nil	− 2·2	9·0	12	0·75	0·016	9·0	12	nil	− 2·2
July 7	17·5	50·8	0·2	4·0	11·0	14	0·79	0·016	20·0	26	0·2	1·8
,, 21	17·5	52·0	nil	1·2	9·0	14	0·64	0·012	29·0	40	0·2	3·0
Aug. 6	17·6	51·0	0·1	− 1·0	9·5	16	0·59	0·011	38·5	56	0·3	2·0
,, 21	17·6	52·0	nil	1·0	10·0	15	0·67	0·013	48·5	71	0·3	3·0
Sept. 5	17·6	49·4	nil	− 2·6	10·0	15	0·67	0·013	58·5	86	0·3	0·4
,, 19	17·6	52·2	nil	2·8	11·5	14	0·82	0·016	70·0	100	0·3	3·2
Oct. 6	17·6	53·5	nil	1·3	14·0	17	0·82	0·016	84·0	117	0·3	4·5
,, 22	17·7	53·1	0·1	− 0·4	11·0	16	0·69	0·013	95·0	133	0·4	4·1
Nov. 6	17·7	53·0	nil	− 0·1	7·0	15	0·47	0·009	102·0	148	0·4	4·0

Table 11 : A4.

Date (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 12	19·8	71·0	—	—	—	—	—	—	—	—	—	—
,, 26	19·8	67·7	nil	– 33	12·0	14	0·86	0·012	12·0	14	nil	– 3·3
June 9	19·9	67·9	0·1	0·2	11·7	14	0·84	0·012	23·7	28	0·1	– 3·1
,, 23	20·0	67·8	0·1	– 0·1	11·7	14	0·84	0·012	35·4	42	0·2	– 3·2
July 7	20·1	67·7	0·1	– 0·1	13·0	14	0·93	0·014	48 4	56	0·3	– 3·3
,, 21	20·1	68·0	nil	0·3	13·0	14	0·93	0·014	61·4	70	0·3	– 3·0
Aug. 6	20·2	68·5	0·1	0·5	14·5	16	0·91	0·013	75·9	86	0·4	– 2·5
,, 21	20·2	66·5	nil	– 2·0	13·0	15	0·87	0·013	88·9	101	0·4	– 4·5
Sept. 5	20·4	66·3	0·2	– 0·2	13·5	15	0·90	0·014	102·4	116	0·6	– 4·7
,, 19	20·2	66·4	– 0·2	0·1	13·5	14	0·96	0·014	115·9	130	0·4	– 4·6
Oct. 6	20·3	68·6	0·1	2·2	16·3	17	0·96	0·014	132·2	147	0·5	– 2·4
,, 22	20·4	68·8	0·1	0·2	14·5	16	0·91	0·013	146·7	163	0·6	– 2·2
Nov. 6	20·2	68·3	– 0·2	– 0·5	8·3	15	0·55	0·008	155·0	178	0·4	– 2·7

Table 12 : A3.

June 12	22·0	101·5	—	—	—	—	—	—	—	—	—	—
,, 23	22·0	97·5	nil	– 4·0	13·0	11	1·18	0·012	13·0	11	nil	– 4·0
July 7	22·0	97·9	nil	0·4	17·5	14	1·25	0·013	30·5	25	nil	– 3·6
,, 21	21·9	100·0	– 0·1	2·1	17·0	14	1·21	0·012	47·6	39	– 0·1	– 1·5
Aug. 6	22·0	97·0	0·1	– 3·0	18·5	16	1·16	0·012	66·0	55	nil	– 4·5
,, 21	22·0	96·0	nil	– 1·0	17·5	15	1·17	0·012	83·5	70	nil	– 5·5
Sept. 5	22·2	93·5	0·2	– 2·5	17·0	15	1·13	0·012	100·5	85	0·2	– 8·0
,, 19	21·8	95·6	– 0·4	2·1	20·0	14	1·43	0·015	120·5	99	– 0·2	– 5·9
Oct. 6	21·9	96·8	0·1	1·2	24·5	17	1·44	0·015	145·0	116	– 0·1	– 4·7
,, 22	22·0	96·3	0·1	– 0·5	20·6	16	1·29	0·013	165·6	132	nil	– 5·2
Nov. 6	22·0	95·2	nil	– 1·1	13·0	15	0·87	0·009	178·6	147	nil	– 6·3

Table 13 : A1.

May 12	24·5	132·0	—	—	—	—	—	—	—	—	—	—
,, 26	24·6	133·8	0·1	1·8	13·7	14	0·98	0·007	13·7	14	0·1	1·8
June 9	24·6	132·0	nil	– 1·8	19·0	14	1·36	0·010	32·7	28	0·1	nil
,, 23	24·6	134·0	nil	2·0	21·0	14	1·50	0·011	53·7	42	0·1	2·0
July 7	24·6	133·2	nil	– 0·8	18·5	14	1·32	0·010	72·2	56	0·1	1·2
,, 21	24·6	138·0	nil	4·8	18·5	14	1·32	0·010	90·7	70	0·1	6·0
Aug. 6	24·8	136·0	0·2	– 2·0	20·0	16	1·25	0·009	110·7	86	0·3	4·0
,, 21	24·7	136·0	– 0·1	nil	19·0	15	1·27	0·009	129·7	101	0·2	4·0
Sept. 5	24·7	136·2	nil	0·2	18·5	15	1·23	0·009	148·2	116	0·2	4·2
,, 19	24·7	135·5	nil	– 0·7	18·5	14	1·32	0·010	166·7	130	0·2	3·5
Oct. 6	24·7	140·4	nil	4·9	21·5	17	1·26	0·009	188·2	147	0·2	8·4
,, 22	24·8	140·8	0·1	0·4	20·0	16	1·25	0·009	208·2	163	0·3	8·8
Nov. 6	24·7	136·9	– 0·1	– 3·9	13·0	15	0·87	0·006	221·2	178	0·2	4·9

TABLE 14.

Summarised Data Concerning the Maintenance Requirements of the Female Plaice, A1–A6.

Fish No.	Initial size. Lth. (cm.)	Initial size. Wt. (gm.)	Final size. Lth. (cm.)	Final size. Wt. (gm.)	Growth. Lth. (cm.)	Growth. Wt. (gm.)	Days in period.	Average weight of food per day. (gm.)	Ratio Food per day/ /mid body-weight per period.
A5	12·2	17·3	13·3	22·0	1·1	4·7	143	0·43	0·022
A6a	15·6	33·0	15·3	27·0	—0·3	—6·0	84	0·34	0·011
b	15·2	35·0	15·2	30·1	nil	—4·9	77	0·34	0·010
A2	17·3	49·0	17·7	53·0	0·4	4·0	148	0·69	0·014
A4	19·8	71·0	20·2	68·3	0·4	—2·7	178	0·87	0·012
A3	22·0	101·5	22·0	95·2	nil	—6·3	147	1·21	0·012
A1	24·5	132·0	24·7	136·9	0·2	4·9	178	1·24	0·009

TABLE 15.

SUMMARISED DATA CONCERNING MAXIMUM REQUIREMENTS AND GROWTH IN MALE AND FEMALE PLAICE.

Fish No.	Sex.	Initial size.		Final size.		Growth.		Period.		Days in Period.	Total food per the period. (gm.)	Average weight of food per day for the period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.
		Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	From	To				
D1	♂	15·0	35·8	19·2	77·1	4·2	41·3	28 : 5	6 : 11	162	475	3·0	11·5
D2	♂	13·5	22·0	17·4	52·1	3·9	30·1	12 : 5	6 : 11	178	358	2·0	11·9
D3	♂	14·0	26·5	17·4	51·0	3·4	24·5	12 : 5	5 : 9	116	250	2·2	10·2
D4	♂	13·5	23·0	16·4	44·5	2·9	21·5	12 : 5	5 : 9	116	196	1·7	9·1
D5	♂	14·6	31·7	16·8	47·2	2·2	15·5	9 : 6	5 : 9	88	159	1·8	10·3
D6	♂	13·1	18·2	15·1	33·0	2·0	14·8	29 : 5	5 : 9	99	159	1·6	10·7
B1	♀	14·7	26·7	18·0	55·7	3·3	29·0	17 : 6	6 : 11	142	331	2·3	11·4
B2	♀	15·5	30·5	18·2	64·1	2·7	33·6	17 : 6	6 : 11	142	352	2·5	10·5
B3	♀	12·9	19·7	17·3	50·3	4·4	30·6	26 : 5	6 : 11	165	296	1·8	9·7
B5	♀	15·5	34·5	19·2	82·5	3·7	48·0	26 : 5	21 : 8	87	308	3·5	8·5

TABLES 16–21.

Maximum Requirements and Growth of Male Plaice.

Table 16 : D1.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 28	15·0	35·8	0·011	—	—	—	—	—	—	—	—	—	—
June 9	16·2	46·0	0·011	1·2	10·2	43·3	4·2	12	3·61	28·5	43	1·2	10·2
,, 23	17·0	51·3	0·010	0·8	5·3	57·1	10·8	14	4·08	11·5	100	2·0	15·5
July 7	17·3	52·5	0·010	0·3	1·2	35·3	29·4	14	2·52	2·3	136	2·3	16·7
,, 21	17·6	58·0	0·011	0·3	5·5	40·0	7·3	14	2·86	10·5	176	2·6	22·2
Aug. 6	17·8	57·7	0·010	0·2	− 0·3	38·6	—	16	2·41	—	214	2·8	21·9
,, 21	18·1	60·5	0·010	0·3	2·8	32·2	11·5	15	2·15	5·0	246	3·1	24·7
Sept. 5	18·3	60·8	0·010	0·2	0·3	41·1	137·0	15	2·74	0·5	288	3·3	25·0
,, 20	18·4	64·3	0·010	0·1	3·5	39·7	11·3	15	2·65	5·8	327	3·4	28·5
Oct. 6	18·8	70·0	0·011	0·4	5·7	54·1	9·5	16	3·38	8·9	381	3·8	34·2
,, 22	19·1	72·2	0·011	0·3	2·2	44·8	20·4	16	2·80	3·1	426	4·1	36·4
Nov. 6	19·2	77·1	0·011	0·1	4·9	48·5	9·9	15	3·23	6·8	475	4·2	41·3

Table 17 : D2.

May 12	13·5	22·0	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	13·5	22·7	0·009	nil	0·7	14·0	20·0	14	1·00	3·2	14	nil	0·7
June 9	14·3	29·7	0·010	0·8	7·0	30·2	4·3	14	2·16	30·8	44	0·8	7·7
,, 23	15·0	33·0	0·010	0·7	3·3	36·0	10·9	14	2·58	11·1	80	1·5	11·0
July 7	15·3	35·2	0·010	0·3	2·2	26·8	12·2	14	1·91	6·7	107	1·8	13·2
,, 21	15·7	39·0	0·010	0·4	3·8	32·7	8·6	14	2·34	10·8	140	2·2	17·0
Aug. 6	16·1	43·2	0·010	0·4	4·2	42·2	10·0	16	2·64	10·8	182	2·6	21·2
,, 21	16·6	46·5	0·010	0·5	3·3	34·0	10·3	15	2·27	7·6	216	3·1	24·5
Sept. 5	16·7	47·0	0·010	0·1	0·5	31·4	62·8	15	2·09	1·1	247	3·2	25·0
,, 20	16·9	46·9	0·010	0·2	− 0·1	16·8	—	15	1·12	—	264	3·4	24·9
Oct. 6	17·1	52·4	0·010	0·2	5·5	35·0	6·4	16	2·19	11·7	299	3·6	30·4
,, 22	17·3	53·0	0·010	0·2	0·6	29·0	48·3	16	1·81	1·1	328	3·8	31·0
Nov. 6	17·4	52·1	0·010	0·1	− 0·9	29·7	—	15	1·98	—	358	3·9	30·1

Table 18 : D3.

May 12	14·0	26·5	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	14·0	25·0	0·009	nil	− 1·5	9·3	—	14	0·66	—	9	nil	− 1·5
June 9	14·4	28·5	0·010	0·4	3·5	24·6	7·0	14	1·76	14·0	34	0·4	2·0
,, 23	14·9	33·3	0·010	0·5	4·8	39·1	8·1	14	2·80	16·8	73	0·9	6·8
July 7	15·5	38·4	0·010	0·6	5·1	34·5	6·8	14	2·46	15·3	107	1·5	11·9
,, 21	16·3	49·0	0·011	0·8	10·6	44·8	4·2	14	3·20	27·6	152	2·3	22·5
Aug. 6	17·0	53·5	0·011	0·7	4·5	48·7	10·8	16	3·04	9·2	201	3·0	27·0
,, 21	17·4	54·5	0·011	0·4	1·0	32·9	32·9	15	2·19	1·9	234	3·4	28·0
Sept. 5	17·4	51·0	0·010	nil	− 3·5	16·4	—	15	1·09	—	250	3·4	24·5

TABLE 19: D4.

Date (1930)	Size of fish. Lth. (cm.)	Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Wt. (gm.)
May 12	13·5	23·0	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	13·5	21·5	0·009	nil	−1·5	11·4	—	14	0·81	—	11	nil	−1·5
June 9	13·7	25·8	0·010	0·2	4·3	19·0	4·4	14	1·36	20·0	30	0·2	2·8
,, 23	14·0	27·0	0·010	0·3	1·2	20·9	17·4	14	1·49	4·6	51	0·5	4·0
July 7	14·3	29·8	0·010	0·3	2·8	21·3	7·6	14	1·52	10·4	73	0·8	6·8
,, 21	14·8	33·5	0·010	0·5	3·7	26·9	7·3	14	1·92	12·4	99	1·3	10·5
Aug. 6	15·5	39·7	0·010	0·7	6·2	35·6	5·7	16	2·22	18·5	135	2·0	16·7
,, 21	16·0	42·0	0·010	0·5	2·3	30·5	13·3	15	2·03	5·8	166	2·5	19·0
Sept. 5	16·4	44·5	0·010	0·4	2·5	30·3	12·1	15	2·02	6·0	196	2·9	21·5

TABLE 20: D5.

June 9	14·6	31·7	0·010	—	—	—	—	—	—	—	—	—	—
,, 23	15·0	33·2	0·010	0·4	1·5	21·9	14·6	14	1·56	4·7	22	0·4	1·5
July 7	15·4	34·8	0·010	0·4	1·6	18·9	11·8	14	1·35	4·8	41	0·8	3·1
,, 21	15·6	38·0	0·010	0·2	3·2	20·8	6·5	14	1·49	9·2	62	1·0	6·3
Aug. 6	16·0	41·0	0·010	0·4	3·0	34·3	11·4	16	2·14	8·0	96	1·4	9·3
,, 21	16·4	42·5	0·010	0·4	1·5	29·4	19·6	15	1·96	3·7	125	1·8	10·8
Sept. 5	16·8	47·2	0·010	0·4	4·7	34·1	7·3	15	2·27	11·1	159	2·2	15·5

TABLE 21: D6.

May 29	13·1	18·2	0·008	—	—	—	—	—	—	—	—	—	—
June 9	13·2	19·3	0·008	0·1	1·1	15·9	14·5	11	1·45	6·0	16	0·1	1·1
,, 23	13·4	20·5	0·009	0·2	1·2	22·6	18·8	14	1·61	6·2	38	0·3	2·3
July 7	13·7	21·6	0·008	0·3	1·1	16·5	15·0	14	1·18	5·3	55	0·6	3·4
,, 21	13·8	24·0	0·009	0·1	2·4	17·1	7·1	14	1·22	11·1	72	0·7	5·8
Aug. 6	14·3	26·0	0·009	0·5	2·0	31·8	15·9	16	1·99	8·3	104	1·2	7·8
,, 21	14·6	28·5	0·009	0·3	2·5	22·8	9·1	15	1·52	9·6	127	1·5	10·3
Sept. 5	15·1	33·0	0·010	0·5	4·5	32·4	7·2	15	2·16	15·8	159	2·0	14·8

TABLES 22–27.

Maximum Requirements and Growth of Female Plaice.

Table 22 : B1.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
June 17	14·7	26·7	0·008	—	—	—	—	—	—	—	—	—	—
,, 23	14·8	28·5	0·009	0·1	1·8	8·4	4·7	6	1·40	6·7	8	0·1	1·8
July 7	15·3	34·4	0·010	0·5	5·9	40·1	6·8	14	2·86	20·7	48	0·6	7·7
,, 21	15·8	43·0	0·011	0·5	8·6	40·2	4·7	14	2·87	25·0	89	1·1	16·3
Aug. 6	16·7	51·0	0·011	0·9	8·0	49·9	6·2	16	3·12	18·6	139	2·0	24·3
,, 21	17·4	58·5	0·011	0·7	7·5	52·2	7·0	15	3·48	14·7	191	2·7	31·8
Sept. 5	17·8	58·9	0·010	0·4	0·4	34·6	86·5	15	2·31	0·7	225	3·1	32·2
,, 20	17·9	59·5	0·010	0·1	0·6	30·1	50·2	15	2·01	1·0	255	3·2	32·8
Oct. 6	18·0	61·6	0·011	0·1	2·1	34·8	16·6	16	2·17	3·5	290	3·3	34·9
,, 22	18·1	55·7	0·010	0·1	− 5·9	19·2	—	16	1·20	—	309	3·4	29·0
Nov. 6	18·0	55·7	0·010	− 0·1	nil	21·6	—	15	1·4	—	331	3·3	29·0

Table 23 : B2.

June 17	15·5	30·5	0·008	—	—	—	—	—	—	—	—	—	—
,, 23	15·5	30·0	0 008	nil	− 0·5	3·8	—	6	0·63	—	4	nil	− 0·5
July 7	15·6	32·2	0·008	0·1	2·2	18·5	8·4	14	1·32	6·7	22	0·1	1·7
,, 21	16·1	42·5	0·010	0·5	10·3	49·9	4·8	14	3·56	32·0	72	0·6	12·0
Aug. 6	16·7	48·3	0·010	0·6	5·8	50·9	8·8	16	3·18	13·6	123	1·2	17·8
,, 21	17·2	54·5	0·011	0·5	6·2	46·5	7·5	15	3·10	12·8	170	1·7	24·0
Sept. 5	17·5	55·8	0·010	0·3	1·3	40·0	30·8	15	2·67	2·4	210	2·0	25·3
,, 20	17·4	60·4	0·011	− 0·1	4·6	42·1	9·2	15	2·81	8·2	252	1·9	29·9
Oct. 6	18·0	63·5	0·011	0·6	3·1	43·1	13·9	16	2·69	5·1	295	2·5	33·0
,, 22	18·2	63·7	0·011	0·2	0·2	28·4	142·0	16	1·77	0·3	323	2·7	33·2
Nov. 6	18·2	64·1	0·011	nil	0·4	28·9	72·2	15	1·93	0·6	352	2·7	33·6

Table 24 : B3.

May 26	12·9	19·7	0·009	—	—	—	—	—	—	—	—	—	—
June 9	13·5	24·1	0·010	0·6	4·4	29·1	6·6	14	2·08	22·3	29	0·6	4·4
,, 23	14·7	30·0	0·009	1·2	5·9	31·6	5·4	14	2·26	24·5	61	1·8	10·3
July 7	15·3	35·3	0·010	0·6	5·3	34·4	6·5	14	2·46	17·7	95	2·4	15·6
,, 21	15·5	36·5	0·010	0·2	1·2	18·2	15·2	14	1·30	3·4	113	2·6	16·8
Aug. 6	15·9	38·8	0·010	0·4	2·3	28·9	12·6	16	1·81	6·3	142	3·0	19·1
,, 21	16·3	42·0	0·010	0·4	3·2	28·7	9·0	15	1·91	8·2	171	3·4	22·3
Sept. 5	16·5	43·8	0·010	0·2	1·8	26·2	14·6	15	1·75	4·3	197	3·6	24·1
,, 20	—	—								x			
Oct. 6	17·2	48·4	0·010	0·7	4·6	49·8	10·8	32	1·56	x	247	4·3	28·7
,, 22	17·4	49·7	0·009	0·2	1·3	23·8	18·3	16	1·49	2·7	271	4·5	30·0
Nov. 6	17·3	50·3	0·010	− 0·1	0·6	25·1	41·8	15	1·67	1·2	296	4·4	30·6

Table 25 : B5.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (c.m.)	Cumulative growth. Wt. (gm)
May 26	15·5	34·5	0·009	—	—	—	—	—	—	—	—	—	—
June 9	15·9	42·5	0·011	0·4	8·0	38·7	4·8	14	2·76	23·2	39	0·4	8·0
,, 23	16·9	53·0	0·011	1·0	10·5	64·5	6·1	14	4·61	24·7	103	1·4	18·5
July 7	17·8	64·0	0·011	0·9	11·0	61·5	5·6	14	4·39	20·8	165	2·3	29·5
,, 21	18·1	69·0	0·012	0·3	5·0	41·5	8·3	14	2·96	7·8	206	2·6	34·5
Aug. 6	18·6	73·8	0·012	0·5	4·8	44·3	9·2	16	2·77	7·0	250	3·1	39·3
,, 21	19·2	82·5	0·012	0·6	8·7	47·8	5·5	15	3·12	1·2	298	3·7	48·0

Table 26 : B4.

May 26	12·3	17·2	0·009	—	—	—	—	—	—	—	—	—	—
June 9	13·0	22·4	0·010	0·7	5·2	26·6	5·1	14	1·90	30·2	27	0·7	5·2
,, 23	14·1	29·2	0·010	1·1	6·8	39·1	5·7	14	2·79	30·4	66	1·8	12·0
July 7	15·1	37·0	0·011	1·0	7·8	42·4	5·4	14	3·03	26·7	108	2·8	19·8
,, 21	15·9	42·0	0·010	0·8	5·0	38·3	7·7	14	2·74	13·5	146	3·6	24·8
Aug. 6	16·5	45·7	0·010	0·6	3·7	37·9	10·2	16	2·37	8·8	184	4·2	28·5
,, 21	16·5	47·5	0·011	nil	1·8	16·4	9·1	15	1·09	3·9	201	4·2	30·3
Sept. 5	16·5	43·8	0·010	nil	−3·7	11·3	—	15	0·75	—	212	4·2	26·6
,, 20	16·4	44·3	0·010	−0·1	0·5	11·3	22·6	15	0·75	1·1	232	4·1	27·1
Oct. 6	16·6	39·1	0·009	0·2	−5·2	32·7	—	16	2·04	—	256	4·3	21·9

Table 27 : B6.

May 12	14·3	27·5	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	14·4	28·0	0·009	0·1	0·5	14·5	29·0	14	1·04	1·8	14	0·1	0·5
June 9	14·5	31·3	0·010	0·1	3·3	26·3	8·0	14	1·88	11·8	41	0·2	3·8
,, 23	15·0	34·0	0·010	0·5	2·7	31·5	11·7	14	2·25	8·6	72	0·7	6·5
July 7	15·2	37·2	0·011	0·2	3·2	27·7	8·7	14	1·98	9·4	100	0·9	9·7
,, 21	15·7	42·5	0·011	0·5	5·3	31·8	6·0	14	2·28	14·3	132	1·4	15·0
Aug. 6	16·2	46·0	0·011	0·5	3·5	35·9	10·3	16	2·24	8·2	168	1·9	18·5
,, 21	16·4	48·5	0·011	0·2	2·5	24·0	9·6	15	1·60	5·4	192	2·1	21·0
Sept. 5	16·5	48·2	0·011	0·1	−0·3	27·6	—	15	1·84	—	219	2·2	20·7
,, 20	16·4	45·6	0·010	−0·1	−2·6	13·8	—	15	0·92	—	233	2·1	18·1

TABLE 28.

Summarised Data Concerning Maximum Requirements and Growth in Male and Female (M) Plaice.

Fish No.	Sex.	Initial size.		Final size.		Growth.		Period.		Days in Period.	Total food per the period. (gm.)	Average weight of food per day for the period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.
		Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	From	To				
M1	♂	15·4	34·0	21·3	117·7	5·9	83·7	12 : 5	6 : 11	178	987	5·5	11·8
M2	♂	15·0	33·7	19·6	79·7	4·6	46·0	2 : 6	6 : 11	157	655	4·1	14·7
M3	♀	15·0	35·0	19·4	82·4	4·4	47·4	14 : 5	6 : 11	176	900	5·1	19·0
M4	♀	13·4	23·3	17·6	59·2	4·2	35·9	14 : 5	6 : 11	176	778	4·4	21·7

TABLES 29 AND 30.

MAXIMUM REQUIREMENTS AND GROWTH OF MALE (M) PLAICE.

TABLE 29 : M1.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 12	15·4	34·0	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	15·8	41·5	0·009	0·4	7·5	50·2	6·7	14	3·6	22·1	50	0·4	7·5
June 9	16·8	49·8	0·010	1·0	8·3	64·1	7·7	14	4·6	20·0	114	1·4	15·8
,, 23	17·0	50·7	0·010	0·2	0·9	65·6	72·9	14	4·7	1·8	180	1·6	16·7
July 7	17·5	61·0	0·011	0·5	10·3	157·6	15·3	14	11·2	20·3	337	2·1	27·0
,, 21	17·9	65·0	0·011	0·4	4·0	81·4	20·4	14	5·8	6·6	419	2·5	31·0
Aug. 6	18·5	74·0	0·012	0·6	9·0	76·4	8·5	16	4·8	13·8	495	3·1	40·0
,, 21	19·3	85·0	0·012	0·8	11·0	82·5	7·5	15	5·5	14·9	578	3·9	51·0
Sept. 20	20·0	89·6	0·011	0·7	4·6	142·5	31·0	30	4·7	2x	720	4·6	55·6
Oct. 6	20·4	102·2	0·012	0·4	12·6	92·0	7·3	16	5·8	14·1	812	5·0	68·2
,, 23	20·7	102·0	0·012	0·3	−0·2	91·0	—	17	5·4	—	903	5·3	68·0
Nov. 6	21·3	117·7	0·012	0·6	15·7	84·0	5·4	14	6·0	15·4	987	5·9	83·7

TABLE 30 : M2.

June 2	15·0	33·7	0·010	—	—	—	—	—	—	—	—	—	—
,, 9	15·0	31·9	0·009	nil	−1·8	15·7	—	7	2·2	—	16	nil	−1·8
,, 23	15·1	33·4	0·010	0·1	1·5	38·2	25·4	14	2·7	4·7	54	0·1	−0·3
July 7	15·5	36·0	0·010	0·4	2·6	66·3	25·5	14	4·7	7·8	120	0·5	2·3
,, 21	15·7	40·0	0·010	0·2	4·0	56·7	14·2	14	4·1	11·1	177	0·7	6·3
Aug. 6	16·4	44·7	0·010	0·7	4·7	69·2	14·7	16	4·3	11·7	246	1·4	11·0
,, 21	16·9	49·0	0·010	0·5	4·3	60·0	14·0	15	4·0	9·2	306	1·9	15·3
Sept. 20	17·8	57·4	0·010	0·9	8·4	111·8	13·3	30	3·7	2x	418	2·8	23·7
Oct. 6	18·3	62·2	0·010	0·5	4·8	86·4	−18·0	16	5·4	−8·4	504	3·3	28·5
,, 23	19·0	71·4	0·010	0·7	9·2	78·0	8·5	17	4·6	14·8	582	4·0	37·7
Nov. 6	19·6	79·7	0·011	0·6	8·3	72·0	8·7	14	5·1	11·6	654	4·6	46·0

TABLES 31 AND 32.

MAXIMUM REQUIREMENTS AND GROWTH OF FEMALE (M) PLAICE.

TABLE 31 : M3.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 14	15·0	35·0	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	15·1	34·8	0·010	0·1	– 0·2	36·0	—	12	3·0	—	36	0·1	– 0·2
June 9	15·5	39·8	0·011	0·4	5·0	55·7	11·1	14	4·0	14·4	92	0·5	4·8
,, 23	16·4	48·8	0·011	0·9	9·0	75·6	8·4	14	5·4	22·6	167	1·4	13·8
July 7	16·8	51·2	0·011	0·4	2·4	153·9	64·1	14	11·0	4·9	321	1·8	16·2
,, 21	17·2	59·0	0·011	0·4	7·8	83·9	10·8	14	6·0	15·2	405	2·2	24·0
Aug. 6	17·6	61·0	0·011	0·4	2·0	73·7	36·8	16	4·6	3·4	479	2·6	26·0
,, 21	18·0	65·0	0·011	0·4	4·0	63·5	15·9	15	4·2	6·6	542	3·0	30·0
Sept. 20	18·6	69·6	0·011	0·6	4·6	119·3	25·9	30	4·0	2x	662	3·6	34·6
Oct. 6	18·8	74·0	0·011	0·2	4·4	88 –	20·0	16	5·5	6·3	750	3·8	39·0
,, 23	19·0	76·2	0·011	0·2	2·2	78·0	35·5	17	4·6	3·0	828	4·0	41·2
Nov. 6	19·4	82·4	0·011	0·4	6·2	72·0	11·6	14	5·1	8·1	900	4·4	47·4

TABLE 32 : M4.

May 14	13·4	23·3	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	13·6	25·2	0·010	0·2	1·9	39·0	20·5	12	3·2	8·1	39	0·2	1·9
June 9	14·2	28·0	0·010	0·6	2·8	57·4	20·5	14	4·1	11·1	96	0·8	4·7
,, 23	14·3	28·7	0·010	0·1	0·7	72·3	103·3	14	5·2	2·5	169	0·9	5·4
July 7	14·7	31·8	0·010	0·4	3·1	70·6	22·8	14	5·0	10·8	239	1·3	8·5
,, 21	15·0	36·5	0·010	0·3	4·7	54·5	11·6	14	3·9	14·8	294	1·6	13·2
Aug. 6	15·1	36·0	0·010	0·1	– 0·5	60·4	—	16	3·8	—	354	1·7	12·7
,, 21	15·8	44·2	0·010	0·7	8·2	68·5	8·4	15	4·6	22·8	423	2·4	20·9
Sept. 20	16·8	50·6	0·011	1·0	6·4	117·5	18·4	30	3·9	2x	540	3·4	27·3
Oct. 6	17·0	52·6	0·011	0·2	2·0	87·5 –	43·7	16	5·5	4·0	628	3·6	29·3
,, 23	17·3	54·2	0·011	0·3	1·6	78·0	48·7	17	4·6	3·0	706	3·9	30·9
Nov. 6	17·6	59·2	0·011	0·3	5·0	72·8	14·6	14	5·2	9·2	778	4·2	35·9

TABLE 33.

Summarised Data Concerning Growth and Intermediate Food Supplies in Male and Female (I) Plaice.

Fish No.	Sex.	Initial size.		Final size.		Growth.		Period.		Days in Period.	Total food per the period. (gm.)	Average weight of food per day for the period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.
		Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	From	To				
I1	♂	15·7	33·7	19·2	65·7	3·5	32·0	13 : 6	6 : 11	146	217	1·5	6·8
I2	♂	15·0	32·0	17·6	56·0	2·6	24·0	12 : 5	6 : 11	178	252	1·4	10·5
I3	♀	12·8	20·3	17·6	59·5	4·8	39·2	14 : 5	6 : 11	176	247	1·4	6·3
I4	♀	14·9	32·0	18·3	67·4	3·4	35·4	18 : 6	6 : 11	141	208	1·5	5·9

TABLES 34 AND 35.

INTERMEDIATE RATIONS AND GROWTH OF MALE (I) PLAICE.

TABLE 34 : I1.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
June 13	15·7	33·7	0·009	—	—	—	—	—	—	—	—	—	—
,, 23	15·9	36·3	0·009	0·2	2·6	12·8	4·9	10	1·28	7·7	13	0·2	2·6
July 7	16·3	39·3	0·009	0·4	3·0	14·0	4·7	14	1·00	8·3	27	0·6	5·6
,, 21	16·5	43·5	0·009	0·2	4·2	17·6	4·2	14	1·26	10·7	44	0·8	9·8
Aug. 6	17·1	48·0	0·009	0·6	4·5	26·0	5·8	16	1·62	10·3	70	1·4	14·3
,, 21	17·7	52·0	0·009	0·6	4·0	24·0	6·0	15	1·60	8·3	94	2·0	18·3
Sept. 19	18·2	57·6	0·010	0·5	5·6	48·0	8·6	29	1·66	2x	142	2·5	23·9
Oct. 6	18·8	64·3	0·010	0·6	6·7	32·0	4·8	17	1·88	11·6	174	3·1	30·6
,, 23	19·1	64·7	0·010	0·3	0·4	25·0	62·5	17	1·47	0·6	199	3·4	31·0
Nov. 6	19·2	65·7	0·010	0·1	1·0	18·0	18·0	14	1·29	1·5	217	3·5	32·0

TABLE 35 : I2.

May 12	15·0	32·0	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	15·2	33·7	0·009	0·2	1·7	14·7	8·6	14	1·05	5·3	15	0·2	1·7
June 9	15·2	31·0	0·009	nil	− 2·7	13·8	—	14	0·99	—	28	0·2	− 1·0
,, 23	15·9	38·8	0·010	0·7	7·8	13·7	1·8	14	0·98	25·1	42	0·9	6·8
July 7	16·2	39·8	0·010	0·3	1·0	14·0	14·0	14	1·00	2·6	56	1·2	7·8
,, 21	16·2	42·0	0·010	nil	2·2	16·3	7·4	14	1·16	5·5	72	1·2	10·0
Aug. 6	16·3	44·0	0·010	0·1	2·0	26·0	13·0	16	1·62	5·0	98	1·3	12·0
,, 21	16·6	46·8	0·010	0·3	2·8	23·5	8·4	15	1·57	6·4	122	1·6	14·8
Sept. 19	17·1	51·0	0·010	0·5	4·2	48·0	11·4	29	1·70	2x	170	2·1	19·0
Oct. 6	17·4	54·6	0·010	0·3	3·6	32·0	8·9	17	1·88	7·1	202	2·4	22·6
,, 23	17·6	55·4	0·010	0·2	0·8	25·6	32·0	17	1·51	1·5	228	2·6	23·4
Nov. 6	17·6	56·0	0·010	nil	0·6	24·2	40·3	14	1·73	1·1	252	2·6	24·0

TABLES 36 AND 37.

INTERMEDIATE RATIONS AND GROWTH OF FEMALE (I) PLAICE.

TABLE 36 : I3.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 14	12·8	20·3	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	12·8	21·3	0·010	nil	1·0	10·9	10·9	12	0·91	4·9	11	nil	1·0
June 9	13·2	23·5	0·010	0·4	2·2	11·2	5·1	14	0·80	10·3	22	0·4	3·2
,, 23	13·7	26·0	0·010	0·5	2·5	11·2	4·5	14	0·80	10·6	33	0·9	5·7
July 7	13·9	28·0	0·010	0·2	2·0	11·2	5·6	14	0·80	7·7	44	1·1	7·7
,, 21	14·4	32·5	0·011	0·5	4·5	17·0	3·8	14	1·21	16·1	61	1·6	12·2
Aug. 6	15·0	37·8	0·011	0·6	5·3	26·0	4·9	16	1·62	16·3	87	2·2	17·5
,, 21	15·7	43·0	0·011	0·7	5·2	23·5	4·5	15	1·57	13·8	111	2·9	22·7
Sept. 19	16·6	50·0	0·011	0·9	7·0	48·0	6·9	29	1·66	2x	159	3·8	29·7
Oct. 6	17·1	56·1	0·011	0·5	6·1	32·0	5·2	17	1·88	12·2	191	4·3	35·8
,, 23	17·5	58·8	0·011	0·4	2·7	28·3	10·5	17	1·70	4·8	219	4·7	38·5
Nov. 6	17·6	59·5	0·011	0·1	0·7	28·0	40·0	14	2·00	1·2	247	4·8	39·2

TABLE 37 : I4.

June 18	14·9	32·0	0·010	—	—	—	—	—	—	—	—	—	—
,, 23	14·9	30·9	0·010	nil	− 1·1	1·7	—	5	0·34	—	2	nil	− 1·1
July 7	15·1	34·0	0·010	0·2	3·1	13·9	4·5	14	0·99	10·0	16	0·2	2·0
,, 21	15·4	39·5	0·010	0·3	5·5	17·3	3·1	14	1·24	16·2	33	0·5	7·5
Aug. 6	15·9	42·0	0·010	0·5	2·5	26·0	10·4	16	1·62	6·3	59	1·0	10·0
,, 21	16·5	48·0	0·010	0·6	6·0	24·0	4·0	15	1·60	14·3	83	1·6	16·0
Sept. 19	17·2	55·3	0·011	0·7	7·3	48·0	6·6	29	1·66	2x	131	2·3	23·3
Oct. 6	17·7	62·7	0·011	0·5	7·4	30·3	4·1	17	1·78	13·4	161	2·8	30·7
,, 23	18·1	65·3	0·011	0·4	2·6	28·2	10·8	17	1·66	4·1	189	3·2	33·3
Nov. 6	18·3	67·4	0·011	0·2	2·1	18·5	8·8	14	1·32	3·2	208	3·4	35·4

TABLES 38–41.

Data from January–April Experiments on Maintenance (Lympstone).

Table 38 : L1w (♂).

Date (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth. Lth. (cm.	Cumulative growth. Wt. (gm.)
Jan. 6	17·6	52·8	—	—	—	—	—	—	—	—	—	—
,, 20	17·6	50·5	nil	− 2·3	5·7	14	0·41	0·008	5·7	14	nil	− 2·3
Feb. 3	17·6	50·2	nil	− 0·3	6·1	14	0·44	0·009	11·8	28	nil	− 2·6
,, 17	17·6	50·9	nil	0·7	8·5	14	0·61	0·012	21·3	42	nil	− 1·9
Mar. 3	17·7	51·8	0·1	0·9	12·6	14	0·90	0·018	33·9	56	0·1	− 1·0
,, 17	17·6	51·0	− 0·1	− 0·8	9·8	14	0·70	0·014	43·7	70	nil	− 1·8
,, 31	17·7	51·8	0·1	0·8	10·5	14	0·75	0·015	54·2	84	0·1	− 1·0
April 14	17·7	52·8	nil	1·0	10·5	14	0·75	0·014	64·7	98	0·1	nil
,, 28	17·7	51·6	nil	− 1·2	10·1	14	0·72	0·014	74·8	112	0·1	− 1·2

Table 39 : L4w (♂).

Jan. 6	21·1	78·8	—	—	—	—	—	—	—	—	—	—
,, 20	21·1	76·9	nil	− 1·9	10·9	14	0·78	0·010	10·9	14	nil	− 1·9
Feb. 3	21·1	77·6	nil	0·7	10·8	14	0·77	0·010	21·7	28	nil	− 1·2
,, 17	21·1	79·4	nil	1·8	13·6	14	0·97	0·011	35·3	42	nil	0·6
Mar. 3	21·2	79·3	nil	− 0·1	15·6	14	1·11	0·014	50·9	56	nil	0·5
,, 17	21·1	81·3	nil	2·0	15·4	14	1·10	0·014	64·3	70	nil	2·5
,, 31	21·1	79·6	nil	− 1·7	13·5	14	0·96	0·012	79·8	84	nil	0·8
April 14	20·9	81·8	− 0·2	2·2	15·4	14	1·10	0·014	95·2	98	− 0·2	3·0
,, 28	20·9	79·0	nil	− 2·8	14·3	14	1·02	0·013	109·5	112	− 0·2	0·2

Table 40 : L5w (♀).

Jan. 6	18·9	69·8	—	—	—	—	—	—	—	—	—	—
,, 20	18·9	69·6	nil	− 0·2	9·0	14	0·64	0·009	9·0	14	nil	− 0·2
Feb. 3	19·0	69·8	0·1	0·2	6·0	14	0·43	0·006	15·0	28	0·1	nil
,, 17	19·0	73·1	nil	3·3	16·1	14	1·15	0·016	31·1	42	0·1	3·3
Mar. 3	19·2	75·9	0·2	2·8	18·0	14	1·29	0·017	49·1	56	0·3	6·1
,, 17	19·5	76·3	0·3	0·4	14·0	14	1·00	0·013	63·1	70	0·6	6·5
,, 31	19·7	77·9	0·2	1·6	13·1	14	0·93	0·012	76·1	84	0·8	8·1
April 14	19·9	79·1	0·2	1·2	10·4	14	0·75	0·010	86·6	98	1·0	9·3
,, 28	20·0	78·2	0·1	− 0·9	9·9	14	0·71	0·009	96·5	112	1·1	8·4

Table 41 : L7w (♀).

Jan. 6	22·7	103·4	—	—	—	—	—	—	—	—	—	—
,, 20	22·7	101·2	nil	− 2·2	13·5	14	0·96	0·009	13·5	14	nil	− 2·2
Feb. 3	22·7	101·1	nil	− 0·1	12·0	14	0·86	0·009	25·5	28	nil	− 2·3
,, 17	22·7	102·4	nil	1·3	8·9	14	0·64	0·006	34·4	42	nil	− 1·0
Mar. 3	22·7	101·5	nil	− 0·9	11·4	14	0·81	0·008	45·8	56	nil	− 1·9
,, 17	22·7	100·2	nil	− 1·3	10·3	14	0·74	0·007	56·1	70	nil	− 3·2
,, 31	22·7	99·9	nil	− 0·3	11·4	14	0·81	0·008	67·5	84	nil	− 3·5
April 14	22·7	100·4	nil	0·5	11·9	14	0·85	0·008	79·4	98	nil	− 3·0
,, 28	22·7	97·6	nil	− 2·8	11·8	14	0·84	0·009	91·2	112	nil	− 5·8

TABLE 42.

SUMMARISED DATA CONCERNING MAINTENANCE REQUIREMENTS OF MALE AND FEMALE PLAICE DURING 1929 AND 1930 (JAN.–APRIL), (PARTLY FROM MY PREVIOUS PAPER).

Fish No.	Sex.	Initial size. Lth. (cm.)	Initial size. Wt. (gm.)	Final size. Lth. (cm.)	Final size. Wt. (gm.)	Growth. Lth. (cm.)	Growth. Wt. (gm.)	Period. From	Period. To	No. of days in period.	Average quantity of food per day for period.	Ratio Food per day/ /mid body-weight for period.	Year.
L1	♂	17·0	50·3	17·6	54·1	0·6	3·8	22 : 8	25 : 11	95	0·90	0·017	1929
		17·6	52·8	17·7	51·6	0·1	—1·2	6 : 1	28 : 4	112	0·58	0·011	1930
L4b	♂	20·8	75·1	21·0	76·9	0·2	1·8	30 : 9	25 : 11	56	1·11	0·015	1929
		21·1	78·8	20·9	79·0	—0·2	0·2	6 : 1	28 : 4	112	0·98	0·012	1930
L5	♀	18·5	62·8	18·6	66·9	0·1	4·1	8 : 8	25 : 11	109	0·88	0·014	1929
		18·9	69·8	20·0	78·2	1·1	8·4	6 : 1	28 : 4	112	0·86	0·012	1930
L7	♀	22·3	104·8	22·7	100·6	0·4	—4·3	4 : 9	25 : 11	82	1·32	0·013	1929
		22·7	103·4	22·7	97·6	nil	—5·8	6 : 1	28 : 4	112	0·81	0·008	1930

TABLE 43.

SUMMARISED DATA SHOWING MAINTENANCE REQUIREMENTS DURING JANUARY–APRIL OF MALE AND FEMALE, "MINIMUM-FED" AND "MAXIMUM-FED" PLAICE.

Fish No.	Sex.	Initial size. Lth. (c.m)	Initial size. Wt. (gm.)	Final size. Lth. (cm.)	Final size. Wt. (gm.)	Growth. Lth. (cm.)	Growth. Wt. (gm.)	Period From	Period To	No. of days in period.	Average quantity of food per day for period.	Ratio Food per day/ /mid body-weight for period.	
L1w	♂	17·6	52·8	17·7	51·8	0·1	—1·0	6 : 1	3 : 3	56	0·61	0·012	MINIMUM FISH.
L4w	♂	21·1	78·8	21·1	79·3	nil	0·5	6 : 1	3 : 3	56	0·91	0·012	
L5w	♀	18·9	69·8	19·2	75·9	0·3	6·1	6 : 1	3 : 3	56	0·88	0·012	
L7w	♀	22·7	103·4	22·7	101·5	nil	—1·9	6 : 1	3 : 3	56	0·67	0·007	
L10w	♂	23·1	117·2	23·1	112·5	nil	—4·7	6 : 1	3 : 3	56	0·02	0·000	MAXIMUM FISH.
L12w	♂	22·0	105·3	22·0	101·7	nil	—3·6	6 : 1	3 : 3	56	0·01	0·000	
L13w	♀	19·2	68·3	19·2	66·3	nil	—2·0	6 : 1	3 : 3	56	0·02	0·000	
L15w	♀	23·1	132·7	23·2	130·3	0·1	—2·4	6 : 1	3 : 3	56	0·02	0·000	

TABLES 44–47.

Maximum Requirements of Male and Female Plaice (Jan.–April).

Table 44 : L10w (♂).

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.³	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
Jan. 6	23·1	117·2	0·010	—	—	—	—	—	—	—	—	—	—
,, 20	23·1	112·5	0·009	nil	− 4·7	7·0	—	14	0·50	—	7	nil	− 4·7
Feb. 3	23·1	111·0	0·009	nil	− 1·5	1·2	—	14	0·09	—	8	nil	− 6·2
,, 17	23·1	110·2	0·009	nil	− 0·8	1·5	—	14	0·11	—	10	nil	− 7·0
Mar. 3	23·1	112·5	0·009	nil	2·3	12·3	5·3	14	0·88	2·1	22	nil	− 4·7
,, 17	23·3	118·0	0·009	0·2	5·5	37·4	6·8	14	2·67	4·9	59	0·2	0·8
,, 31	23·5	123·8	0·009	0·2	5·8	46·4	8·0	14	3·31	4·9	106	0·4	6·6
April 14	23·7	129·3	0·009	0·2	5·5	55·6	10·1	14	3·97	4·4	162	0·6	12·1
,, 28	23·7	128·2	0·009	nil	− 1·1	62·5	—	14	4·46	—	224	0·6	11·0

Table 45 : L12w (♂).

Jan. 6	22·0	105·3	0·010	—	—	—	—	—	—	—	—	—	—
,, 20	22·0	102·1	0·010	nil	− 3·2	0·1	—	14	0·01	—	nil	nil	− 3·2
Feb. 3	22·0	100·4	0·009	nil	− 1·7	0·1	—	14	0·01	—	nil	nil	− 4·9
,, 17	22·0	100·0	0·009	nil	− 0·4	0·4	—	14	0·03	—	1	nil	− 5·3
Mar. 3	22·0	101·7	0·010	nil	1·7	10·5	6·2	14	0·75	1·7	11	nil	− 3·6
,, 17	22·0	103·7	0·010	nil	2·0	37·9	16·9	14	2·71	2·0	49	nil	− 1·6
,, 31	22·0	103·6	0·010	nil	− 0·1	15·8	—	14	1·13	—	65	nil	− 1·7
April 14	22·0	103·0	0·010	nil	− 0·6	17·3	—	14	1·24	—	82	nil	− 2·3
,, 28	22·3	111·5	0·010	0·3	8·5	27·3	3·2	14	1·95	8·2	109	0·3	6·2

Table 46 : L13w (♀).

Jan. 6	19·2	68·3	0·010	—	—	—	—	—	—	—	—	—	—
,, 20	19·2	66·3	0·009	nil	− 2·0	0·9	—	14	0·06	—	1	nil	− 2·0
Feb. 3	19·2	65·0	0·009	nil	− 1·3	1·0	—	14	0·07	—	2	nil	− 3·3
,, 17	19·2	64·0	0·009	nil	− 1·0	1·8	—	14	0·13	—	4	nil	− 4·3
Mar. 3	19·2	66·3	0·009	nil	2·3	12·6*	5·5	14	0·90	3·6	16	nil	− 2·0
,, 17	19·3	71·5	0·010	0·1	5·2	35·1	6·7	14	2·51	7·8	51	0·1	3·2
,, 31	19·5	74·0	0·010	0·2	2·5	40·1	16·1	14	2·87	3·5	92	0·3	5·7
April 14	19·5	75·5	0·010	nil	1·5	42·9	28·6	14	3·06	2·0	135	0·3	7·2
,, 28	19·8	80·8	0·010	0·3	5·3	47·5	9·0	14	3·39	7·0	182	0·6	12·5

Table 47 : L15w (♀).

Jan. 6	23·1	132·7	0·011	—	—	—	—	—	—	—	—	—	—
,, 20	23·1	129·5	0·011	nil	− 3·2	3·0	—	14	0·21	—	3	nil	− 3·2
Feb. 3	23·2	128·0	0·010	0·1	− 1·5	0·9	—	14	0·06	—	4	0·1	− 4·7
,, 17	23·2	126·0	0·010	nil	− 2·0	1·2	—	14	0·09	—	5	0·1	− 6·7
Mar. 3	23·2	130·3	0·010	nil	4·3	12·5†	2·9	14	0·89	3·4	18	0·1	− 2·4
,, 17	23·5	135·1	0·010	0·3	4·8	39·4	8·2	14	2·81	3·7	57	0·4	2·4
,, 31	23·5	138·8	0·011	nil	3·7	45·1	12·2	14	3·22	2·7	102	0·4	6·1
April 14	23·5	152·4	0·012	nil	13·6	43·6	3·2	14	3·11	9·8	146	0·4	19·7
,, 28	23·7	128·8	0·010	0·2	− 23·6‡	46·6	—	14	3·33	—	192	0·6	− 3·9

* May be 10·3. 1 daily ration of doubtful value. † May be 10·4. See footnotes to Table 46.
‡ Spawned during this period.

TABLES 48–51.

Maintenance Requirements of Male Plaice.

Table 48 : L1.

Date (1930)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth.	
	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)							Lth. (cm.)	Wt (gm.)
May 12	17·9	62·2	—	—	—	—	—	—	—	—	—	—
,, 26	18·0	59·5	0·1	− 2·7	6·5	14	0·47	0·008	6·5	14	0·1	− 2·7
June 9	18·0	59·9	nil	0·4	9·9	14	0·71	0·012	16·4	28	0·1	− 2·3
,, 23	18·0	59·3	nil	− 0·6	9·9	14	0·71	0·012	26·3	42	0·1	− 2·9
July 7	18·0	59·0	nil	− 0·3	10·6	14	0·76	0·013	36·9	56	0·1	− 3·2
,, 21	18·0	57·3	nil	− 1·7	10·6	14	0·76	0·013	47·5	70	0·1	− 4·9
Aug. 4	18·0	57·7	nil	0·4	12·4	14	0·89	0·015	59·9	84	0·1	− 4·5
,, 18	18·0	58·0	nil	0·3	12·2	14	0·87	0·015	72·1	98	0·1	− 4·2
Sept. 1	18·0	56·5	nil	− 1·5	11·6	14	0·83	0·015	83·7	112	0·1	− 5·7
,, 15	18·0	56·8	nil	0·3	19·7	14	1·41	0·025	103·4	126	0·1	− 5·4
,, 29	18·1	57·1	0·1	0·3	12·7	14	0·91	0·016	116·1	140	0·2	− 5·1
Oct. 13	18·1	56·1	nil	− 1·0	12·6	14	0·90	0·016	128·7	154	0·2	− 6·1
,, 27	18·1	55·9	nil	− 0·2	13·7	14	0·98	0·017	142·4	168	0·2	− 6·3
Nov. 10	18·1	57·5	nil	1·6	13·9	14	0·98	0·017	156·3	182	0·2	− 4·7
,, 24	18·1	59·2	nil	1·7	12·3	14	0·88	0·015	168·6	196	0·2	− 3·0

Table 49 : L2.

May 26	20·0	65·0	—	—	—	—	—	—	—	—	—	—
June 9	20·0	64·8	nil	− 0·2	11·9	14	0·85	0·013	20·2	14	nil	− 0·2
,, 23	20·0	64·3	nil	− 0·5	11·9	14	0·85	0·013	32·1	28	nil	− 0·7
July 7	20·0	62·2	nil	− 2·1	12·6	14	0·90	0·014	44·7	42	nil	− 2·8
,, 21	20·0	60·1	nil	− 2·1	14·2	14	1·01	0·017	58·9	56	nil	− 4·9
Aug. 4	20·0	60·2	nil	0·1	17·1	14	1·22	0·020	76·0	70	nil	− 4·8
,, 18	20·0	61·2	nil	1·0	16·9	14	1·21	0·020	92·9	84	nil	− 3·8
Sept. 1	20·0	60·0	nil	− 1·2	16·0	14	1·14	0·019	108·9	98	nil	− 5·0
,, 15	20·2	62·6	0·2	2·6	25·8	14	1·84	0·028	134·7	112	0·2	− 2·4
,, 29	20·2	63·8	nil	1·2	14·2	14	1·02	0·016	148·9	126	0·2	− 1·2
Oct. 13	20·2	65·1	nil	1·3	12·9	14	0·92	0·014	161·8	140	0·2	0·1
,, 27	20·2	69·5	nil	4·4	11·6	14	0·83	0·012	173·4	154	0·2	4·5
Nov. 10	20·2	70·3	nil	0·8	7·3	14	0·52	0·008	180·7	168	0·2	5·3
,, 24	20·2	70·1	nil	− 0·2	6·6	14	0·47	0·007	187·3	182	0·2	5·1

TABLE 50 : L3.

Date (1930)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth.	
	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)							Lth. (cm.)	Wt. (gm.)
May 12	21·5	90·3	—	—	—	—	—	—	—	—	—	—
,, 26	21·5	83·5	nil	− 6·8	5·4	14	0·39	0·004	5·4	14	nil	− 6·8
June 9	21·5	82·4	nil	− 1·1	12·5	14	0·89	0·011	17·9	28	nil	− 7·9
,, 23	21·5	81·1	nil	− 1·3	15·1	14	1·08	0·013	33·0	42	nil	− 9·2
July 7	21·5	81·1	nil	nil	16·5	14	1·18	0·014	49·5	56	nil	− 9·2
,, 21	21·5	79·1	nil	− 2·0	16·5	14	1·18	0·014	66·0	70	nil	− 11·2
Aug. 4	21·5	79·8	nil	0·7	18·5	14	1·32	0·017	84·5	84	nil	− 10·5
,, 18	21·5	78·7	nil	− 1·1	17·9	14	1·28	0·016	102·4	98	nil	− 11·6
Sept. 1	21·5	77·8	nil	− 0·9	18·0	14	1·29	0·017	120·4	112	nil	− 12·5
,, 15	21·5	77·5	nil	− 0·3	21·2	14	1·51	0·019	141·6	126	nil	− 12·8
,, 29	21·6	74·4	0·1	− 3·1	14·4	14	1·03	0·014	156·0	140	0·1	− 15·9
Oct. 13	21·6	75·1	nil	0·7	14·8	14	1·06	0·014	170·8	154	0·1	− 15·2
,, 27	21·6	75·5	nil	0·4	14·1	14	1·01	0·013	184·9	168	0·1	− 14·8
Nov. 10	21·6	76·3	nil	0·8	12·6	14	0·90	0·014	197·5	182	0·1	− 14·0
,, 24	21·6	78·6	nil	2·3	11·8	14	0·84	0·011	209·3	196	0·1	− 11·7

TABLE 51 : L4 (a and b).

(a)												
May 12	18·5	65·5	—	—	—	—	—	—	—	—	—	—
,, 26	18·5	64·8	nil	− 0·7	7·6	14	0·54	0·009	7·6	14	nil	− 0·7
June 9	18·5	63·8	nil	− 1·0	8·7	14	0·62	0·010	16·3	28	nil	− 1·7
,, 23	18·5	62·2	nil	− 1·6	9·9	14	0·71	0·011	26·2	42	nil	− 3·3
July 7	18·5	62·1	nil	− 0·1	11·5	14	0·82	0·013	37·7	56	nil	− 3·4
,, 21	18·5	62·5	nil	0·4	11·5	14	0·82	0·013	49·2	70	nil	− 3·0
Aug. 4	18·6	64·6	0·1	2·1	12·0	14	0·86	0·014	61·2	84	0·1	− 0·9
,, 18	18·6	63·5	nil	− 1·1	9·9	14	0·71	0·011	71·1	98	0·1	− 2·0
Sept. 1	18·7	63·0	0·1	− 0·5	11·1	14	0·79	0·012	82·2	112	0·2	− 2·5
(b)												
Sept. 15	24·4	149·6	—	—	—	—	—	—	—	—	—	—
,, 29	24·4	142·8	nil	− 6·8	9·4	14	0·67	0·005	9·4	14	nil	− 6·8
Oct. 13	24·4	145·1	nil	2·3	15·4	14	1·10	0·008	24·8	28	nil	− 4·5
,, 27	24·4	147·2	nil	2·1	13·2	14	0·94	0·006	38·0	42	nil	− 2·4
Nov. 10	24·6	147·2	0·2	nil	12·2	14	0·87	0·006	50·2	56	0·2	− 2·4
,, 24	24·7	149·5	0·1	2·3	12·3	14	0·88	0·006	62·5	70	0·3	− 0·1

TABLE 52.

SUMMARISED DATA: MAINTENANCE REQUIREMENTS OF MALE PLAICE.

Fish No.	Initial size. Lth. (cm.)	Initial size. Wt. (gm.)	Final size. Lth. (cm.)	Final size. Wt. (gm.)	Growth. Lth. (cm.)	Growth. Wt. (gm.)	Days in period.	Average weight of food per day. (gm.)	Ratio Food per day/ /mid body-weight for period.
L1	17·9	62·2	18·1	57·5	0·2	−4·7	182	0·86	0·015
L2	20·0	65·0	20·2	70·3	0·2	5·3	168	1·03	0·015
L3	21·5	90·3	21·6	76·3	0·1	−14·0	182	1·09	0·013
L4 (a)	18·5	65·5	18·7	63·0	0·2	−2·5	112	0·74	0·012
L4 (b)	24·4	149·6	24·6	147·2	0·2	−2·4	56	0·89	0·006

TABLES 53–56.

Maintenance Requirements of Female Plaice.

Table 53 : L5.

Date (1930)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth.	
	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)							Lth. (cm.)	Wt. (gm.)
May 12	14·7	28·9	—	—	—	—	—	—	—	—	—	—
,, 26	14·7	28·6	nil	− 0·3	5·2	14	0·37	0·013	5·2	14	nil	− 0·3
June 9	14·7	27·8	nil	− 0·8	7·0	14	0·50	0·018	12·2	28	nil	− 1·1
,, 23	14·7	26·6	nil	− 1·2	7·8	14	0·56	0·021	20·0	42	nil	− 2·3
July 7	14·7	25·7	nil	− 0·9	9·9	14	0·71	0·027	29·9	56	nil	− 3·2
,, 21	14·7	25·3	nil	− 0·4	11·5	14	0·82	0·032	41·4	70	nil	− 3·6
Aug. 4	14·7	25·7	nil	0·4	12·0	14	0·86	0·034	53·4	84	nil	− 3·2
,, 18	14·7	25·9	nil	0·2	11·8	14	0·84	0·033	65·2	98	nil	− 3·0
Sept. 1	14·7	26·0	nil	0·1	11·6	14	0·83	0·032	76·8	112	nil	− 2·9
,, 15	14·7	26·1	nil	0·1	16·2	14	1·16	0·045	93·0	126	nil	− 2·8
,, 29	14·7	25·8	nil	− 0·3	11·0	14	0·79	0·031	104·0	140	nil	− 3·1
Oct. 13	14·7	27·7	nil	1·9	14·2	14	1·01	0·038	118·2	154	nil	− 1·2
,, 27	14·8	28·7	0·1	1·0	12·3	14	0·88	0·034	130·5	168	0·1	− 0·2
Nov. 10	14·8	29·1	nil	0·4	11·2	14	0·80	0·028	141·7	182	0·1	0·2
,, 24	14·9	31·3	0·1	2·2	10·9	14	0·78	0·026	152·6	196	0·2	2·4

Table 54 : L6 (a and b).

(a)												
May 12	18·0	69·9	—	—	—	—	—	—	—	—	—	—
,, 26	18·0	62·9	nil	− 7·0	6·1	14	0·44	0·007	6·1	14	nil	− 7·0
June 9	18·0	61·3	nil	− 1·6	10·7	14	0·76	0·012	16·8	28	nil	− 8·6
,, 23	18·0	59·8	nil	− 1·5	11·8	14	0·84	0·014	28·6	42	nil	− 10·1
July 7	18·0	61·1	nil	1·3	14·0	14	1·00	0·017	42·6	56	nil	− 8·8
,, 21	18·0	62·2	nil	1·1	12·4	14	0·89	0·013	55·0	70	nil	− 7·7
Aug. 4	18·0	63·8	nil	1·6	12·0	14	0·86	0·014	67·0	84	nil	− 6·1
,, 18	18·0	65·3	nil	1·5	10·5	14	0·75	0·012	77·5	98	nil	− 4·6
Sept. 1	18·0	64·6	nil	− 0·7	7·5	14	0·54	0·008	85·0	112	nil	− 5·3
(b)												
Sept. 29	17·3	56·2	—	—	—	—	—	—	—	—	—	—
Oct. 13	17·4	60·2	0·1	4·0	8·5	14	0·61	0·010	85	14	0·1	4·0
,, 27	17·6	64·3	0·2	4·1	4·6	14	0·33	0·005	13·1	28	0·3	8·1
Nov. 10	17·7	64·9	0·1	0·6	0·5	14	0·03	—	13·6	42	0·4	8·7
,, 24	17·8	67·7	0·1	2·8	3·0	14	0·21	0·003	16·6	56	0·5	11·5

Table 55: L7.

Date (1930)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Ratio of food per day/ /average body-wt. for period.	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Cumulative growth.	
	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)							Lth. (cm.)	Wt. (gm.)
June 23	18·0	58·5	—	—	—	—	—	—	—	—	—	—
July 7	18·1	57·1	0·1	− 1·4	11·2	14	0·80	0·014	11·2	14	0·1	− 1·4
„ 21	18·1	57·4	nil	0·3	12·6	14	0·90	0·016	23·8	28	0·1	− 1·1
Aug. 4	18·1	58·1	nil	0·7	12·6	14	0·90	0·016	36·4	42	0·1	− 0·4
„ 18	18·1	57·9	nil	− 0·2	9·9	14	0·71	0·012	46·3	56	0·1	− 0·6
Sept. 1	18·1	57·8	nil	− 0·1	10·1	14	0·72	0·012	56·4	70	0·1	− 0·7
„ 15	18·1	59·2	nil	1·4	19·4	14	1·39	0·024	75·8	84	0·1	0·7
„ 29	18·2	59·2	0·1	nil	8·8	14	0·63	0·011	84·6	98	0·2	0·7
Oct. 13	18·2	59·2	nil	nil	8·1	14	0·58	0·010	92·7	112	0·2	0·7
„ 27	18·2	60·2	nil	1·0	8·1	14	0·58	0·010	100·8	126	0·2	1·7
Nov. 10	18·2	60·4	nil	0·2	7·1	14	0·51	0·008	107·9	140	0·2	1·9
„ 24	18·2	61·0	nil	0·6	7·0	14	0·50	0·008	114·9	154	0·2	2·5

Table 56: L8.

May 12	18·8	56·8	—	—	—	—	—	—	—	—	—	—
„ 26	18·8	56·8	nil	nil	7·9	14	0·56	0·010	7·9	14	nil	nil
June 9	18·8	50·9	nil	− 5·9	8·7	14	0·62	0·012	16·6	28	nil	− 5·9
„ 23	18·8	51·3	nil	0·4	14·8	14	1·06	0·021	31·4	42	nil	− 5·5
July 7	18·8	50·8	nil	− 0·5	14·6	14	1·04	0·020	46·0	56	nil	− 6·0
„ 21	18·8	52·5	nil	1·7	15·1	14	1·08	0·021	61·1	70	nil	− 4·3
Aug. 4	18·8	52·6	nil	0·1	13·4	14	0·96	0·018	74·5	84	nil	− 4·2
„ 18	18·8	53·0	nil	0·4	13·4	14	0·96	0·018	87·9	98	nil	− 3·8
Sept. 1	18·8	53·0	nil	nil	13·0	14	0·93	0·018	100·9	112	nil	− 3·8
„ 15	18·8	54·7	nil	1·7	19·3	14	1·38	0·026	120·2	126	nil	− 2·1
„ 29	18·9	55·1	0·1	0·4	11·2	14	0·80	0·014	131·3	140	0·1	− 1·7
Oct. 13	18·9	55·1	nil	nil	8·7	14	0·62	0·011	140·9	154	0·1	− 1·7
„ 27	18·9	55·1	nil	nil	8·7	14	0·62	0·011	148·7	168	0·1	− 1·7
Nov. 10	18·9	55·8	nil	0·7	8·7	14	0·62	0·011	157·4	182	0·1	− 1·0
„ 24	18·9	57·8	nil	2·0	8·0	14	0·57	0·010	165·4	196	0·1	1·0

TABLE 57.

SUMMARISED DATA : MAINTENANCE REQUIREMENTS OF FEMALE PLAICE.

Fish No.	Initial size. Lth. (cm.)	Initial size. Wt. (gm.)	Final size. Lth. (cm.)	Final size. Wt. (gm.)	Growth. Lth. (cm.)	Growth. Wt. (gm.)	Days in period.	Average weight of food per day. (gm.)	Ratio Food per day/ /mid body-weight per period.
L5	14·7	28·9	14·8	29·1	0·1	0·2	182	0·78	0·027
L6 (a)	18·0	69·9	18·0	64·6	nil	—5·3	112	0·76	0·011
L6 (b)	17·3	56·2	17·7	64·9	0·4	8·7	42	0·32	0·005
L7	18·0	58·5	18·2	60·4	0·2	1·9	140	0·77	0·013
L8	18·8	56·8	18·9	55·8	0·1	—1·0	182	0·86	0·015

TABLE 58.

Summarised Data: Maximum Requirements and Growth of Male and Female Plaice.

Fish No.	Sex.	Initial size.		Final size.		Growth.		Period.		Days in Period.	Total food per the period. (gm.)	Average weight of food per day for the period (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.
		Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	Lth. (cm.)	Wt. (gm.)	From	To				
L9 a	♂	18·4	67·4	18·9	78·3	0·5	10·9	12 : 5	23 : 6	42	126	3·0	11·6
L9 b		21·2	92·5	22·1	104·5	0·9	12·0	27 : 6	10 : 11	136	545	4·0	45·4
L10 a	♂	17·2	55·6	17·7	56·9	0·5	1·3	12 : 5	4 : 8	84	242	2·9	186·1
L10 b		21·4	73·9	23·1	127·7	1·7	53·8	4 : 8	10 : 11	98	515	5·3	9·6
L11 a	♂	21·8	101·2	22·7	118·8	0·9	17·6	12 : 5	1 : 9	112	469	4·2	26·6
L11 b		22·6	120·1	23·8	160·8	1·2	40·7	29 : 9	10 : 11	42	267	6·4	6·5
L12 a	♂	19·3	75·1	21·3	105·6	2·0	30·5	12 : 5	1 : 9	112	471	4·2	15·4
L12 b		20·3	86·8	20·8	102·7	0·5	15·9	29 : 9	10 : 11	42	175	4·2	11·0
L13	♀	20·0	73·7	22·0	114·6	2·0	40·9	12 : 5	10 : 11	182	819	4·5	20·0
L14 a	♀	17·0	50·5	20·6	97·8	3·6	47·3	12 : 5	1 : 9	112	546	4·9	11·5
L14 b		25·1	173·2	26·1	205·3	1·0	32·1	15 : 9	10 : 11	56	409	7·3	12·7
L15	♀	20·1	75·7	22·1	115·7	2·0	40·0	12 : 5	10 : 11	182	896	4·9	22·4
L16 a	♀	19·5	79·0	20·7	102·8	1·2	23·8	12 : 5	23 : 6	42	209	5·0	8·8
L16 b		20·8	104·9	24·5	192·8	3·7	87·9	7 : 6	10 : 11	126	827	6·6	9·4

TABLES 59–62.

Maximum Requirements and Growth of Male Plaice.

Table 59 : L9 (a and b).

Date. (1930)	Size of fish. Lth. (cm.)	Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Wt. (gm.)
(a)													
May 12	18·4	67·4	0·011	—	—	—	—	—	—	—	—	—	—
,, 26	18·5	69·0	0·011	0·1	1·6	21·1	13·2	14	1·51	2·4	21	0·1	1·6
June 9	18·8	77·6	0·012	0·3	8·6	63·2	7·3	14	4·51	12·5	84	0·4	10·2
,, 23	18·9	78·3	0·012	0·1	0·7	42 0	60·0	14	3·00	0·9	126	0·5	10·9
(b)													
June 27	21·2	92·5	0·010	—	—	—	—	—	—	—	—	—	—
July 7	21·3	92·6	0·010	0·1	0·1	48·0	480·0	10	4·80	0·1	48	0·1	0·1
,, 21	21·5	94·8	0·010	0·2	2·2	63·1	28·7	14	4·51	2·4	111	0·3	2·3
Aug. 4	21·2	96·6	0·010	– 0·3	1·8	56·9	31·6	14	4·06	1·9	168	nil	4·1
,, 18	21·7	101·2	0·010	0·5	4·6	60·9	13·2	14	4·35	4·8	229	0·5	8·7
Sept. 1	21·8	101·1	0·010	0·1	– 0·1	61·6	—	14	4·40	—	290	0·6	8·6
,, 15	21·9	95·9	0·009	0·1	– 5·2	38·2	—	14	2·73	—	329	0·7	3·4
,, 29	22·0	100·5	0·010	0·1	4·6	50·7	11·0	14	3·62	4·8	379	0·8	8·0
Oct. 13	22·0	103·8	0·010	nil	3·3	66·4	20·1	14	4·74	3·3	446	0·8	11·3
,, 27	22·1	108·1	0·010	0·1	4·3	59·1	13·7	14	4·22	4·1	505	0·9	15·6
Nov. 10	22·1	104·5	0·010	nil	– 3·6	40·5	—	14	2·89	—	545	0·9	12·0
,, 24	22·1	104·6	0·010	nil	0·1	20·1	201·0	14	1·44	0·1	565	0·9	12·1

Table 60 : L10 (a and b).

Date. (1930)	Size of fish. Lth. (cm.)	Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Wt. (gm.)
(a)													
May 12	17·2	55·6	0·011	—	—	—	—	—	—	—	—	—	—
,, 26	17·2	53·8	0·011	nil	– 1·8	28·8	—	14	2·06	—	29	nil	– 1·8
June 9	17·4	57·7	0·011	0·2	3·9	65·5	16·8	14	4·68	7·2	94	0·2	2·1
,, 23	17·7	60·0	0·011	0·3	2·3	45·5	19·8	14	3·25	4·0	140	0·5	4·4
July 7	17·7	60·7	0·011	nil	0·7	41·9	59·9	14	2·99	1·2	182	0·5	5·1
,, 21	17·7	59·9	0·011	nil	– 0·8	38·4	—	14	2·74	—	220	0·5	4·3
Aug. 4	17·7	56·9	0·010	nil	– 3·0	20·8	—	14	1·49	—	241	0·5	1·3
(b)													
Aug. 4	21·4	73·9	0·008	—	—	—	—	—	—	—	—	—	—
,, 18	21·6	84·3	0·008	0·2	10·4	59·4	5·7	14	4·24	14·1	59	0·2	10·4
Sept. 1	21·8	89·8	0·009	0·2	5·5	68·8	12·5	14	4·91	6·5	128	0·4	15·9
,, 15	22·0	97·5	0·009	0·2	7·7	66·9	8·7	14	4·78	8·6	195	0·6	23·6
,, 29	22·3	107·7	0·010	0·3	10·2	81·8	8·0	14	5·84	10·5	277	0·9	33·8
Oct. 13	22·7	119·1	0·010	0·4	11·4	96·8	8·5	14	6·91	10·6	374	1·3	45·2
,, 27	22·9	123·0	0·010	0·2	3·9	83·1	21·3	14	5·94	3·3	457	1·5	49·1
Nov. 10	23·1	127·7	0·010	0·2	4·7	57·9	12·3	14	4·14	3·8	515	1·7	53·8
,, 24	23·2	129·6	0·010	0·1	1·9	28·6	15·1	14	2·04	1·5	543	1·8	55·7

TABLE 61 : L11 (a and b).

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
(a)													
May 12	21·8	101·2	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	21·9	100·2	0·010	0·1	– 1·0	40·2	—	14	2·87	—	40	0·1	– 1·0
June 9	21·9	96·6	0·009	nil	– 3·6	51·6	—	14	3·69	—	92	0·1	– 4·6
,, 23	22·0	102·3	0·010	0·1	5·7	59·1	10·4	14	4·22	5·9	151	0·2	1·1
July 7	22·1	105·0	0·010	0·1	2·7	60·8	22·5	14	4·34	2·6	212	0·3	3·8
,, 21	22·3	110·3	0·010	0·2	5·3	62·5	11·8	14	4·46	5·0	274	0·5	9·1
Aug. 4	22·4	114·6	0·010	0·1	4·3	62·6	12·2	14	4·47	3·9	337	0·6	13·4
,, 18	22·5	120·0	0·011	0·1	5·4	68·2	12·6	14	4·87	4·7	405	0·7	18·8
Sept. 1	22·7	118·8	0·010	0·2	– 1·2	61·9	—	14	4·42	—	467	0·9	17·6
(b)													
Sept. 29	22·6	120·1	0·010	—	—	—	—	—	—	—	—	—	—
Oct. 13	22·9	136·9	0·010	0·3	16·8	75·0	4·5	14	5·36	13·9	75	0·3	16·8
,, 27	23·5	158·5	0·012	0·6	21·6	103·3	4·8	14	7·36	15·8	178	0·9	38·4
Nov. 10	23·8	160·8	0·012	0·3	2·3	88·5	38·5	14	6·32	1·5	267	1·2	40·7
,, 24	23·9	166·2	0·012	0·1	5·4	45·1	8·4	14	3·23	3·4	312	1·3	46·1

TABLE 62 : L12 (a and b).

(a)													
May 12	19·3	75·1	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	19·6	82·3	0·011	0·3	7·2	51·6	7·2	14	3·69	9·6	52	0·3	7·2
June 9	20·0	86·9	0·011	0·4	4·6	64·7	14·1	14	4·62	5·6	116	0·7	11·8
,, 23	20·2	89·3	0·011	0·2	2·4	61·8	25·7	14	4·41	2·8	178	0·9	14·2
July 7	20·4	90·5	0·011	0·2	1·2	56·7	47·2	14	4·05	1·3	235	1·1	15·4
,, 21	20·5	95·1	0·011	0·1	4·6	55·0	12·0	14	3·93	5·1	290	1·2	20·0
Aug. 4	20·8	99·9	0·011	0·3	4·8	58·9	12·3	14	4·21	5·0	349	1·5	24·8
,, 18	21·1	104·3	0·011	0·3	4·4	63·3	14·4	14	4·52	4·4	412	1·8	29·2
Sept. 1	21·3	105·6	0·011	0·2	1·3	59·3	45·6	14	4·24	1·2	471	2·0	30·5
(b)													
Sept. 29	20·3	86·8	0·010	—	—	—	—	—	—	—	—	—	—
Oct. 13	20·4	92·1	0·011	0·1	5·3	61·0	11·5	14	4·36	6·1	61	0·1	5·3
,, 27	20·7	99·0	0·011	0·3	6·9	61·5	8·9	14	4·39	7·5	122	0·4	12·2
Nov. 10	20·8	102·7	0·011	0·1	3·7	52·3	14·1	14	3·74	3·7	175	0·5	15·9
,, 24	20·9	105·4	0·012	0·1	2·7	36·5	13·5	14	2·61	2·6	211	0·6	18·6

TABLES 63–66.

Maximum Requirements and Growth of Female Plaice.

Table 63 : L13.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.^{3}	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 12	20·0	73·7	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	20·3	85·7	0·010	0·3	12·0	53·9	4·5	14	3·85	16·3	54	0·3	12·0
June 9	20·6	88·2	0·010	0·3	2·5	74·9	30·0	14	5·35	2·9	129	0·6	14·5
,, 23	20·7	94·6	0·011	0·1	6·4	71·7	11·2	14	5·12	7·3	200	0·7	20·9
July 7	20·8	100·2	0·011	0·1	5·6	69·3	12·4	14	4·95	5·9	270	0·8	26·5
,, 21	21·0	103·7	0·011	0·2	6·5	62·3	9·6	14	4·45	6·5	332	1·0	33·0
Aug. 4	21·3	109·1	0·011	0·3	2·4	66·0	27·5	14	4·71	1·3	398	1·3	35·4
,, 18	21·3	109·3	0·011	nil	0·2	66·1	330·0	14	4·72	0·2	464	1·3	35·6
Sept. 1	21·3	106·4	0·011	nil	−2·9	63·5	—	14	4·54	—	528	1·3	32·7
,, 15	21·4	107·0	0·011	0·1	0·6	48·4	80·6	14	3·46	0·6	576	1·4	33·3
,, 29	21·5	108·9	0·011	0·1	1·9	46·0	24·2	14	3·29	1·8	622	1·5	35·2
Oct. 13	21·7	120·0	0·012	0·2	11·1	77·9	7·0	14	5·56	10·2	700	1·7	46·3
,, 27	22·0	123·1	0·012	0·3	3·1	75·8	24·5	14	5·41	2·6	776	2·0	49·4
Nov. 10	22·0	114·6	0·011	nil	−8·5	45·5	—	14	3·25	—	821	2·0	40·9
,, 24	22·0	121·1	0·012	nil	6·5	22·4	3·4	14	1·60	5·7	844	2·0	47·4

Table 64 : L14 (a and b).

(a)													
May 12	17·0	50·5	0·010	—	—	—	—	—	—	—	—	—	—
,, 26	17·8	66·8	0·012	0·8	16·3	40·9	2·5	14	2·92	32·1	41	0·8	16·3
June 9	18·7	78·0	0·012	0·9	11·2	77·9	7·0	14	5·56	16·8	119	1·7	27·5
,, 23	19·1	83·5	0·012	0·4	5·5	75·0	13·6	14	5·36	7·1	194	2·1	33·0
July 7	19·3	86·8	0·012	0·2	3·3	71·0	21·8	14	5·07	4·0	265	2·3	36·3
,, 21	19·6	93·4	0·012	0·3	6·6	74·4	11·3	14	5·32	7·6	339	2·6	42·9
Aug. 4	20·1	97·7	0·012	0·5	4·3	75·0	17·4	14	5·36	4·6	414	3·1	47·2
,, 18	20·3	97·1	0·012	0·2	−0·6	67·0	—	14	4·79	—	481	3·3	46·6
Sept. 1	20·6	97·8	0·011	0·3	0·7	66·5	95·0	14	4·75	0·7	548	3·6	47·3
(b)													
Sept. 15	25·1	173·2	0·011	—	—	—	—	—	—	—	—	—	—
,, 29	25·4	182·2	0·011	0·3	9·0	72·9	8·1	14	5·21	5·2	73	0·3	9·0
Oct. 13	25·9	200·4	0·012	0·5	18·2	115·0	6·3	14	8·21	10·0	188	0·8	27·2
,, 27	26·1	211·3	0·012	0·2	10·9	119·4	11·0	14	8·53	5·4	307	1·0	38·1
Nov. 10	26·1	205·3	0·012	nil	−6·0	101·8	—	14	7·27	—	409	1·0	32·1
,, 24	26·1	204·4	0·011	nil	−0·9	26·9	—	14	1·92	—	436	1·0	31·2

TABLE 65 : L15.

Date. (1930)	Size of fish. Lth. (cm.)	Size of fish. Wt. (gm.)	Wt./ /Lth.³	Growth per period. Lth. (cm.)	Growth per period. Wt. (gm.)	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Average food per day during each period. (gm.)	Percentage growth in wt.	Total food to date (gm.)	Cumulative growth. Lth. (cm.)	Cumulative growth. Wt. (gm.)
May 12	20·1	75·7	0·009	—	—	—	—	—	—	—	—	—	—
,, 26	20·2	85·2	0·010	0·1	9·5	61·0	6·4	14	4·36	12·5	61	0·1	9·5
June 9	20·8	96·7	0·011	0·6	11·5	94·2	8·2	14	6·73	13·5	155	0·7	21·0
,, 23	21·0	102·1	0·011	0·2	5·4	86·4	16·0	14	6·17	5·6	242	0·9	26·4
July 7	21·1	106·5	0·011	0·1	4·4	68·8	15·6	14	4·91	4·3	310	1·0	30·8
,, 21	21·2	108·6	0·011	0·1	2·1	70·6	33·6	14	5·04	1·0	381	1·1	32·9
Aug. 4	21·5	111·6	0·011	0·3	3·0	71·0	23·7	14	5·07	2·8	452	1·4	35·9
,, 18	21·6	114·1	0·011	0·1	2·5	72·6	29·0	14	5·19	2·2	525	1·5	38·4
Sept. 1	21·6	110·4	0·011	nil	− 3·7	65·2	—	14	4·66	—	590	1·5	34·7
,, 15	21·7	111·3	0·011	0·1	0·9	60·4	67·1	14	4·31	0·8	650	1·6	35·6
,, 29	21·9	115·3	0·011	0·2	4·0	66·9	16·7	14	4·78	3·6	717	1·8	39·6
Oct. 13	22·1	118·7	0·011	0·2	3·4	77·3	22·7	14	5·52	3·0	794	2·0	43·0
,, 27	22·1	120·4	0·011	nil	1·7	57·4	33·8	14	4·10	1·4	852	2·0	44·7
Nov. 10	22·1	115·7	0·011	nil	− 4·7	44·0	—	14	3·14	—	896	2·0	40·0
,, 24	22·1	114·4	0·011	nil	− 1·3	20·9	—	14	1·49	—	917	2·0	38·7

TABLE 66 : L16 (a and b).

(a)													
May 12	19·5	79·0	0·011	—	—	—	—	—	—	—	—	—	—
,, 26	19·8	88·5	0·011	0·3	9·5	51·7	5·4	14	3·69	12·0	52	0·3	9·5
June 9	20·5	99·3	0·011	0·7	10·8	84·4	7·8	14	6·03	12·3	136	1·0	20·3
,, 23	20·7	102·8	0·011	0·2	3·5	73·4	21·0	14	5·24	3·5	209	1·2	23·8
(b)													
July 7	20·8	104·9	0·012	—	—	—	—	—	—	—	—	—	—
,, 21	21·5	114·7	0·012	0·7	9·8	72·2	7·4	14	5·14	9·3	72	0·7	9·8
Aug. 4	22·0	126·4	0·012	0·5	11·7	82·2	7·0	14	5·87	10·2	154	1·2	21·5
,, 18	22·5	136·7	0·012	0·5	10·3	90·4	8·8	14	6·46	8·1	245	1·7	31·8
Sept. 1	22·9	142·3	0·012	0·4	5·6	89·0	15·9	14	6·36	4·1	334	2·1	37·4
,, 15	23·1	153·5	0·012	0·2	11·2	85·4	7·6	14	6·10	7·9	420	2·3	48·6
,, 29	23·6	158·7	0·012	0·5	5·2	76·4	14·7	14	5·46	3·4	496	2·8	53·8
Oct. 13	24·0	177·7	0·013	0·4	19·0	121·5	6·4	14	8·68	12·0	618	3·2	72·8
,, 27	24·3	187·0	0·013	0·3	9·3	106·2	11·4	14	7·59	5·2	724	3·5	82·1
Nov. 10	24·5	192·8	0·013	0·2	5·8	98·2	16·9	14	7·01	3·1	822	3·7	87·9
,, 24	24·6	201·8	0·014	0·1	9·0	67·5	7·5	14	4·82	4·6	890	3·8	96·9

A Statistical Study of Growth and Maintenance in the Plaice (*Pleuronectes platessa* L.).

By

Ben Dawes, A.R.C.S., D.I.C., F.L.S.

With 5 Figures in the Text.

CONTENTS.

I. Introduction and Methods.

The data for this paper were obtained from experiments carried out at Cawsand and Lympstone under the auspices of the Marine Biological Association during the years 1929–30 and subject to the direction of Dr. E. J. Allen, F.R.S. The aim of the experiments was to determine the maintenance requirements and growth efficiency of plaice during the third season of growth, and to ascertain what fraction of total food taken by such fish is available for growth promotion. To some extent this aim has already been realised, for in two previous papers (**1** and **2**) many data have been presented and discussed and interesting conclusions bearing upon growth and maintenance have been put forward. To these papers the reader is referred also for a full description of the experimental methods employed and the practical difficulties encountered. In one important respect, however, the results of the work remain incompletely expressed due to the purely arithmetic mode of treatment of the data, which remain in rather unwieldy form and show a heterogeneity entirely due to variable

performances. In the first instance it was essential to emphasise this variability, but ultimately the indices of growth efficiency and maintenance must relate to populations rather than to individuals if they are to be of maximum assistance to fishery research. The aim of the present paper is to remedy this deficiency by applying appropriate statistical treatment to the data, thus enabling them to be presented in more compact and more satisfactory form. At the outset it is desired to thank Mr. T. Edser of the "S" Branch of the Ministry of Agriculture and Fisheries for his suggestion that the work be undertaken and for invaluable assistance willingly rendered.

A glance at my previous papers will serve to show that the experiments were divided up into periods of approximately a fortnight in duration, so that each period may be regarded as a separate experiment yielding definite results. In the present paper, it is intended to consider these periods as units, after reducing by simple proportion where necessary to periods of 14 days. Larger masses of data are thereby rendered available and can be dealt with statistically; the individual is the plaice used in one unit period of 14 days. Weight increase (to be expressed in grammes) and food taken (to be expressed as a percentage of the initial body-weight) are the only growth characteristics utilised, and factors such as temperature are of necessity ignored, except in as far as the mean temperature differs from one place to another and from one year to the next. The aim of the work may be more closely defined as being to determine the maintenance requirements and growth efficiency of the average member of a plaice community during the "average" fortnight of the third season of growth.

In setting out the data initially, weight changes were considered to the nearest 0·1 gm., food quantities to the nearest 1 per cent, but in compiling the tables, grouping was effected into 1·0 gm. and in 10 per cent classes, except in the case of the L.W. experiments, where 1·0 gm. and 5 per cent classes were formed. Males and females were considered separately in order to ascertain the possibility of marked differences in degree of correlation or in steepness of the regression lines, and Cawsand and Lympstone results were kept separate for similar reasons. All calculations have been made by the use of four-figure logarithms, have been carried out twice independently, and then finally checked. In my previous papers many scraps of data were omitted for the sake of brevity since they did not materially affect conclusions formed, but in the present paper all available data have received due consideration. It is usual in work of this kind to reject extreme variates following upon the use of Chauvenet's criterion and prior to calculation of statistical characteristics, but in this case suspected extreme variates are relatively numerous and it was deemed advisable to let them stand.

RESULTS.

II. Size Data.

The primary consideration of defining as closely as possible the size limits of and the distribution of sizes in the various statistical populations is made in Table 1, where relevant summarised size data are shown.

TABLE 1.

Summarised Body-Weight Data Defining the Statistical Populations.

Population.	Sex.	No. of Fish.	Weight Distribution (gm.). Lower. Limit	Lower Quartile Q1.	Median Q2.	Upper Quartile Q3.	Upper Limit.	Arithmetic Mean (gm.) $\bar{X} \pm \frac{\sigma_x}{\sqrt{n}}$	Standard Deviation (gm.) $\pm \sigma_x \pm \frac{\sigma_x}{\sqrt{2n}}$
C1929	♂	175	13	21·7	29·9	43·2	105	35·2±1·3	18·0±1·0
,,	♀	189	15	27·0	38·6	57·2	105	44·6±1·6	22·0±1·1
C 1930	♂	181	18	33·9	46·4	64·0	118	52·7±1·8	24·2±1·3
,,	♀	194	17	32·5	47·3	61·6	141	54·1±2·1	29·5±1·5
L 1929	♂	117	21	57·7	79·0	109·8	159	84·0±3·0	32·1±2·1
,,	♀	111	27	61·1	74·2	112·7	186	90·4±4·0	41·7±2·8
L 1930	♂	119	54	63·4	79·8	102·8	166	86·7±2·5	27·7±1·8
,,	♀	119	25	59·2	73·1	109·6	211	86·1±4·1	44·8±2·9

Under the heading of " Weight Distribution " lower and upper size limits are indicated, as are also lower, median, and upper quartiles, these being the sizes below which 25, 50, and 75 per cent of the variates occur in each population, and therefore merely convenient indices of the grouping of each 25 per cent of the variates. The outstanding feature of the distributions is that they are not normal, the median being far below the mid-point of the total range. The populations thus include a majority of small individuals, the sampling among large individuals being more than merely correspondingly inferior in view of the extended distribution above the upper quartile. It is also noticeable that the quartiles of the Lympstone populations are fairly uniform and dissimilar to those of the Cawsand populations. One would be inclined to expect that since the populations are thus rendered statistically distinct, this distinction would be reflected into subsequent correlative findings, as the unit of growth is 1·0 gm., that of food 1 per cent of the body-weight at the outset of the experimental period.

The peculiarity of the distributions mentioned above is emphasised by the differences between the medians and the means, $\frac{1}{n}\Sigma(f.X)$, as is shown in Table 1. The means are in every instance considerably greater than the medians. When probable errors are taken into account, the means are fairly uniform as regards sex, but clearly distinct in the C and L groups, even though generally speaking all plaice considered are two-year-olds.

The most convenient measure of dispersion is the standard deviation,

and since this index is to be used consistently throughout the present paper it is essential first of all to define it as the "square-root of the arithmetic mean of the squares of all deviations, deviations being measured from the arithmetic mean of the observations" (Yule, **4**, p. 134). Here, with its standard error, it is

$$\sigma_x = \sqrt{\tfrac{1}{n}\Sigma(f.D^2)} \pm \frac{\sigma_x}{\sqrt{2n}}$$

It can be converted readily into the mean deviation, $\frac{1}{n}(f.D)$ irrespective of the sign of D, by multiplying by ·7979, the standard error into the probable error of the determination by multiplying by ·6745. The meaning of the index has been admirably illustrated by Mr. Ford (Ford,* **3**, p. 256).

In Table 1 it is seen that, with the exception of the L. 1930 ♂ population, standard deviations happen to form an ascending series from the top of the table to the bottom. The degree of dispersion of body-weights is thus greater in L. than in C. groups, as in the case of means.

It is to be observed, however, that the degree of dispersion is not a reliable index of growth, since maintained individuals of all sizes are included in the populations.

III. Growth Data.

Examination of the columns under the heading "Distribution of Weight Changes" in Table 2 will serve to indicate that in all populations

TABLE 2.

Growth Data.

Population.	Sex.	No. of Fish.	Distribution of Weight Changes (gm.). Lower Limit.	Lower Quartile Q1.	Median Q2.	Upper Quartile Q3.	Upper Limit.	Mean Growth (gm.) $\left(\bar{x} \pm \frac{\sigma}{\sqrt{n}}\right)$	Standard Deviation (gm.) $\left(\pm \sigma_x \pm \frac{\sigma_x}{\sqrt{2n}}\right)$
C 1929	♂	153	− 6	− 0·6	0·9	2·9	13	1·3±0·3	3·2±0·2
,,	♀	161	− 7	− 0·2	0·8	3·1	14	1·6±0·3	3·3±0·2
C 1930	♂	163	− 5	0·0	1·3	3·4	12‡	1·9±0·2	3·0±0·2
,,	♀	171	− 5	− 0·3	1·4	3·6	11	1·7±0·2	3·1±0·2
L 1929	♂	100	− 7	− 1·2	1·1	7·5	17†	2·7±0·6	6·0±0·4
,,	♀	101	− 8	− 1·1	0·7	7·9	22	3·2±0·7	6·6±0·5
L 1930	♂	106	− 7	− 0·7	0·9	3·7	11††	1·7±0·4	4·1±0·3
,,	♀	107	− 8	− 0·2	1·4	4·9	12*	2·7±0·5	5·0±0·3

† 1 observation 25 gm.
‡ 1 ,, 16 gm.
†† 1 ,, 22 gm.; 1 observation 17 gm.
* 1 ,, each 19, 18, and 16 gm.

* In all subsequent references, whether in tables or text, the error of the standard deviation and other statistical characteristics cited is the standard error, which it will be remembered is greater than the probable error of the determination.

weight losses reaching 5–8 gm. occur in 25 per cent of cases, while in 50 per cent of cases weight increases never exceed 1·4 gm., and maximum increases may be as low as 0·7 gm. These latter cases clearly include the vast majority of maintained individuals, freely-growing individuals forming the bulk of the upper 50 per cent of each population. In this respect the C. and L. groups are fairly uniform whereas the upper quartiles are generally higher in the L. groups, which indicates at once a higher degree of growth in approximately half the total number of freely-growing individuals. This feature is expecially well marked during 1929. As will now be expected, mean growth is much greater among the L. groups, ranging from 1·7–3·2 gm. as against a range of 1·3–1·9 gm. among the C. groups. Dispersion in the upper parts of the populations is also greater, medians and upper quartiles ranging from 3·7–25 gm. in the L. groups as against a range of 2·9–16 gm. in the C. groups. Differences of degree of dispersion are best shown with respect to standard deviations, however, which vary between 4·1 and 6·6 gm. in the L. populations and between 3·0 and 3·3 gm. in the C. populations, with insignificant standard errors in each case. Clearly, degree of growth is distinctly different in the two sets of populations.

IV. Food Data.

The principal features of the distribution of food quantities are shown in Table 3. The median is clearly much lower in the case of the L. populations, excepting L. 1930 ♀. The figures show that 50 per cent of the first

TABLE 3.

Food Data

Population.	Sex.	No. of Fish.	Distribution of Food Quantities (= % ages of Bd.-wt.) Lower Limit.	Lower Quartile Q1.	Median Q2.	Upper Quartile Q3.	Upper Limit.	Mean Ration % $\left(\bar{y} \pm \frac{\sigma_y}{\sqrt{n}}\right)$	Standard Deviation $\left(\pm \sigma_y \pm \frac{\sigma_y}{\sqrt{2n}}\right)$
C 1929	♂	153	1	23·3	41·9	118·6	266	73·7±5·1	63·0±3·6
,,	♀	161	2	22·6	38·4	96·0	249	59·9±3·9	49·2±2·7
C 1930	♂	163	9	21·3	45·4	81·6	200	56·1±3·2	41·1±2·3
,,	♀	171	3	18·5	41·7	80·5	257	58·7±4·0	52·4±2·8
L 1929	♂	100	2	15·1	25·0	102·5	249	56·2±5·3	53·4±3·8
,,	♀	101	3	14·6	24·7	92·5	226	53·1±5·4	53·7±3·8
L 1930	♂	106	6	18·3	29·2	63·4	120	40·2±2·5	25·7±1·8
,,	♀	107	2	18·8	42·3	65·9	116	44·4±2·6	27·0±1·8

three L. populations took percentages less than 29·3, 50 per cent of any C. population taking percentages greater than 38·3. Since the portion of each population receiving such low percentages is largely if not entirely formed of maintained individuals, it follows that the maintenance demands (expressed as percentages of body-weight) at Lympstone were smaller than those at Cawsand. Weight decreases at Lympstone were slightly

greater than at Cawsand, but apparently not correspondingly so, while temperatures were slightly higher at the former place (Dawes, **1** and **2**). But in view of the fact that sizes were much greater at Lympstone it seems safe to infer that such differences in maintenance demands as are noted above are connected with, if not entirely due to, size differences. The inference also receives some support from the much smaller lower quartiles in the L. populations.

Upper quartiles and upper limits are greater in C. populations of a particular year than in L. populations of the corresponding year, especially so during 1930. Standard deviations are considerably greater in the 1929 groups and are generally greater in the C. groups when particular years are considered. The especially low standard deviations of the L. 1930 populations are connected with low growth characteristics, both degree of growth and appetite being smaller during 1930 than during the preceding year.

V. Correlation between Food and Growth.

It is evident from the foregoing that both growth in weight and food percentages taken are highly variable. This was clearly indicated also in my previous papers, where it was also shown that similar high variability characterises growth efficiency, i.e. the capacity to utilise food for purposes of growth. But high values of weight increase are generally associated with high food percentages and it is with this association that we are now concerned. Tables 8–15 are built up by noting the frequency with which particular associations of the x and y variables occur, which frequencies are grouped and arranged in arrays to form correlation tables.

The index of correlation is the correlation coefficient r, which is a pure number lying between the limits -1 and $+1$. It is positive if large values of x are associated with large values of y, negative if small values of x are associated with large values of y, and conversely. If the two variables are independent, i.e. if there is no correlation, $r=0$. It is calculated from the formula,

$$r=\frac{p}{\sigma_x\ \sigma_y},$$

where σ_x and σ_y are the standard deviations of x and y variables and where p is a measure of variance, being the product of deviations from the arbitrary origin minus the product of the difference between arbitrary and true means, i.e.

$$p=\frac{\Sigma(x-\bar{x})\,(y-\bar{y})}{n}-(D_x\,D_y)$$

Taking the C. 1929 populations and making use of the tables cited, we have :—

(Table 8) [♂]

$$D_x=\frac{51}{153}=\cdot 3 \text{ gm.}$$

$$D_y=\frac{-20}{153}=-\cdot 1307\times 10\%$$

(Table 9) [♀]

$$D_x=\frac{97}{161}=\cdot 6030 \text{ gm.}$$

$$D_y=\frac{-82}{161}=-\cdot 5093\times 10\%$$

(Table 2)

$\sigma_x=3\cdot 178$ (calculated value)

$\sigma_x=3\cdot 354$ gm.

(Table 3)

$\sigma_y=6\cdot 302\times 10\%$

$$p=\frac{1498}{153}-(\cdot 3\times -\cdot 1307)$$

$$=9\cdot 792+\cdot 044$$

$$=9\cdot 836$$

$$r=\frac{9\cdot 836}{3\cdot 178\times 6\cdot 302}=\cdot 4912$$

$\sigma_y=4\cdot 916\times 10\%$

$$p=\frac{1264}{161}-(\cdot 603\times -\cdot 5093)$$

$$=7\cdot 852+\cdot 307$$

$$=8\cdot 159$$

$$r=\frac{8\cdot 159}{3\cdot 354\times 4\cdot 916}=\cdot 4950$$

Data for the remaining populations were treated in the same way, using Tables 2 and 3 and 10–15, and the list of correlation coefficients presented in Table 4 was obtained by the use of the values of p shown. It is seen that in every case there occurs a moderately high degree of correlation. The standard errors are greater in the case of C. populations but are nowhere of sufficiently high value to preclude the probability of fairly high correlation not due to mere chance. The values of r are highest among L. populations, lowest among the C. populations, higher during 1930 in C. groups, during 1929 in L. groups. There is close similarity for the sexes during any particular year.

The diagrams in Figs. 1 and 2 are made by representing the frequencies each by a single ring in its appropriate position. They refer to the C. 1929 populations (♂ and ♀) and they indicate the degree of correlation diagrammatically. The regression lines shown are drawn in after calculation of the regression coefficients from the formulæ

$$b_x=\frac{r\,\sigma_x}{\sigma_y\times 10};\qquad b_y=\frac{r\,\sigma_y\times 10}{\sigma_x}$$

The lines cut each other in the means $\bar{x}$ and $\bar{y}$ and the angle they make with each other indicates the degree of correlation ; an angle of approximately 90° would represent independency of the variables.

Continuing the examples previously taken (C. 1929), we have :—

[♂]	[♀]
$b_x = \frac{\cdot 4912 \times 3 \cdot 178}{63 \cdot 02} = \cdot 0248$	$b_x = \frac{\cdot 495 \times 3 \cdot 354}{49 \cdot 16} = \cdot 0338$
$b_y = \frac{\cdot 4912 \times 63 \cdot 02}{3 \cdot 178} = 9 \cdot 738$	$b_y = \frac{\cdot 495 \times 49 \cdot 16}{3 \cdot 354} = 7 \cdot 256$

b_x is the regression of x on y, i.e. the regression function given by the

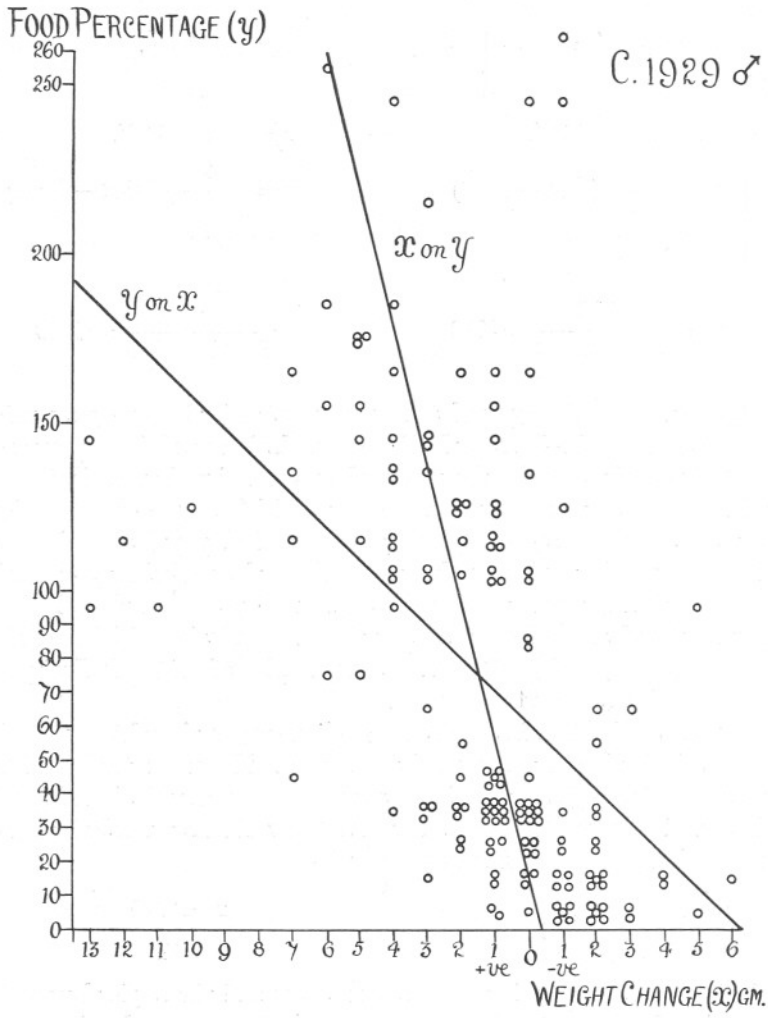

FIG. 1.—Correlation diagram for the male plaice population of Cawsand, 1929. The regression lines were drawn in lastly and are based upon the regression coefficients calculated. The diagram is a graphical presentation of Table 8.

equation $x=\bar{x}-b_x(y-\bar{y})$, by the regression of y on x, i.e. the regression function given by the equation $y=\bar{y}-b_y(x-\bar{x})$. Since the primary aim is to deduce weight increase (x) from available food percentage (y), the more important regression line from the point of view of this work is that

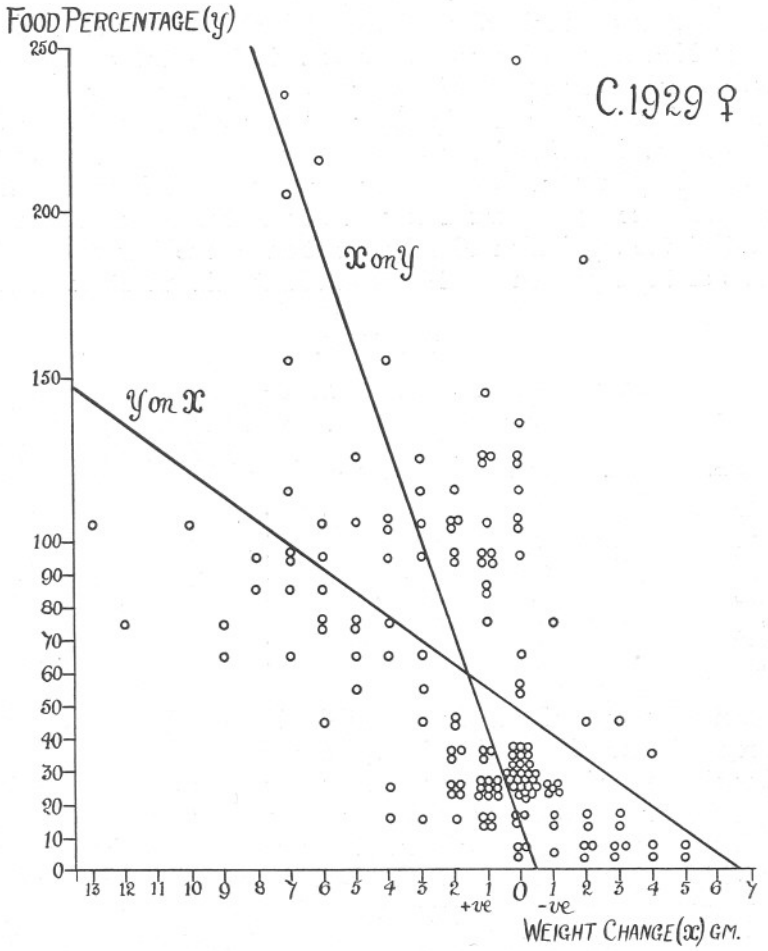

FIG. 2.—Correlation diagram for the female plaice population of Cawsand, 1929, with regression lines drawn in as in Fig. 1. The diagram is a graphical presentation of Table 9.

of x on y. The regression coefficient b_x indicates the order of change in x, i.e. weight increase or decrease, resulting on the average from unit change in y, i.e. food percentage, since $x=b_xy$. Similarly, b_y indicates the order of change in y with unit change in x. In the above example the slope of the regression line of x on y is appreciably steeper in the case of males

where b_x is smaller. Similarly, the slope of the regression line of y on x is correspondingly steeper, since the correlation coefficients are identical. This is shown diagrammatically in Figs. 1 and 2, where the regression lines are drawn into the correlation dot diagrams.

The regression coefficients for all populations were calculated by the method illustrated in the above example and they are shown in Table 4 along with corresponding standard errors. It is seen that only in the instance of the C. 1929 populations are the differences between the regression coefficients of the sexes significant, when standard errors are taken into account. Even in this instance some of this significance is lost when it is considered that the chances of the true values lying within $\pm 2\times$ standard error are approximately merely of the order of 20 to 1, and that the application of this correction in one instance renders values of the regression coefficients confluent. In all other cases it

TABLE 4.

REGRESSION AND CORRELATION COEFFICIENTS.

Population.	Sex.	Product of Deviations from Mean (p).	Correlation Coeff. $r=\frac{p}{\sigma_x\,\sigma_y\,10}\pm\frac{1-r^2}{\sqrt{n}}$	Regression Coeff. $b_x=\frac{r\sigma_x}{\sigma_y}\pm\frac{\sigma_x\sqrt{1-r^2}}{\sigma_y\sqrt{n}}$	Regression Coeff. $b_y=\frac{r\sigma_y}{\sigma_x}\pm\frac{\sigma_y\sqrt{1-r^2}}{\sigma_x\sqrt{n}}$
C 1929	♂	9·84	0·49±·06	·025±·003	9·7±1·4
,,	♀	8·16	0·49±·06	·034±·005	7·3±1·0
C 1930	♂	7·89	0·63±·03	·047±·005	8·5±0·9
,,	♀	10·35	0·64±·03	·038±·004	10·8±1·0
L 1929	♂	25·09	0·78±·04	·088±·007	6·9±0·6
,,	♀	24·97	0·70±·05	·086±·009	5·8±0·9
L 1930	♂	6·47	0·63±·04	·100±·012	3·9±0·5
,,	♀	8·19	0·61±·04	·112±·014	3·3±0·4

is practically certain that no difference exists between the sexes as regards the regression functions during either year at either place.

But these functions vary slightly from year to year and vary considerably between the C. and L. populations, the Cawsand populations yielding much steeper regression lines than the Lympstone ones, and thus indicating a higher growth efficiency. And although variable factors such as temperature might conceivably produce such differences in the regression functions, there appear to be good grounds for believing that size differences, which are well marked between the C. and L. populations as we have seen, are the factors principally involved. That the differences in the regression functions are significant is shown in Table 4, the greatest value for b_x in any C. population being ·047, while in any L. population the least value of the corresponding coefficient is ·086, with an insignificant standard error in each case. These results are shown graphically in Figs. 3–5, where the regression lines for the remaining populations are presented.

In all the above cases it has been assumed that the regression lines are linear, an assumption which is by no means justifiable unless the approximation to linearity is measured and found to be reasonably close. Such a measure of the closeness to linearity is available in the form of the "correlation ratio" of Professor Pearson (η_{xy}). This ratio, which is the correlation ratio of x on y, "measures the approach of values of x

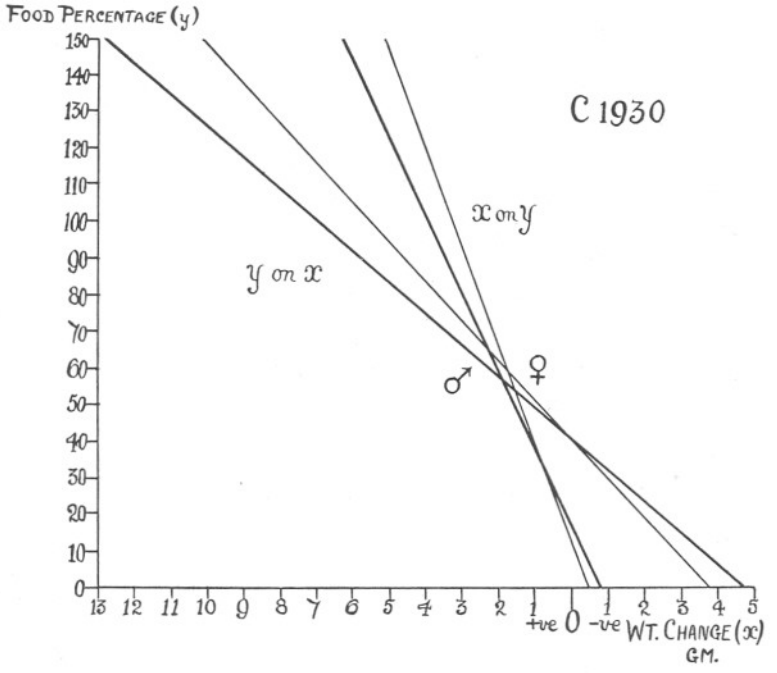

FIG. 3.—Diagram showing the positions and slopes of the regression lines for male and female plaice populations of Cawsand, 1930. Although this is not a correlation diagram, yet it is strictly based upon Tables 10 and 11.

associated with given values of y to a single valued relationship of any form" (Yule, **4**, p. 205). Each table provides two such ratios, the second being η_{yx} or the correlation ratio of y on x, the significance of which will be clear.

The correlation ratios for the various populations were calculated from the formulæ :—

$$\eta_{xy}=\frac{\sigma_{mx}}{\sigma_x}\ ; \qquad \eta_{yx}=\frac{\sigma_{my}}{\sigma_y}$$

where σ_x and σ_y=standard deviations of x and y respectively,
σ_{mx} and σ_{my} = standard deviation of the means of the x and y arrays, respectively.

The way in which the formulæ are derived is shown in *loc. cit.* and it is

sufficient here merely to indicate that η_{xy} and η_{yx} are invariably greater than the correlation coefficient r, and that the difference between these quantities indicates the departure from linearity, $\eta^2 - r^2$ measuring the divergence of the actual line through the means of the arrays from the line of regression. At the same time, it should be observed that " owing to

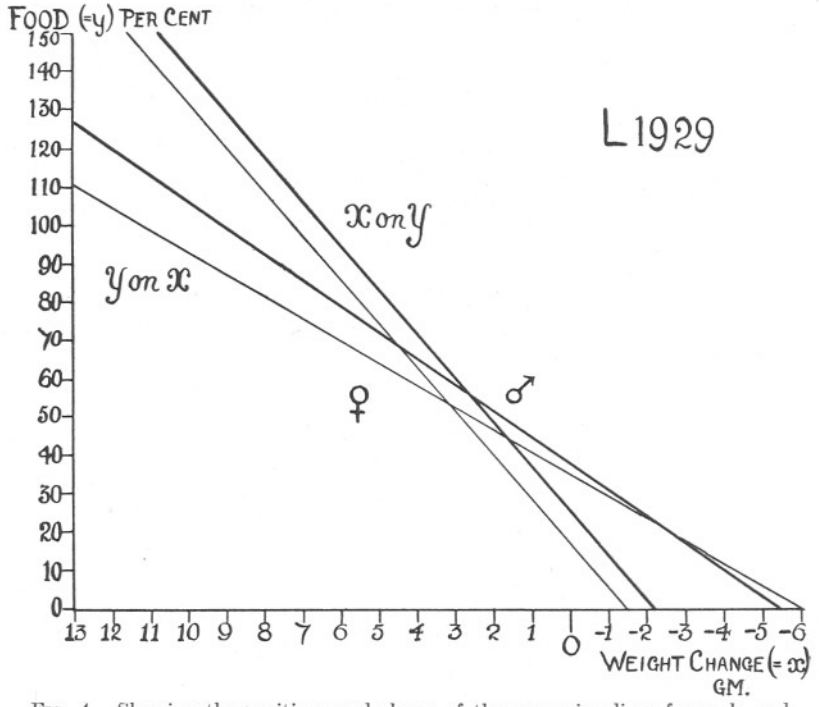

FIG. 4.—Showing the positions and slopes of the regression lines for male and female plaice populations of Lympstone, 1929, based upon Tables 12 and 13.

fluctuations of sampling, r and η are almost certain to differ slightly, even though the regression may be truly linear (Yule, **4**, p. 206).

TABLE 5.

DATA FOR ESTIMATING THE DEPARTURE OF THE REGRESSION LINES FROM LINEARITY.

Population.		Standard Deviations of Means of Arrays. σ_{mx}	σ_{my}	Standard Deviations (gm.). σ_x	σ_y	Correlation Ratios. η_{xy}	η_{yx}	Correlation Coeff. r	$\eta_{xy}^2 - r^2$	$\eta_{yx}^2 - r^2$
C 1929	♂♀	2·2	37·5	3·2	63·0	·70	·60	·49	·25	·12
,,	♂♀	2·3	27·1	3·3	49·2	·71	·55	·49	·26	·06
C 1930	♂♀	2·1	30·1	3·0	40·1	·70	·73	·63	·09	·14
,,	♂♀	2·4	36·7	3·1	52·4	·76	·70	·64	·19	·08
L 1929	♂♀	5·1	49·6	6·0	53·4	·84	·93	·78	·10	·26
,,	♂♀	5·6	48·5	6·6	53·7	·86	·90	·70	·25	·32
L 1930	♂♀	2·7	18·9	4·1	25·7	·67	·74	·63	·05	·15
,,	♂♀	3·4	19·7	5·0	27·0	·67	·73	·61	·08	·16

Values have been obtained for the correlation ratios of all populations and are shown in Table 5, together with the standard deviations from which they were calculated. If these values are compared with those of the regression coefficients, which are also shown in the table, it will be seen that in some cases the departure from linearity is fairly slight. In 4 instances, $\eta_{xy}^2 - r^2 \leqq \cdot 10$ although in other instances it increases to ·26; in 2 instances, $\eta_{yx}^2 - r^2 \leqq \cdot 08$ while in others it ranges from ·12 to ·32. During 1930 the approach to linearity of the regression lines is much closer than during 1929, but if it is justifiable to assume linearity in one

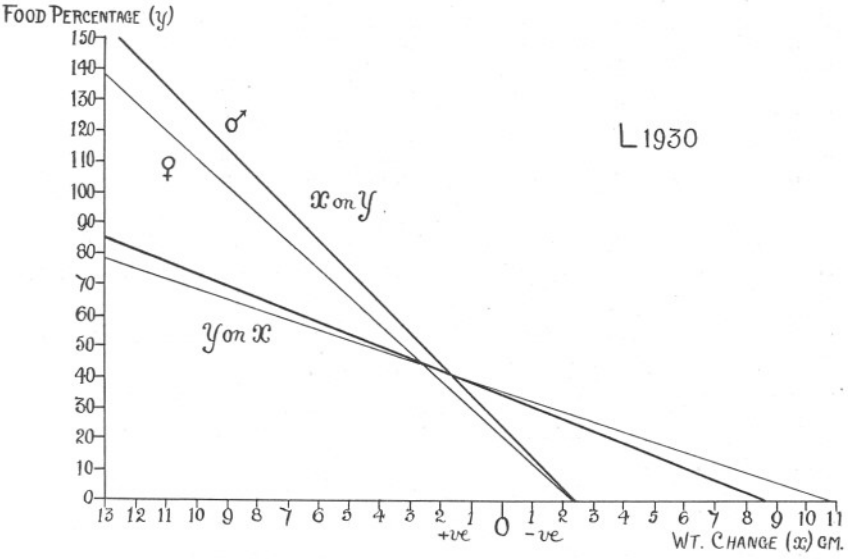

Fig. 5.—Showing the positions and slopes of the regression lines for male and female plaice populations of Lympstone, 1930. Based upon Tables 14 and 15.

instance it is justifiable in others, especially since the aim of the work is to obtain only approximate indices, and although the regression lines strictly are not straight it is sufficient for our purpose to assume that they are.

By substituting mean values and regression coefficients in the regression equations, equations of the form $x = b_x y + \text{const.}$ and $y = b_y x + \text{const.}$ are obtained. A set of pairs of such equations are provided in Table 6. The constants in equations (1) indicate how far the regression lines of x on y are displaced to the right in Figures 1–5, and it is seen that the C. and L. populations show striking differences in this respect, the constant being at least thrice the C. value in the corresponding L. population. In equations (2) the constants show how far the regression line of y on x is

displaced vertically in the same figures, and in this case there is no well-marked difference other than that shown by the C. 1929 populations, especially the male one.

TABLE 6.

REGRESSION EQUATIONS OF THE FORM $x=b_xy+$const. AND $y=b_yx+$ const., WITH VALUES OF EACH VARIATE WHEN THE VALUE OF THE OTHER IS ZERO.

Population.	Sex.	Equation (1) x=(gm.)	Equation (2) y=(%)	In (1), when x=0 y=(%)	In (2), when y=0 x=(gm.)	In (1), when x=·05 y=(%)	In (1), when x=1·0 y=(%)
C 1929	♂	·025 Y − ·49	9·7 X+60·7	19	− 6	40	60
,,	♀	·034 Y − ·42	7·3 X+48·3	12	− 7	27	42
C 1930	♂	·047 Y − ·73	8·5 X+40·0	16	− 5	26	37
,,	♀	·038 Y − ·47	10·8 X+39·8	12	− 4	26	39
L 1929	♂	·088 Y − 2·19	6·9 X+37·1	25	− 5	31	36
,,	♀	·086 Y − 1·41	5·8 X+34·8	16	− 6	22	28
L 1930	♂	·100 Y − 2·34	3·9 X+33·6	23	− 9	28	33
,,	♀	·112 Y − 2·31	3·3 X+35·5	21	− 11	25	30

If in equations (1) we make x=0, the evaluation of y will then provide a measure of maintenance requirements in terms of percentage of the initial body-weight. A list of such evaluations of y are shown in Col. 5 of Table 6, and are seen to provide greater indices in males than in females and at Lympstone than at Cawsand. This latter is contrary to previous findings both in my previous paper and in the present one where quartiles of the y variate are discussed, and it calls for an explanation.

The figures in Col. 5 of Table 6 are misleading unless it is borne in mind that there is a significant difference in the steepness of the regression lines of the C. and L. populations. These lines are much steeper in the C. populations, which implies that the change in y corresponding to unit change in x is greater in this case. When x=0, y is greater in the L. than in the C. populations, i.e. maintenance demands, as percentages, are greater. But when x=·5 the significance of the difference is lost, and when x=1·0 the values of y are considerably greater in the C. populations, as is shown in Table 6, especially during 1929. For pure maintenance, the larger L. individuals appear to require slightly higher food percentages than do the C. individuals, but this result is more apparent than real, since if very small increases are considered the reverse is the case. Increases greater than ·5 gm. required greater food percentages in the case of C. than in the case of L. populations, as is shown by a study of the regression equations.

The above-mentioned feature of relative efficiency in the C. and L. populations is brought out rather better in Table 7. The ratio $b_xX^{100}/\bar{X}$

TABLE 7.

REGRESSION COEFFICENTS INFERRED FOR STANDARD PLAICE OF 100 (b_x) AND 1 GM. (b_y) RESPECTIVELY.

Population.	C 1929 ♂	C 1929 ♀	C 1930 ♂	C 1930 ♀	L 1929 ♂	L 1929 ♀	L 1930 ♂	L 1930 ♀
$\overline{X}$	35·2	44·6	52·7	54·1	84·0	90·4	86·7	86·1
$b_x \times 100/\overline{X}$	·07	·08	·09	·07	·10	·10	·12	·13
$b_y/\overline{X}$	·28	·16	·16	·20	·08	·06	·04	·04

indicates the degree of change in x related to unit change in y for a standard plaice of 100 gm., which change is slightly greater in the L. groups, thus suggesting greater efficiency in these groups. This suggestion is furthered when the ratio $b_y/\overline{X}$ is considered, when the degree of change in y per gm. of fish corresponding to unit change in x is found to be very much greater in the C. groups, i.e. efficiency is not as great.

By making y=0 in equation (2) (Table 6) the values of x obtained indicate the probable weight decreases during starvation for the various populations, these being slightly greater in the L. populations (5–11 gm.) than in the C. populations (4–7 gm.).

VI. L.W. EXPERIMENTS.

It remains to consider briefly the winter experiments carried out at Lympstone during the early months of 1930. They are of especial interest because the individuals used were carried through from the experiments of 1929, which enables the results to bear comparison with those of the L. 1929 populations, thus affording also a comparison between winter and summer performances. The sexes have been grouped together, since the number of individuals of one sex is too small to allow of reliable statistical treatment.

The following size data indicate how closely the L.W. population compares with the L. 1929 ones (see Table 1) :

[$\overline{X}$] Mean weight :— 90·6$\pm$2·9 gm.
[σ_x] Standard deviation :—24·5$\pm$2·1 gm.

The principal differences between the populations as regards size of individuals is thus seen to be one of degree of dispersion, this naturally being much smaller in the L.W. populations.

As would be anticipated, growth is much more restricted, as the following figures indicate :

($\bar{x}$) Mean growth :— 0·6$\pm$0·3 gm.
(σ_x) Standard deviation :—2·6$\pm$0·2 gm.

Mean growth in the case of the L. 1929 populations is roughly five times as great, standard deviation more than twice as great (Table 2).

Food percentages taken are very substantially smaller.

($\bar{y}$) Mean food :— 18·7 $\pm$1·9 per cent.
(σ_y) Standard deviation :—14·6 $\pm$1·3 per cent.

Each of these values is approximately only one-third of the corresponding values in the case of the L. 1929 populations (cp. Table 3).

As in the case of all other populations a fairly high degree of correlation occurs between food and growth, since from Table 16,

$$p=\frac{322}{62}-(\cdot629\times\cdot742)$$
$$=4\cdot727$$

and

$$r=\frac{p}{\sigma_x\,\sigma_y}=\frac{4\cdot727}{2\cdot57\times2\cdot93}=\cdot6276\ (\cdot63\pm\cdot08).$$

The correlation coefficient is smaller, however, than those of the L. 1929 populations, which are ·78 (♂) and ·70 (♀) respectively (Table 4).

The regression coefficients of x on y, i.e. b_x, of the L. 1929 populations were seen to be distinctly uniform, the differences between the sexes being negligible (Table 4). The corresponding coefficient of the L.W. populations provides a striking contrast, for

$$b_x=\frac{\cdot628\times2\cdot57}{2\cdot93\times5}=\cdot110\ (\pm\cdot017).$$

Change in x corresponding to unit change in y is thus, on the average, greater during the winter months than during the summer months, in the ratio of 110 : 87, i.e. growth efficiency is enhanced even though growth is restricted. (Note : Strictly, this relates to the onset of a new growth season, that of 1930, since the individuals showing growth are those which have passed through the winter period of growth inhibition. In this connection it is interesting to observe that the L.W. regression coefficient b_x agrees very closely with the corresponding coefficients of the L. 1930 groups.)

By substitution of mean values ($\bar{x}$ and $\bar{y}$) in the regression equation, the following equation is obtained :

$$x=\cdot110y-1\cdot43$$

By making x=0, it is found that y=13, so that, on the average, maintenance demands are reduced during the winter months in the ratio of $^{13}/_{16-25}$. If small weight increases are permitted, the reduction is more strongly marked, for when x=·5, y=17, so that the ratio becomes $^{17}/_{28-36}$.

Corresponding contrast is seen in the case of the regression of y on x, for the regression coefficient

$$b_y = \frac{\cdot 628 \times 2 \cdot 93 \times 5}{2 \cdot 57} = 3 \cdot 576\ (3 \cdot 6 \pm \cdot 6)$$

(cp. Table 4, L. 1929). After substitution of means, the regression equation becomes

$$y = 3 \cdot 58x + 20 \cdot 8.$$

Thus the regression line of y on x is shifted nearer to the y zero co-ordinate, that of x on y being shifted nearer to the x zero co-ordinate, during the winter months. Moreover, both regression lines are considerably less steep than during the previous summer.

VII. Notation Used.

$\bar{X}$	Mean weight.
σ_x	Standard deviation of weight.
$\bar{x}$	Mean growth in weight.
σ_x	Standard deviation of growth.
$\bar{y}$	Mean percentage of initial body-weight as food.
D_x	Difference between arbitrary and true weight means.
D_y	Difference between arbitrary and true percentage means.
f	Frequency.
n	Total number of frequencies.
Σ	Summation.
r	Correlation coefficient.
b_x	Regression coefficient of x on y.
b_y	Regression coefficient of y on x.
x, y	Any value of the variates within ranges stated.
p	Product of deviations from means.
σ_{mx}	Standard deviations of means of x arrays.
σ_{my}	Standard deviations of means of y arrays.
η_{xy}	Correlation ratio of x on y.
η_{yx}	Correlation ratio of y on x.
$\eta^2 - r^2$	A measure of the divergence of the actual line through the means of arrays from line of regression.

VIII. SUMMARY.

The aim of the paper has been to treat the data of the Plaice experiments on Growth and Maintenance, carried out at Cawsand and Lympstone during 1929 and 1930, in a statistical manner. The experiments for each sex, year and place have been resolved into experiments with an

average plaice during the "average" 14 days of the third growth season. Growth and food-percentage indices have been provided and a fairly high degree of correlation between food and growth has been indicated, and shown to be uniform for the sexes. Regression coefficients indicating the facility with which food is utilised for purposes of growth have been worked out and have been shown to vary with place and year, but not with sex. Maintenance demands have been evaluated and shown to be slightly greater in males than in females. The diminished demands during winter months have also been evaluated. The outstanding features of the results are the distinct differences shown between the Cawsand and Lympstone plaice, which differences it is suggested arise out of size differences to a large extent.

IX. REFERENCES.

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TABLE 8.

Correlation Table of Percentage of Body-Wt. as food and Wt. Increase. Cawsand Males [1929].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x).																				Total	f×Dy	f×D²y
	13	12	11	10	9	8	7	6	5	4	3	2	+ve 1	0	−ve 1	2	3	4	5	6			
265															1						1	19	361
255								1													1	18	324
245										1				1	1						3	51	867
235																					0	0	0
225																					0	0	0
215											1										1	14	196
205																					0	0	0
195																					0	0	0
185								1		1											2	22	242
175									3												3	30	300
165							1			1		1	1	1							5	45	405
155								1	1				1								3	24	192
145	1								1	1	2		1								6	42	294
135							1			2	1			1							5	30	180
125				1								3	2		1						7	35	175
115		1					1		1	2		1	3								9	36	144
105										2	2	1	3	2							10	30	90
95	1		1							1					1				1		5	10	20
85														2							2	2	2
75								1	1												2	0	0
65											1					1	1				3	−3	3
55												1				1					2	−4	8
45							1					1	5	1							8	−24	72
35										1	3	3	9	9	1	2					28	−112	448
25												2	3	4	2	2					13	−65	325
15											1		2	3	4	5		2		1	18	−108	648
5													2	1	5	5	2		1		16	−112	784
Total	2	1	1	1	0	0	4	4	7	12	11	13	32	25	16	16	3	2	2	1	153	−20	6080
f×Dx	24	11	10	9	0	0	24	20	28	36	22	13	0	−25	−32	−48	−12	−10	−12	−7	+51		
f×D²x	288	121	100	81	0	0	144	100	112	108	44	13	0	25	64	144	48	50	72	49	1563		
np(x−x̄) (y−ȳ)	108	44	20	45	0	0	96	185	196	204	42	4	0	44	60	258	60	60	30	42	1498		

TABLE 9.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Cawsand Females [1929].

Percentage of Body-wt. as Food (= y)	Wt. Increase (gm.) (= x).																							
	14	13	12	11	10	9	8	7	6	5	4	3	2	+ve 1	0	−ve 1	2	3	4	5	6	7	Total	f×Dy	f×D²y
245															1								1	18	324
235																							1	17	289
225																							0	0	0
215																							1	15	225
205																							1	14	196
195																							0	0	0
185																	1						1	12	144
175																							0	0	0
165																							0	0	0
155								1															2	18	162
145														1									1	8	64
135	1													1	1								3	21	147
125												1		3	2								7	42	252
115								1				1	1		1								4	20	100
105		1			1				1	1	2	1	3	1	2								13	52	208
95							1	2	1		1	1	2	4	1								13	39	117
85							1	1	1					2									5	10	20
75			1			1			2	2	1			1		1							9	9	9
65						1		1		1	1	1			1								6	0	0
55										1		1			2								4	−4	4
45									1			1	2				1	1					6	−12	24
35													3	3	9				1				16	−48	144
25											1		4	9	17	5							36	−144	576
15											1	1	1	4	3	2	2	2				1	17	−85	425
5															3	1	3	3	2	2			14	−84	504
Total	1	1	1	0	1	2	2	8	7	6	8	8	16	29	43	9	7	6	3	2	0	1	161	−82	3934
f×Dx	13	12	11	0	9	16	14	48	35	24	24	16	16	0	−43	−18	−21	−24	−15	−12	0	−8	+97		
f×D²x	169	144	121	0	81	128	98	288	175	96	72	32	16	0	43	36	63	96	75	72	0	64	1869		
$n_p(x-\bar{x})(y-\bar{y})$	91	48	11	0	36	8	35	318	120	44	36	20	−11	0	77	70	54	120	75	72	0	40	1264		

TABLE 10.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Cawsand Males [1930].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x). 16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	+ve 1	0	−ve 1	2	3	4	5	Total	f×Dy	f×D²y
205														1									1	16	256
165													1										1	12	144
155									1				1										2	22	242
145					1					1													2	20	200
135									1	1		1	2			1							6	54	486
125												1	1	1									3	24	192
115						1									1	3							5	35	245
105						1	1		3			1	3										9	54	324
95											1		2	1							1		5	25	125
85	1												2		2	2	1						8	32	128
75												4		3	3								10	30	90
65												1		2	2	4	2						11	22	44
55													2	3	3	1	1		2				12	12	12
45									1		1		2	1	3	2	3			1			14	0	0
35														1		4	3	1					9	−9	9
25															5	8	10	4		1			28	−56	112
15														1	2	7	11	8	6	1			36	−108	324
5																						1	1	−4	16
Total	1	0	0	0	1	2	1	0	6	2	2	8	16	14	21	32	31	15	6	3	1	1	163	+181	2949
f×Dx	15	0	0	0	11	20	9	0	42	12	10	32	48	28	21	0	−31	−30	−18	−12	−5	−6	+146		
f×D²x	225	0	0	0	121	200	81	0	294	72	50	128	144	56	21	0	31	60	54	48	25	36	1646		
np(x−x̄)(y−ȳ)	60	0	0	0	110	130	54	0	266	114	25	148	261	82	15	0	47	62	54	20	−25	24	1447		

TABLE 11.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Cawsand Females [1930].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x).																			
	11	10	9	8	7	6	5	4	3	2	+ve 1	0	−ve 1	2	3	4	5	Total	f×Dy	f×D²y
255											1							1	20	400
245									1									1	19	361
235																		0	—	—
225									1									1	17	289
215																		0	—	—
205																		0	—	—
195			1							1								2	28	392
185																		0	—	—
175				1														1	12	144
165				1	1		2											4	44	484
155		2					1											3	30	300
145				2		1	1	1		1								7	63	567
135						1	1											2	16	128
125							1		1									3	21	147
115	1		1				1	1			1							5	30	180
105					1				1	1								3	15	75
95					1	2		1	1									5	20	80
85							2		1	2								5	15	45
75							1	2	2									5	10	20
65				1			1	1	1	3	2						1	10	10	10
55						1	3	1	3	3	1	3						15	0	0
45						1		1	2	4	5	1		1				15	−15	15
35										2	3	4		1				10	−20	40
25								1	1	3	3	5	5	2	2		1	23	−69	207
15							1	1		4	4	16	9	7	4		1	47	−188	752
5													2			1		3	−15	75
Total	1	2	2	5	3	6	15	10	15	24	20	31	16	11	6	1	3	171	+63	4711
f×Dx	9	16	14	30	15	24	45	20	15	0	−20	−62	−48	−44	−30	−6	−21	−43		
f×D²x	81	128	98	180	75	96	135	40	15	0	20	124	144	176	150	36	147	1645		
np(x−x̄) (y−ȳ)	54	160	140	252	100	96	201	32	55	0	8	144	183	148	110	30	42	1755		

TABLE 12.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Lympstone Males [1929].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x).																	+ve		−ve									
	25	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0	1	2	3	4	5	6	7	Total	f×Dy	f×D²y
245	1																										1	19	361
175						1																					1	12	144
165									1					1													2	22	242
155										1																	1	10	100
145			1					1			2	1															5	45	405
135									1			1	1														3	24	192
125					2			1							1												4	28	196
115											1			1		2											5	30	180
105										1				1				2									4	20	50
95		1		1																							3	12	48
85			1	1								1	1					1									5	10	45
75																											0	0	0
65								1								1			1								3	3	3
55										1																	1	0	0
45																1			1	1							3	−3	3
35																						1					1	−2	4
25															1	1	4	2	5	2	1						16	−48	144
15												1			1	3	1	4	5	7	3	2	2	3	2	1	35	−140	560
5																		1			1	2	2		1		7	−35	175
Total	1	1	2	2	2	1	0	3	2	3	4	4	2	3	3	8	5	10	12	10	6	5	4	3	3	1	100	+12	2852
f×Dx	23	15	28	26	24	11	0	27	16	21	24	20	8	9	6	8	0	−10	−24	−30	−24	−25	−24	−21	−24	−9	+75		
f×D²x	529	225	392	338	288	121	0	243	128	147	144	100	32	27	12	8	0	10	48	90	96	125	144	147	192	81	3667		
np(x−x̄)(y−ȳ)	437	60	168	91	168	132	0	153	152	105	180	80	44	66	0	−3	0	14	70	105	64	100	108	84	104	36	2518		

TABLE 13.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Lympstone Females [1929].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x). 22	21	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	+ve 3	2	1	0	−ve 1	2	3	4	5	6	8	(f) Total	f×Dy	f×D²y
225												1																	1	17	289
205										1																			1	15	225
195													1																1	14	196
185													1																1	13	169
175															1														1	12	144
165																													0	0	0
155																													1	10	100
145								1						1															2	18	162
135					1			1				1					1												4	32	256
125										1					1														2	14	98
115			1												1				1										3	18	108
105		1				1		1			1					1		1											6	30	150
95				1				1			1																		3	12	48
85	1				1					1																			3	9	27
75							1																						1	2	4
65							1				1										1					1			4	4	4
55												1									1								2	0	0
45																					2								4	−4	4
35																						1							1	−2	4
25																1		3	1	4	4	2	1		2				18	−54	162
15																			3	5	7	2	3	5	3	2		1	31	−124	496
5																					3	5			2		1		11	−55	275
Total	1	1	1	1	2	2	2	4	1	3	3	3	2	1	3	2	1	5	5	9	18	10	4	5	7	3	1	1	101	−19	2921
f×Dx	18	17	14	13	24	22	20	36	8	21	18	15	8	3	6	2	0	−5	−10	−27	−72	−50	−24	−35	−56	−27	−10	−12	−83		
f×D²x	324	289	196	169	288	242	200	324	64	147	108	75	32	9	12	2	0	5	20	81	288	250	144	245	448	243	100	144	4449		
np(x−x̄)(y−ȳ)	54	85	84	52	132	165	30	234	−8	175	60	125	108	27	50	2	0	5	18	96	224	205	90	140	224	63	50	48	2538		

TABLE 14.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Lympstone Males [1930].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x).																							
	22	17	11	10	9	8	7	6	5	4	3	2	+ve 1	0	−ve 1	2	3	4	5	6	7	Total	f×Dy	f×D²y
115										1												1	8	64
105																						0	0	0
95			1		1																	2	12	72
85				2					1													3	15	75
75	1					1	1		2	1		2	1	1								10	40	160
65		1					1	1	5	1	2	2	1	1	1							16	48	144
55									1	3		1	2		1	1		1				10	20	40
45									1		1				1							3	3	3
35											1	1		1			1	1	1			6	0	0
25									1			3	5	7	5	3						24	−24	24
15										1		3	2	9	7	2	2					26	−52	104
5												2		1							2	5	−15	45
Total	1	1	1	2	1	1	2	1	11	7	4	14	11	20	15	6	3	2	1	0	2	106	+55	731
f×Dx	21	16	10	18	8	7	12	5	44	21	8	14	0	−20	−30	−18	−12	−10	−6	0	−16	+72		
f×D²x	441	256	100	162	64	49	72	25	176	63	16	14	0	20	60	54	48	50	36	0	128	1834		
np(x−x̄) (y−ȳ)	84	48	60	90	48	28	42	15	120	57	14	1	0	21	26	15	16	−10	0	0	48	723		

TABLE. 15.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Lympstone Females [1930].

Percentage of Body-wt. as Food (=y).	Wt. Increase (gm.) (=x).																												
	19	18	17	16	12	11	10	9	8	7	6	5	4	3	2	+ve 1	0	−ve 1	2	3	4	5	6	7	8	Total	f×Dy	f×D²y
115						2																				2	14	98
105																										0	0	0
95						1						1														2	10	50
85				1			1			1	1	1	1	1	1											8	32	128
75	1				2	1	1				1			1												7	21	63
65		1				1	1	2		1	1		2	3	3	1	2	1								19	38	76
55						1					1	1			1	1				1	1					7	7	7
45								1							2	2	5						1			11	0	0
35								1							2	1	1	1				1			1	8	−8	8
25															1	2	7	3								13	−26	52
15											1		1		3	4	9	4	2			1	1			26	−78	234
5													1	1		1								1		4	−16	64
Total	1	1	0	1	2	6	3	4	0	2	5	3	5	6	13	12	24	9	2	1	1	2	2	1	1	107	−6	780
f×Dx	17	16	0	14	20	54	24	28	0	10	20	9	10	6	0	−12	−48	−27	−8	−5	−6	−14	−16	−9	−10	+73		
f×D²x	289	256	0	196	200	486	192	196	0	50	80	27	20	6	0	12	96	81	32	25	36	98	128	81	100	2687		
np(x−x̄) (y−ȳ)	51	32	0	56	60	225	72	21	0	30	28	30	2	9	0	18	76	51	24	−5	−6	28	24	36	10	872		

TABLE 16.

Correlation Table of Percentage of Body-Wt. as Food and Wt. Increase. Lympstone Winter ♂ and ♀ [1930].

	Wt. Increase (gm.) (=x).																
								+ve		−ve							
	8	7	6	5	4	3	2	1	0	1	2	3	4	5	Total	f×Dy	f×D²y
65				1											1	10	100
60								1							1	9	81
55				1		1									2	16	128
50										1					1	7	49
45			1												1	6	36
40			1												1	5	25
35				1	1		1								3	12	48
30				1											1	3	9
25	1					2		1							4	8	16
20							3	2	2	2					9	9	9
15							2	3	2	2	2	1			12	0	0
10					1		2	2	4	2	1	1			13	−13	13
5									1	5	4	2		1	13	−26	52
Total	1	0	2	4	2	3	8	9	9	12	7	4	0	1	62	+46	566
f×Dx	8	0	12	20	8	9	16	9	0	−12	−14	−12	0	−5	+39		
f×D²x	64	0	72	100	32	27	32	9	0	12	28	36	0	25	437		
$n_p(x-\bar{x})(y-\bar{y})$	16	0	66	125	12	36	10	11	0	3	18	15	0	10	322		

Growth in Length during the Transition from Larva to Adolescent in the Pilchard and Sprat.

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With 1 Figure in the Text.

Introduction.

In a previous paper (Ford, **1**) it was shown that during the transition from larva to adolescent in the herring, there was a progressive alteration in position of the anus and fins relative to one another and to the vertebrae. Simple models of tape and elastic were utilised to demonstrate how such changes in position could be induced on the assumption that different intervals along the body grew in length at unequal rates. It will be recalled that for the herring it was accepted that two such intervals, namely, (1) from the back of the head, along the dorsal surface, to the first ray of the dorsal fin ; and (2) from the insertion of the pelvics, along the ventral surface to the anus, remained at a steady unchanging length throughout the transition stages. Meanwhile, other body-intervals increased in length, each at its own rate.

With the necessary material available for the study, similar investigations have since been made for the sprat and the pilchard, and it is the purpose of the present publication to discuss the results so obtained.

Methods.

As in the case of the young herrings, determinations of the length of the following body-intervals were made (see Fig. 1) :—

Head	Hd.
Back of head to first ray of dorsal fin . .	Hd. to D^1.
First ray of dorsal fin to base of caudal peduncle .	D^1 to Caud. Ped.
Back of head to pelvics	Hd. to Pv.
Pelvics to anus	Pv. to An.
Anus to base of caudal peduncle . . .	An. to Caud. Ped.
Snout to base of caudal peduncle . . .	L_B.

Having completed the measurement, the data were grouped into classes according to the length of (L_B–Hd.), that is to say, according to the length of the distance from the back of the brain to the base of the caudal peduncle.

The Pilchard (*Clupea pilchardus* Walbaum).

The data for a total of 261 measured specimens were as shown in Table 1. (See p. 979.) Examining the figures relating to the two intervals (Hd. to D^1) and (Pv. to An.), it is seen that (Hd. to D^1) varies but little from an average figure of about 10·5 mm., whereas the values of (Pv. to An.) tend to increase as the value of (L_B–Hd.) increases. The pilchard thus resembles the herring in that the length from the back of the brain to the first dorsal ray appears to remain steady throughout the transition from larva to adolescent, but differs from the herring in that the distance from the pelvics to the anus increases instead of remaining unchanged throughout metamorphosis.

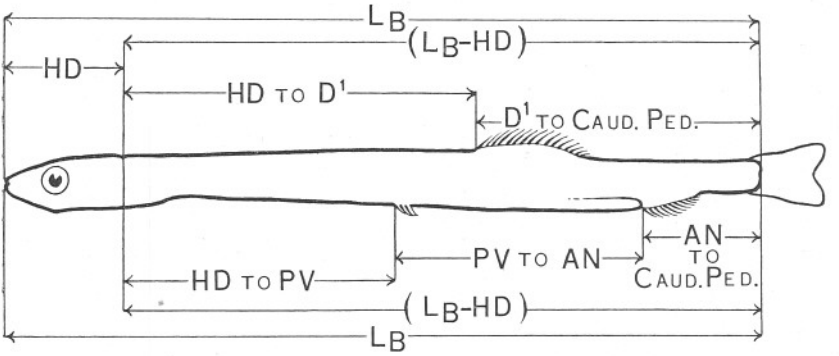

Fig. 1.—Diagrammatic representation of young clupeoid to illustrate meaning of symbols used in the text.

Snout to end of caudal peduncle	L_B.
Snout to back of head	Hd.
Back of head to end of caudal peduncle	(L_B–Hd.)
Back of head to first ray of dorsal fin	Hd. to D^1.
First dorsal ray to end of caudal peduncle	D^1 to Caud. Ped.
Back of head to pelvics	Hd. to Pv.
Pelvics to anus	Pv. to An.
Anus to end of caudal peduncle	An. to Caud. Ped.

With regard to the data in general, it has been determined that the length of a given body-interval can be expressed in terms of (L_B–Hd.) in accordance with a simple equation of the form :

$$Y=M(X)+C$$

TABLE 1.

AVERAGE VALUES (MM.) FOR EACH OF THE FOLLOWING VALUES OF L_B–HD :—

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Hd. . .	3·5	3·8	3·7	4·2	4·9	5·0	—	6·2	6·3	6·3	6·7	7·0	7·1	7·6	7·6	8·6	9·3	9·5	9·5
Hd. to D^1 .	10·0	9·8	10·5	10·5	10·6	10·8	—	10·2	10·2	10·2	10·2	10·1	10·4	10·3	10·8	10·4	10·8	10·7	12·0
D^1 to Caud. Ped. .	8·0	9·2	9·5	10·5	11·4	12·2	—	14·8	15·8	16·8	17·8	18·9	19·6	20·7	21·2	22·6	23·2	24·3	24·0
Hd. to Pv. .	6·4	6·8	7·3	7·9	8·4	8·7	—	9·75	10·2	10·4	10·8	11·0	11·5	11·8	12·4	12·7	13·6	14·5	15·0
Pv. to An. .	7·8	8·0	8·3	8·2	8·2	8·3	—	8·0	8·0	8·4	8·4	8·8	9·0	9·2	9·2	9·6	8·8	9·3	9·0
An. to Caud. Ped. .	3·6	4·2	4·4	4·9	5·4	6·0	—	7·25	7·8	8·2	8·8	9·2	9·5	10·0	10·4	10·7	11·6	11·2	12·0
Total No. of Spec. .	5	9	19	15	5	6	—	12	30	39	26	22	21	17	17	9	5	3	1

TABLE 2.

VALUES CALCULATED FROM EQUATIONS—VALUES OF (L_B–HD).

	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Hd. to D^1 .	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5	10·5
D^1 to Caud. Ped. .	7·5	8·5	9·5	10·5	11·5	12·5	13·5	14·5	15·5	16·5	17·5	18·5	19·5	20·5	21·5	22·5	23·5	24·5	25·5
Hd. to Pv. .	6·43	6·87	7·31	7·75	8·19	8·63	9·06	9·50	9·94	10·37	10·81	11·25	11·68	12·12	12·56	13·00	13·44	13·87	14·31
Pv. to An. .	8·07	8·13	8·19	8·25	8·31	8·37	8·44	8·50	8·56	8·63	8·69	8·75	8·82	8·88	8·94	9·00	9·06	9·13	9·19
An. to Caud. Ped. .	3.5	4·0	4·5	5·0	5·5	6·0	6·5	7·0	7·5	8·0	8·5	9·0	9·5	10·0	10·5	11·0	11·5	12·0	12·5

The following equations have been found to give values which approximate reasonably closely to the observed figures :—

(1) (Hd. to D^1) $=10{\cdot}5$.
(2) (D^1 to Caud. Ped.) $=(L_B\text{–Hd.})-10{\cdot}5$.
(3) (Hd. to Pv.) $={\cdot}4375\ (L_B\text{–Hd.})-1{\cdot}44$.
(4) (Pv. to An.) $={\cdot}0625\ (L_B\text{–Hd.})+6{\cdot}94$.
(5) (An. to Caud. Ped.) $=(L_B\text{–Hd.})-(\text{Hd. to Pv.})-(\text{Pv. to An.})$.

How nearly the calculated values approximate to the raw data may be learned by comparing Table 2 with Table 1. (See p. 979.) Accepting equations 1 to 5 above, it is possible to make the following statements :—

For each unit of increase in (L_B–Hd.).

(1) Hd. to D^1 increases by 0·0000 unit.
(2) D^1 to Caud. Ped. ,, ,, 1·0000 ,,
(3) Hd. to Pv. ,, ,, 0·4375 ,,
(4) Pv. to An. ,, ,, 0·0625 ,,
(5) An. to Caud. Ped. ,, ,, 0·5000 ,,

THE SPRAT (*Clupea sprattus* L.).

The corresponding data for a total of 136 sprats were :—

TABLE 3.

AVERAGE VALUES (MM.) FOR EACH OF THE FOLLOWING VALUES OF (L_B–Hd.).

	18	19	20	21	22	23	24	25	26
Hd.	3·75	3·7	3·9	4·0	4·3	4·7	4·9	5·1	5·5
Hd. to D^1	9·25	9·6	10·0	10·7	10·7	11·1	11·7	11·9	11·8
D^1 to Caud. Ped.	8·75	9·4	10·0	10·3	11·3	11·9	12·3	13·1	14·2
Hd. to Pv.	7·1	7·5	8·1	8·8	9·2	9·7	10·7	11·5	11·5
Pv. to An.	6·4	6·4	6·7	6·4	6·5	6·2	5·6	6·5	5·7
An. to Caud. Ped.	4·5	5·1	5·2	5·8	6·3	7·1	7·7	7·0	8·8
Total No. of Spec.	8	19	15	19	25	16	14	14	6

Referring as before to the values of (Hd. to D^1) and (Pv. to An.), it is seen that the former interval increases as the value of (L_B–Hd.) increases, while the latter oscillates about a mean of 6·3, with perhaps a tendency even to decrease as (L_B–Hd.) increases. Thus the sprat agrees with the herring in that the distance from the pelvics to the anus does not increase during the transition from larva to adolescent, but differs from it in that the distance from the back of the brain to the first dorsal ray

increases instead of remaining at a steady length. Comparing the sprat with the pilchard, it is seen that the interval (Hd. to D^1) increases in the sprat but remains steady in the pilchard, whereas the interval (Pv. to An.) remains steady in the sprat but increases in the pilchard. These comparisons may be summarised thus :—

	HERRING.	PILCHARD.	SPRAT.
Hd. to D^1 . .	Constant.	Constant.	Increases with L_B.
Pv. to An. . .	Constant.	Increases with L_B.	Constant.

Utilising the data in general, it has been found that the following equations may be used as mathematical summaries for the sprat :—

(1) (Hd. to D^1) $=\cdot412\ (L_B\text{–Hd.})+1\cdot79$.
(2) (D^1 to Caud. Ped.) $=(L_B\text{–Hd.})-(\text{Hd. to } D^1)$.
(3) (Hd. to Pv.) $=\cdot571\ (L_B\text{–Hd.})-3\cdot2$.
(4) (Pv. to An.) $=6\cdot26$.
(5) (An. to Caud. Ped.) $=(L_B\text{–Hd.})-(\text{Hd. to Pv.})-(\text{Pv. to An.})$.

In Table 4, the values calculated from the above equations are shown for values of (L_B–Hd.), ranging from 18 mm. to 26 mm. As was the case with the pilchard, it is seen that the calculated values (given in Table 4) are not greatly different from the observed data (given in Table 3).

TABLE 4.

VALUES OF (L_B–HD.).

	18	19	20	21	22	23	24	25	26
Hd. to D^1 . . .	9·2	9·61	10·02	10·44	10·85	11·26	11·67	12·09	12·50
D^1 to Caud. Ped. . .	8·8	9·39	9·98	10·56	11·15	11·74	12·33	12·91	13·50
Hd. to Pv. . . .	7·09	7·66	8·23	8·8	9·37	9·94	10·52	11·09	11·66
Pv. to An. . . .	6·26	6·26	6·26	6·26	6·26	6·26	6·26	6·26	6·26
An. to Caud. Ped. . .	4·65	5·08	5·51	5·94	6·37	6·80	7·22	7·65	8·08

Thus for each unit of increase in the length of (L_B–Hd.) :

(1) Hd. to D^1) increases by ·412 unit.
(2) D^1 to Caud. Ped. ,, ,, ·588 ,,
(3) Hd. to Pv. ,, ,, ·571 ,,
(4) Pv. to An. ,, ,, ·000 ,,
(5) An. to Caud. Ped. ,, ,, ·429 ,,

COMPARISONS BETWEEN SPECIES.

Consider, first, the growth in length along the dorsal surface. An increase of one unit in the length of (L_B–Hd.) is in each species the sum

of the increases of (Hd. to D^1) and (D^1 to Caud. Ped.). These latter are as follows :—

INCREASES PER UNIT INCREASE IN (L_B–Hd.).

	Herring.	Pilchard.	Sprat.
Hd. to D^1	nil	nil	·412
D^1 to Caud. Ped. . .	1·0	1·0	·588
Total . .	1·0	1·0	1·000

Thus for each unit increase in the length of (L_B–Hd.) the first dorsal ray is being brought relatively nearer the head in all three species, but more slowly in the sprat than in the herring or pilchard.

Unit increase in length of (L_B–Hd.) along the *ventral* surface is shared among three intervals, namely (Hd. to Pv.), (Pv. to An.), and (An. to Caud. Ped.). In the three species these individual increments are :—

INCREASES PER UNIT INCREASE IN (L_B–Hd.).

	Herring.	Pilchard.	Sprat.
(Hd. to Pv.) . . .	·455	·4375	·571
(Pv. to An.) . . .	nil	·0625	nil
(An. to Caud. Ped.) . .	·545	·5000	·429
Total . .	1·000	1·0000	1·000

It is seen that in the sprat the greater part of each unit increase in (L_B–Hd.) is added to the interval (Hd. to Pv.), whereas in both the herring and pilchard, particularly the former, the major increase is in the interval (An. to Caud. Ped.). Dropping the use of symbols, this is to say that in the sprat the greater part of each unit increase in the body-length is added in front of the pelvic fins, whereas in the herring and pilchard it is added post-anally.

It is instructive, also, to consider the changes in relative positions of the pelvic fins and anus as the result of unit increase in the length of (L_B–Hd.). Referring to Table 2, it is noted that in a pilchard in which (L_B–Hd.) is 18 mm. the interval (Hd. to Pv.) measures 6·43 mm. When (L_B–Hd.) is 19 mm. the interval (Hd. to Pv.) is 6·87 mm. That is to say, an increase of 1 mm. in (L_B–Hd.) results in an alteration of the proportion $\frac{\text{(Hd. to Pv.)}}{\text{(L_B–Hd.)}}$ from $\frac{6{\cdot}43}{18}$ to $\frac{6{\cdot}87}{19}$, or from ·357 to ·361. In effect this means that as the result of unit increase in (L_B–Hd.) the pelvics make a relative movement away from the head. Again referring to Table 2, it is noted that in a pilchard in which (L_B–Hd.) is 18 mm. the interval (An. to Caud. Ped.) is 3·5 mm., whereas at 19 mm. the same interval measures 4·0 mm. Thus an increase of 1 mm. in (L_B–Hd.) results

in an alteration of the proportion $\frac{\text{(An. to Caud. Ped.)}}{(L_B\text{–Hd.})}$ from $\frac{3{\cdot}5}{18}$ to $\frac{4{\cdot}0,}{19}$ or from ·19 to ·21. This implies a relative movement of the anus towards the head. Hence in the pilchard each unit increase in (L_B–Hd.) causes a slight alteration in relative position of both pelvic fins and anus, the movement being *away* from the head in the case of the pelvics, but *towards* the head in the case of the anus.

Turning to the sprat, it is seen from Table 4 that when (L_B–Hd.) is 18 mm. the interval (Hd. to Pv.) measures 7·09 mm., while at 19 mm. it is 7·66 mm. long. For unit increase in (L_B–Hd.) therefore the proportion $\frac{\text{(Hd. to Pv.)}}{(L_B\text{–Hd.})}$ changes from $\frac{7{\cdot}09}{18}$ to $\frac{7{\cdot}66,}{19}$ or from ·39 to ·40. Hence, as in the pilchard, the pelvics make a relative movement away from the head, but it is here very slight. Table 4 also shows that in the sprat in which (L_B–Hd.) is 18 mm. the interval (An. to Caud. Ped.) measures 4·65 mm., while at 19 mm. it is 5·08 mm. Unit increase in (L_B–Hd.) results in an alteration of the proportion $\frac{\text{(An. to Caud. Ped.)}}{(L_B\text{–Hd.})}$ from $\frac{4{\cdot}65}{18}$ to $\frac{5{\cdot}08,}{19}$ or from ·26 to ·27. Hence, as in the pilchard, there is a relative movement of the anus towards the head for each unit increase in (L_B–Hd.). Now it has already been shown (Ford, **1**) that in the herring the pelvics move backward and the anus forward relatively as (L_B–Hd.) increases, so that all three species are alike in this respect.

Before finishing this discussion of growth along the ventral surface, attention is directed to the relative lengths of the ventral body-intervals as (L_B–Hd.) increases. From Table 2 it is learned that in the pilchard of 18 mm. the interval (Hd. to Pv.) is shorter than (Pv. to An.), but that with increasing length of (L_B–Hd.) the difference between these two intervals becomes less and less until at 23 mm. the interval (Hd. to Pv.) actually exceeds that of (Pv. to An.). From then onwards the margin of excess increases steadily. In the sprat, however (see Table 4), the interval (Hd. to Pv.) is already greater than (Pv. to An.) when (L_B–Hd.) is at its smallest length of 18 mm., and successive increases in (L_B–Hd.) merely augment the initial difference between the two intervals. Again, in both the pilchard and sprat the length of (Pv. to An.) at 18 mm. is greater than that of (An. to Caud. Ped.), but as the fish grows in length the difference between the intervals diminishes until both are of the same length. This occurs at ca. 28 mm. in the pilchard, but at ca. 21·5 mm. in the sprat. At greater lengths of (L_B–Hd.) the interval (An. to Caud. Ped.) is longer than (Pv. to An.).

Having considered growth in length along the dorsal surface, as distinct from that along the ventral surface, it is now desirable to discuss the one in conjunction with the other. We have seen that in the three species the dorsal fin makes a relative movement towards the head, the pelvics away from the head, and the anus towards it. How does the position of the first dorsal ray alter with respect to the pelvics and anus? Consider, first, the situation with regard to the first dorsal ray and the pelvics. The first dorsal ray is gradually shifting towards the head, but the pelvics away from it, and this holds in all three species. If carried on long enough, therefore, the time must come when the first dorsal ray, initially situated at a level well posterior to the pelvics, will come to lie immediately above the pelvics, and then later to be in front of them. This does actually occur in both the herring and pilchard, but in the sprat the process of relative shift appears to cease before the first dorsal ray has quite reached the level of the pelvics. A glance at the diagrams given by Lebour (**2**) will confirm this.

In the case of the first dorsal ray and the anus, we have seen that both tend to move relatively towards the head. Obviously, therefore, it is necessary to take into account the rate at which each is moving. On page 980 it was shown that for unit increase in (L_B–Hd.), the resultant increase in the interval (D^1 to Caud. Ped.) in the pilchard was 1·0 unit. This means that the first dorsal ray is brought 1 mm. farther away from the end of the caudal peduncle. During this time the interval (An. to Caud. Ped.) increases by ·5 mm., which means that the anus is brought farther forward by ·5 mm. The anus and the first dorsal ray have thus become still further separated by (1·0 − ·5) = ·5 mm. In the case of the sprat, unit increase in (L_B–Hd.) brings about an increase of ·588 mm. in the interval (D^1 to Caud. Ped.), and of ·429 mm. in the interval (An. to Caud. Ped.). The anus and the first dorsal ray in this species thus become further separated by (·588 − ·429) = ·159 mm. as compared with ·5 mm. in the pilchard. Similar working with the herring shows that the additional separation amounts to ·455 mm.

SUMMARY.

Growth in length during the transition from larva to adolescent in the pilchard and sprat has been analysed, and simple straight-line equations deduced from observed data have been used to demonstrate how the different intervals along the dorsal and ventral surfaces of the body alter in length and proportion as development proceeds.

In the herring, pilchard, and sprat at least one of the body-intervals remains for all practical purposes unaltered in length during the transition. In the herring there are two such intervals, namely, (1) the

distance from the back of the brain along the dorsal surface to the insertion of the first dorsal fin-ray, and (2) the distance from the insertion of the pelvic fins along the ventral surface to the anus. In the pilchard and sprat one of the above two remains stationary, but the other increases in length ; in the pilchard the fixed interval is the distance from the back of the brain to the first dorsal fin-ray, and in the sprat it is the distance from the pelvics to the anus.

In the herring and pilchard the greater part of each unit of increase in the length of the body ventrally from the back of the head to the end of the caudal peduncle is added in front of the pelvic fins, whereas in the sprat this is added post-anally.

Along the dorsal surface the first ray of the dorsal fin in the herring, pilchard, and sprat is gradually brought to lie relatively nearer and nearer to the head as development continues. Along the ventral surface the pelvics and anus also undergo alteration in relative position, the pelvics *away* from the head but the anus *towards* it.

In the herring and pilchard the relative forward movement of the first dorsal ray and the relative backward movement of the pelvics is carried on sufficiently to cause a " cross-over " in position on the body, so that whereas initially the first dorsal ray is posterior to the pelvic fins, it is eventually brought to lie anterior to the pelvics. In the sprat this does not occur, and the first dorsal ray remains posterior to the pelvics throughout development.

In the herring, pilchard and sprat a greater proportion of each unit increase in total length is added to the distance from the first dorsal ray to the end of the caudal peduncle than to the distance from the anus to the end of the caudal peduncle, so that as development proceeds the first dorsal ray becomes further and further removed from the anus.

During development the relative lengths of the different body-intervals alter appreciably. In the pilchard the distance from the back of the head to the pelvic fins is at first shorter than that from the pelvics to the anus, but ultimately it becomes the greater of the two. Similarly the distance from the anus to the end of the caudal peduncle commences by being smaller than that from the pelvics to the anus, but eventually comes to exceed it.

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2. Lebour, M. V. The Larval and Post-Larval Stages of the Pilchard, Sprat and Herring from Plymouth District. Journ. Mar. Biol. Assoc., N.S., Vol. XII, No. 3, 1921.

Changes in Length during the Larval Life and Metamorphosis of the Freshwater Eel (*Anguilla vulgaris* Turt.).

By

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With 5 Figures in the Text.

Introduction.

In other papers (Ford, **2** and **3**) attention was directed to a study of the changes in length which occur during the transformation of the transparent eel-shaped larval clupeoid into the silvery and scaled adolescent fish. The change in position of the anus and fins relative to the vertebræ was considered in connection with the altering proportions of the different body intervals as development proceeds, and simple models were used to illustrate important features.

Now the freshwater eel has its transparent larval stage and metamorphosis. As in the clupeoid, length-proportions change during development, while anus and fins undergo marked migrations with respect to the myomeres. It was therefore thought to be of no little interest to analyse the length-changes during development in a manner similar to that adopted for the herring, sprat and pilchard. Professor Johannes Schmidt most kindly supplied me with material upon which to work, and I have made much use of data already published by him in reports on his great pioneer investigations. I have also drawn extensively from the data given by Dr. Leon Bertin in his paper on the migrations of the anus in the eels during ontogeny. I may be permitted to add that much which follows is suggestive in nature, rather than proven fact. Nevertheless, it should prove of interest in its direct bearing upon questions of fundamental biological importance.

Following the principle adopted by the Italian zoologist Massimo Sella in 1911, Schmidt (**6**, pages 9 and 10) determined the total length and the length of the tail (ano-caudal distance) for each of a representative series of larval *Anguilla vulgaris* Turt. and plotted in a graph the ratio $\left(\frac{\text{total length}}{\text{length of tail}}\right)$ for eight average values of the total length. Schmidt's

figure is reproduced here in Figure 1. It will be seen that for a total length of 15 mm. the above ratio has a value of 4·35, whereas at a total length of 85 mm. it has fallen to 3·20. That is to say, at a total length of 15 mm. the ano-caudal distance is $\frac{15}{4{\cdot}35}$ =3·45 mm., and at 85 mm. it is $\frac{85}{3{\cdot}2}$=26·55 mm.

In the accompanying Figure 2, the line AB measures 15 units of length, of which PB represents 3·45 units. CD is drawn parallel to AB and measures 85 units of length, of which QD represents 26·55 units. The straight line connecting point A with point C is at right-angles to AB

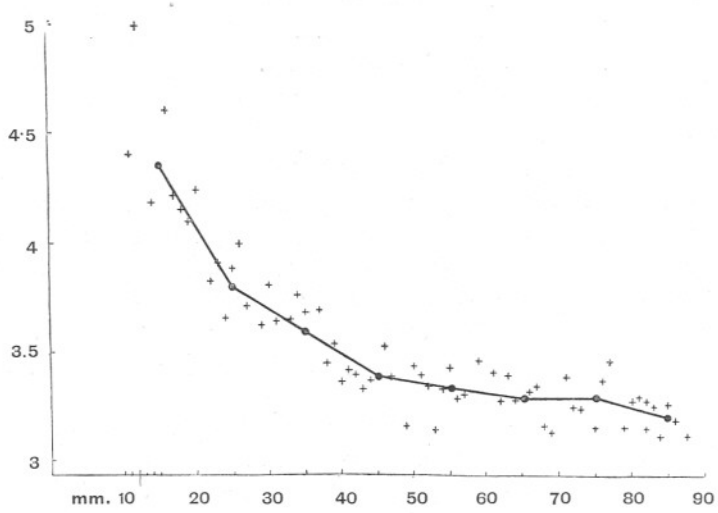


FIG. 1.—European Fresh-Water Eel (*Anguilla vulgaris* Turt.). Showing ratio between total length and length of tail during larval development. (After Schmidt, **6**, page 10, figure 3.)

(or CD) and is of a length equal to the difference between the lengths of AB and CD, namely, 85—15=70 units. Furthermore, AC is divided into equal intervals of 10 units at points *a* to *f*, and straight lines are drawn parallel to AB (or CD) from each of the points *a* to *f* to intersect PQ and BD.

Now it is obvious that in taking the step of 10 units downwards from point A to point *a*, the length *ag* is greater than AB by an amount equal to one-seventh of the difference (CD–AB) which would be brought about by proceeding the whole distance of 70 units from A to C. Similarly, *pg* exceeds PB by an amount equal to one-seventh of the difference between QD and PB.

Let us assume that this figure is a diagrammatic representation of the manner in which a larval freshwater eel at Schmidt's 15 mm. stage

grows in length to the 85 mm. stage, PB and QD being the corresponding lengths of the tail (ano-caudal distances). The values of the total length and length of tail for successive steps of 10 units along AC in the direction of point C, and of the ratio $\left(\frac{\text{Total length}}{\text{Length of tail}}\right)$ are :—

TOTAL LENGTH.	LENGTH OF TAIL.	$\left(\frac{\text{TOTAL LENGTH}}{\text{LENGTH OF TAIL.}}\right)$
15	3·45	4·35
25	6·75	3·70
35	10·05	3·48
45	13·35	3·37
55	16·65	3·30
65	19·95	3·26
75	23·25	3·23
85	26·55	3·20

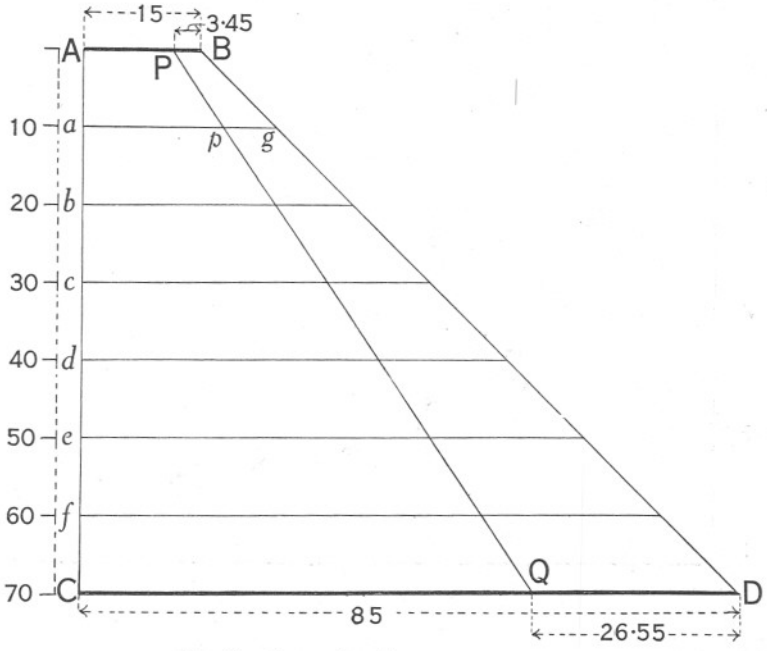


FIG. 2.—For explanation see text page 988.

In Figure 3 the values of the ratio $\left(\frac{\text{Total length}}{\text{Length of tail}}\right)$ have been superimposed on Schmidt's figures (see my Figure 1) and it will be seen that they are quite a fair approximation. In other words, there is evidence for the

assumption that *during growth as a larva, the length of the tail increases uniformly by 3·3 mm. for each increase of 10 mm. in the total length.*

This being so, it can be shown by simple calculation that *the pre-anal length increases uniformly by 6·7 mm. for each increase of 10 mm. in the total length.*

These two deductions may be expressed in the form of equations, thus :—

$$Y_m = 0{\cdot}33\ M - 1{\cdot}50$$
$$Z_m = 0{\cdot}67\ M + 1{\cdot}50$$

where Y_m=Ano-caudal distance at a total length of M millimetres
Z_m=Pre-caudal length ,, ,, ,,

Calculating the value of Y_m when M is 12,

$$Y_{12} = 0{\cdot}33\ (12) - 1{\cdot}5$$
$$= 3{\cdot}96 - 1{\cdot}5$$
$$= 2{\cdot}46$$

The value of the ratio $\left(\frac{\text{Total Length}}{Y_{12}}\right)$ is thus $\frac{12}{2{\cdot}46} = 4{\cdot}88$.

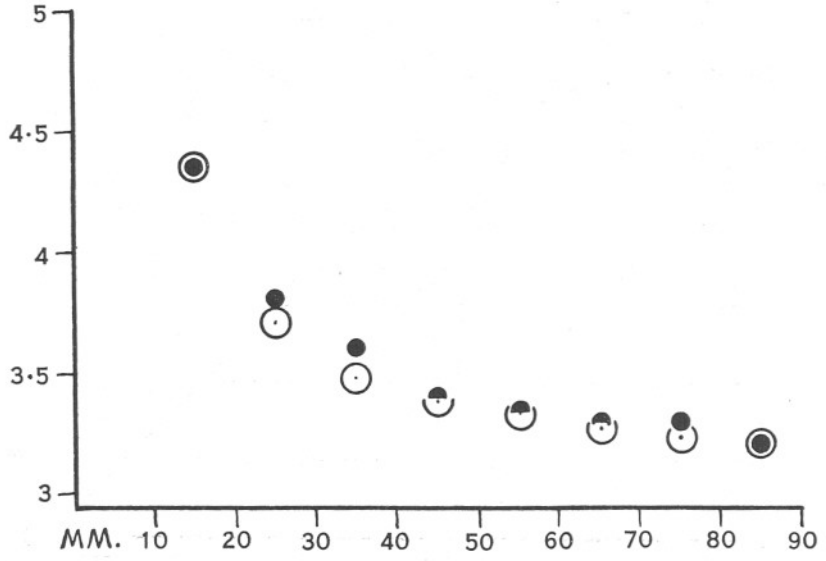


FIG. 3.—Ratio between total length and length of tail during development. Solid black dots are Schmidt's averages (see Fig. 1). Dots within circles are values calculated as explained in text in page 989.

Consulting Schmidt's graph once more (*vide* my Figure 1) it is seen that the solitary record for the ratio at a total length of 12 mm. is about 4·98, a value not greatly different from the above one of 4·88.

The increase in the proportionate length of the tail from the smallest

to the largest larva results in a relative movement of the anus along the ventral surface of the body in the direction of the head. It is important to note, however, that the anus appears not to change its position with respect to the myomere under which it lies. Writing on this point, Bertin (**1**, page 329) summarises the observations by Lea, Grassi and Schmidt on the position of the anus in leptocephaline stages of *Anguilla vulgaris* varying from 8·5 mm. to 83 mm. in length—observations which clearly demonstrate that the anus remains under practically the same myomere throughout. It can be stated, therefore, that growth in length along the vertebral column must agree with that along the ventral surface of the body in being relatively greater post-anally than pre-anally. Otherwise the anus would alter its position with respect to myomeres as growth proceeded. Nor is there any evidence that growth in length along the dorsal surface of the body is of a different nature, since the dorsal fin possesses its full complement of rays at an early leptocephaline stage and its anterior end appears to remain in a constant position relative to the anus throughout leptocephaline life. Thus it may be concluded that *the leptocephalus as a whole increases in length differentially, growth in length being greater post-anally than pre-anally. Neither anus nor dorsal fin alter their position relative to the myomeres.*

Length-Changes during Metamorphosis.

As an introduction to the study of the changes in length which occur during the transformation of the flattened leptocephalus into the rounded elver, I draw attention to a footnote to one of Schmidt's earlier papers (Schmidt, **4**, page 167) on the metamorphosis :—

" It is very interesting to note the gradual change in the nerves which pass to the rays and interspinous rays in the dorsal and anal fins. Though all or at any rate the majority of the rays are present even in the 1st stage, yet both the dorsal and the anal fin are much shorter than in the following stages. In the 1st stage we see how the nerves emerge from the column *far in front of even the beginning of the fins* and are therefore *closely packed together* opposite the fins themselves. In the following stages, when the front part of the fins grows much forwards the nerves become *shortened* and more *separated*, and at the same time their direction relative to the longitudinal axis is quite changed (from being almost parallel or forming a very acute angle at the most with this they become almost perpendicular to it)."

It is a point of great significance that in the fully-grown leptocephalus the rays of the fins are innervated, *not* from the myomeres immediately above or beneath which they lie, but from myomeres some considerable distance in front. Using a binocular microscope, it is possible to trace in

a formalin-preserved leptocephalus the path of an individual nerve from its ending in the fin, forward to the myomere from which it emerges. In a leptocephalus 68 mm. long, having a total of 115 myomeres, I determined that the nerve supplying the first ray of the dorsal fin emerged from the 25th myomere (counted from the head). In contrast with this, the fin ray itself lay immediately above the 65th myomere, that is, forty myomeres farther back towards the tail. Similarly, the first anal ray, lying beneath the 71st myomere, was innervated from the 35th myomere. The observed particulars of this leptocephalus may be summarised thus :—

Length (Snout to end of body) . .	68 mm.
Total number of myomeres . .	115
Snout to 25th myomere . . .	18 mm.
Snout to 35th myomere . . .	25·5 mm.
Snout to 40th myomere . . .	29 mm.
Snout to 46th myomere . . .	33 mm.
Snout to 65th myomere . . .	46 mm.
Snout to 71st myomere . . .	49·5 mm.

In Figure 4A I have given a diagrammatic representation of the leptocephalus, incorporating the above data together with an indication of the paths of the nerves emerging from selected myomeres. I next draw attention to Figure 4B which lies immediately below Figure 4A. Instead of using the outline of a leptocephalus, that of an elver has been employed, the total length being the same. No change has been made in the position of the myomeres, but the nerves emerging from them have been made to pass out at right-angles to the vertebral column, instead of running far back as in Figure 4A. By so doing, however, the position of the dorsal and anal fins with respect to the myomeres, and the proportions of the several body intervals have been greatly altered. The first dorsal ray has come forward forty myomeres to lie over the 25th myomere, while the distance from the snout to the first dorsal ray has become shortened from 46 mm. to 18 mm. The distance from the first dorsal ray to the posterior end of the body, on the other hand, has increased from 22 mm. to 50 mm. Similarly, the anus has advanced thirty-six myomeres and now lies under the 35th myomere, while the distance from the snout to the anus has been reduced from 49·5 mm. to 25·5 mm. The ano-caudal distance has increased from 18·5 mm. to 42·5 mm.

Comparison with the measurements of actual specimens reveals the fact that Figure 4B is a good representation of the proportions of an elver at a length of 68 mm. The significance of this lies in the fact that a close approximation to the elver has been reached by a simple readjustment of the characters of the leptocephalus so that fins and anus are made to lie

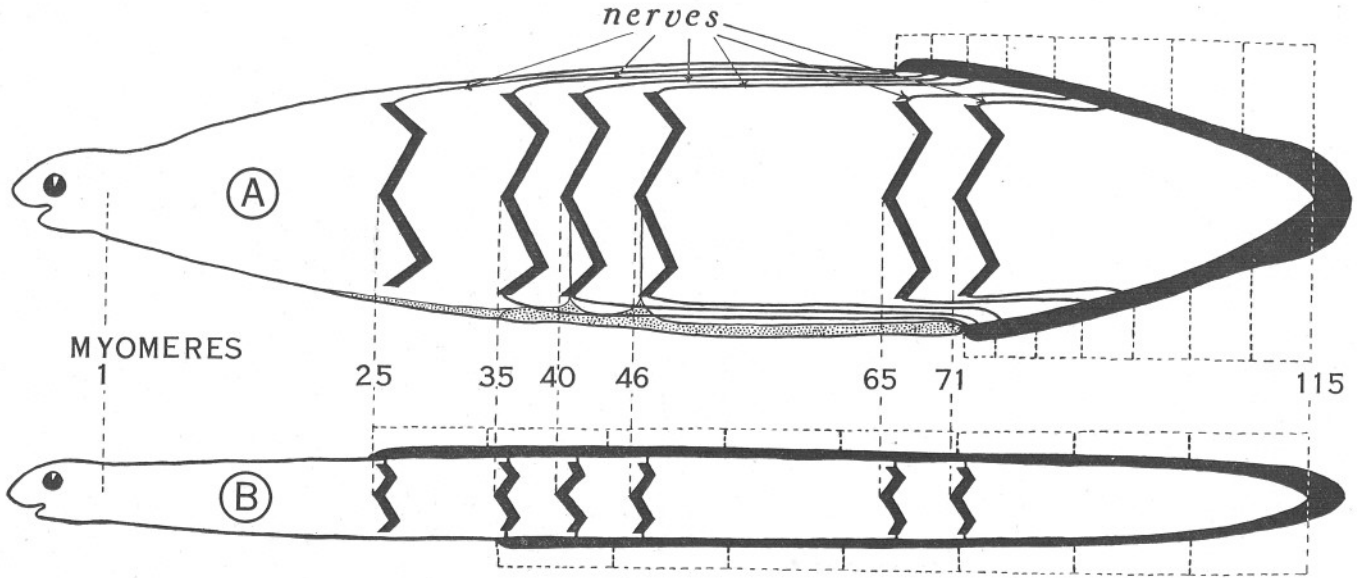


FIG. 4A.—Diagrammatic representation of leptocephalus described in text in page 992. Six myomeres and the dorsal and anal fins are shown in solid black. The nerves from the myomeres to the fins run almost parallel to the spinal column for the great part of their length.

FIG. 4B.—Hypothetical elver deduced from the leptocephalus represented in Fig. 4A. The myomeres remain in the same position as in the leptocephalus, but the nerves are now placed at right-angles to the spinal column. The new positions of the dorsal and anal fins are indicated in solid black.

immediately opposite the myomeres from which they are innervated, instead of being held remote from them.

It is at once realised that the length-changes of the intervals along the dorsal and ventral surfaces of the body during metamorphosis are very different from those which take place while the fish is growing as a leptocephalus. Before metamorphosis, every interval steadily increases in length, growth as a whole being such that the first dorsal ray and anus come gradually to occupy a position relatively nearer the head, although neither changes its orientation with respect to the myomeres. But while the fish is actually undergoing metamorphosis, some intervals increase rapidly in length at the direct expense of others, so that the resultant forward movements of the first dorsal ray and anus are not relative but real. Moreover, in the process of moving, the first dorsal ray and the anus entirely change their position with respect to the myomeres.

Biological Significance of Results.

If Figures 4A and 4B really depict the principle underlying the transformation of the leptocephalus into the elver, save only that no account is taken of the undoubted shrinkage in total length, then there remain many interesting morphological problems to be solved. How do the nerves shorten ? How does the dorsal fin grow forward at the expense of the predorsal portion of the upper surface ? How does the anus come to lie so much further forward ? Some further information concerning the forward movement of the fins and anus can alone be offered here. The examination of the fins of the leptocephalus shows that the fin rays are closely packed anteriorally, but become progressively wider and wider apart towards the posterior end (see Fig. 4A). It may well be, therefore, that the first ray moves forward as the result of the rapid growth of tissues between the fin-rays, causing the fin to " open out " (rather as a collapsible bellows lengthens as it is opened out), until ultimately the rays are uniformly wide apart over a longer length (as suggested in Fig. 4B). Concerning the movement of the anus, Bertin (**1**, page 332) speaks of the autonomous shortening of the digestive tube, and the descriptions given by Schmidt show that the rectal portion of the larval gut gradually shortens during metamorphosis.

It cannot have escaped attention that Figures 4A and 4B raise an interesting question in phylogeny. Which is the more primitive position of the anus—posterior as in the leptocephalus, or anterior as in the elver ? In the leptocephalus, the anus lies a considerable distance behind the myomere from which it is apparently innervated, but moves forward to lie beneath this myomere in the elver. Thus, in effect, Figures 4A and 4B may be interpreted to imply that *the leptocephalus is a specialised form of*

larva in which the anus is temporarily held in a posterior position, moving forward to its true position during metamorphosis.

In this connection, it is instructive to refer to a Table given by Bertin (**1**, page 333, Table VI) in which the French investigator has summarised data concerning the number of pre-anal myomeres and total myomeres in the leptocephaline and adult stages of 15 species of eel. Bertin calculates for each species what he calls "l'amplitude des déplacements anaux," as a convenient measure of the anal displacement during metamorphosis. This amplitude is in the form of a percentage $\left(\frac{a_2 - a_1}{t}\right) 100$, where a_1 and a_2 are the numbers of pre-anal myomeres in the leptocephaline and adult stages respectively, while t is the total number of myomeres for the species in question. It will be easily understood that if the value of this percentage-amplitude is small for a given species, the anus has migrated over a small number of myomeres, compared with the total number of myomeres in the fish. Conversely, a high value of the percentage-amplitude indicates that the anus has moved over a high proportion of the total number of myomeres. It is evident from Bertin's calculations that species differ greatly in the magnitude of the anal displacement during metamorphosis, for the values of his percentage-amplitude range from 0% to 49% in the 15 species for which data are given.

It is, however, important to observe that the value of the percentage-amplitude appears to be dependent upon the position the anus occupies in the leptocephalus. If the anus is far back towards the tail of the leptocephalus in relation to the myomeres, the percentage-amplitude is comparatively high, whereas if the anus is already well forward in the leptocephalus, the percentage-amplitude is small. It is as if in all species there were an attempt during metamorphosis to bring the anus forward to a fixed position in the adult, so that the number of pre-anal myomeres shall be about one-third of the total number. Hence, if in a leptocephalus the anus lies far back, there is a relatively large forward movement of the anus during metamorphosis ; conversely, if in the leptocephalus the anus is well forward, little movement is necessary during metamorphosis to bring the anus to its adult position.

As an example, we may use the data on which Figures 4A and 4B are based. In the leptocephalus of the freshwater eel (Fig. 4A) the anus lies beneath the 71st myomere, but in the elver (Fig. 4B) it is under the 35th. The total number of myomeres is 115. Thus, in the elver the ratio $\left(\frac{\text{number of pre-anal myomeres}}{\text{total number of myomeres}}\right)$ is $\frac{35}{115}$, which is approximately $\frac{1}{3}$. During metamorphosis, the anus has moved from the 71st to the 35th myomere, so that the percentage-amplitude is $\left(\frac{71-35}{115}\right) 100$, or 31%.

Actually, the ratio $\left(\frac{\text{number of pre-anal myomeres}}{\text{total number of myomeres}}\right)$ in the adult is not invariably the same, but differs from species to species. Nevertheless, the values of this ratio tend to group themselves about an average of $\frac{1}{3}$, whereas in the leptocephalus, the corresponding values are widely separated and show no such tendency to group. That this is so is seen in the following Table which summarises Bertin's data for all the species dealt with by him, except *Sphagebranchus cœcus* which he regards as a "mélange probable de deux races" :—

Number of Species having the following values of ratio $\left(\frac{\text{Number of pre-anal myomeres}}{\text{Total number of myomeres}}\right)$:—

	·2–·29	·3–·39	·4–·49	·5–·59	·6–·69	·7–·79	·8–·89	·9–·99
Adult	4	6	4	–	–	–	–	–
Leptocephalus	1	2	4	1	2	2	1	1

Thus, with regard to the position of the anus in relation to the myomeres, the eel species considered by Bertin agree more closely the one with the other in the adult stage than in the leptocephalus—a fact which is of some significance when considering the question of the morphology of the ancestral larva of the eel. It certainly lends support to the view that in the latter the anus lay beneath the myotome from which it was innervated, and was situated in the fore part of the body. Those present-day leptocephalid larvæ which have the anus far back beneath a posterior myotome, although the corresponding spinal nerves arise from an anterior point, must, in this event, be regarded as specialised forms. The degree of specialisation in a given leptocephalus may be estimated by calculating the value of Bertin's "percentage-amplitude" of the anal displacement during metamorphosis. If the value is large, the specialisation is great. To judge from Bertin's data, it would seem that the leptocephaline stages of the species of Synaphobranchus, Congermuræna, Conger, and Anguilla must be considered highly specialised, whereas those of Sphagebranchus, Saurenchelys, Nettastoma, and Muræna are the least so.

Now Schmidt (**5**, page 340) has already suggested the division of the Eel-fishes into two biological groups : (1) those which spawn far from the coasts over great depths, and (2) those which spawn in comparatively shallow water inside or near the 200 m. line. In his first group Schmidt places *Conger vulgaris*, *Conger* (=*Congermuræna*) *mystax*, and *Anguilla vulgaris*. These are species which, as indicated above, have highly specialised larvæ. To his second group Schmidt refers *Ophichthys* (=*Sphagebranchus*) *imberbis*, and *Muræna helena*—and these are species in which the leptocephalus is least specialised.

The conception of a specialised larva is thus brought into direct association with that of an adult habit. Eels which spawn far from the coast

have a specialised leptocephalus, while those which spawn in coastal waters have not. Furthermore, from our discussion of the structure of the ancestral larval eel, we see the possibility that both it and the primitive parent were inhabitants of inshore waters.

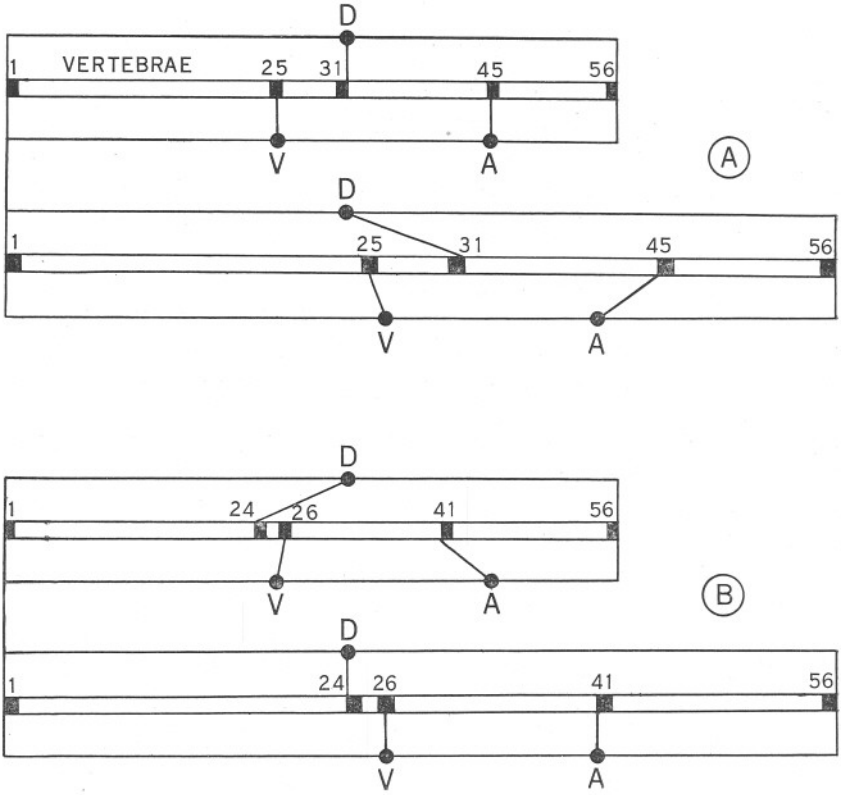
Anguilla and Clupea.

In the growth-changes during early life, the eel, herring, sprat, and pilchard agree in some respects but differ in others. In each instance, the early larva is transparent with the anus situated beneath a posterior myomere. This larva grows and ultimately becomes transformed into an adolescent bearing the familiar characters of the adult. In doing so, the anus is brought forward in relation to the myomeres, and fins undergo a marked change in position. Furthermore, it has been shown in the preceding pages of this paper and elsewhere (Ford, **2** and **3**) that such changes in length-relations can be expressed in terms of the varying rates at which the different body-intervals alter in length as development proceeds.

This generalised agreement between the eel and the clupeoids has its interest, but there are equally important differences. We have seen that the leptocephalus grows in length while still retaining its typical leptocephaline form. Although growth in length is differential, being greatest at the tail-end, the anus and fins do not alter their position relative to the myomeres during this growth as a leptocephalus. The marked readjustment of body proportions whereby the anus and fins assume their adult position takes place as a distinct process of metamorphosis from leptocephalus to elver. In the larval clupeoids, however, differential growth in length is such that the anus and fins steadily change their position relative to the myotomes as the larva increases in length. This amounts to a process of gradual transformation into an adolescent of larger size, as opposed to one in which a larva first grows as a larva, and then changes to an adolescent by a distinct act of metamorphosis. The end result may be the same in the two cases, in that the anus is brought forward to its adult position, but the " timing " of the developmental events leading to the end result is different. In the clupeoid, growth in total length and anal migration proceed simultaneously; in the eel, growth in total length takes place while the fish is yet a leptocephalus, and the anal migration is postponed until later.

We know that the larval life of the eel is very lengthy compared with that of the clupeoid, and we have discussed the probability that the leptocephalus is a specialised larval form, organised in a manner suited to the conditions imposed by the oceanic spawning of the eel. We have suggested that the position of the anus in the after part of the body of the

leptocephalus is one of the special modifications, and have referred to the manner in which the spinal nerves have become drawn-out so that they end at a point much farther back than their origin in the spinal cord. What is the situation in the young of the clupeoid ? What can we learn



FIGS. 5A and 5B.—*Clupea harengus*. Possible alternatives in innervation of young stages. (See text in page 999.)

D = First ray of dorsal fin. V = Pelvic fins. A = Anus.

5A. Upper. Length 88 units.
Nerves assumed to leave vertebral column at right-angles.

5A. Lower. Length 119·5 units.
Nerves originate and end at points identical with those shown in Fig. 5A. Upper.

5B. Lower. Length 119·5 units.
Nerves assumed to leave vertebral column at right angles.

5B. Upper. Length 88 units.
Nerves originate and end at points identical with those shown in Fig. 5B. Lower.

from a study of the nerves in successive stages of development ? Unfortunately, it is not possible by simple gross examination as with the leptocephalus to trace the spinal nerves of the clupeoid larva from source to end point, nor have I, as yet, found opportunity to conduct the necessary

micro-examination which would provide an answer to this question. But there are two alternatives which are well worth considering here. The spinal nerves of the clupeoid larva either pass out at right angles to the spinal cord so that they innervate parts of the body immediately opposite to their origin, or, failing this, they run out obliquely to innervate parts of the body which are not immediately above or below their origin.

Consider these alternatives as applied to the herring. Given the following data concerning a post-larva and an adolescent (from Ford, **2**) :—

BODY INTERVAL.	POST-LARVA.	ADOLESCENT.
	(Units of Length.)	
Body Length	88·0	119·5
Head to 1st ray of Dorsal Fin . .	49·0	49·0
Head to Pelvics	39·0	54·9
Pelvics to Anus	30·5	30·5

In Figure 5A, upper, constructed in accordance with the above data for the post-larva, the nerves supplying certain points have been represented by lines drawn at right angles from the vertebræ. Figure 5A, lower, is constructed on the data for the adolescent, and lines have been drawn linking the same origin and end-point of nerves shown in Figure 5A, upper. It is seen that in the adolescent the path of each nerve is now oblique to the vertebral column, whereas in the post-larva it was at right-angles to it. In this case the adolescent is, so to speak, a distortion of the post-larva.

The other alternative is illustrated in Figures 5B, upper, and 5B, lower. It is here simpler first to construct a representation of the adolescent, as in Figure 5B, lower, inserting nerves at right-angles to the vertebral column. The figure for the post-larva (Fig. 5B, upper) in next drawn with the nerve origins and endings as in Figure 5B, lower. It is seen that it is now the post-larva and not the adolescent in which the nerves take an oblique course. In other words, the post-larva is now a distortion of the adolescent.

Which of these two is to be regarded as approaching the true state of affairs is a matter which can be settled by dissection, and is worth investigation, since it is of direct interest in the study of the evolutionary history of the fishes concerned. It is hoped that further investigation on this question will be made in the near future.

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Relative Growth of the abdomen and the carapace of the Shore-Crab *Carcinus maenas.**

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With 5 Figures in the Text.

Introduction.

In 1920 the senior author undertook some experiments on shore-crabs (*Carcinus maenas*) to see whether the development of their secondary sexual characters was altered by thyroid or pituitary feeding. To carry these out, it was first necessary to find the normal relative growth-rate of these characters, and a number of measurements were undertaken for the purpose. Some further measurements were made by the senior class in Zoology at Oxford as an exercise. By then, however, it had become apparent that the interpretation of the measurements of the normal crabs offered more interesting problems than the endocrine experiments, which turned out to be wholly negative, but that more accurate methods of measurement were necessary for their solution. Accordingly the junior author undertook to devise and carry out these measurements.

The common shore-crab can be strongly recommended as material for many types of investigation. For biometric work it offers the advantage of a hard skeleton. As class-material in biometric study it is cheap and easily handled. It is good for the study of growth-problems, since it has an "unlimited" growth and since the cast moults can be measured with as great an accuracy as the whole animal. It is easily kept in captivity far from the sea. Specimens up to 1 or 2 inches' carapace-length, kept in ½ to 1 inch of sea-water in covered finger-bowls or (cheaper !) in tongue or potted-meat jars, need only to be fed and have their water changed twice a week; and larger specimens can equally well be kept if larger receptacles are provided. A few preliminary trials indicate that injections into the muscles or haemocoel can be satisfactorily made through the

* Studies in Heterogonic Growth, No. V.

arthrodial membranes at the base of the limbs, or between thorax and abdomen. The crabs can be kept healthy on meat or still better on fish, but will accept, and thrive on, a large variety of foods. Finally, it is an abundant and easily-obtained species, and it is apparently rather variable.

All specimens with a Sacculina externa were of course rejected, since sacculinisation is known to increase the breadth of the abdomen in both sexes. Some specimens with Sacculina interna are no doubt included in the population measured ; however, the error thus introduced will not be large, partly because such individuals are not common, partly because sacculinisation will not have had time to produce much effect on the abdomen before the parasite becomes external.

In larger individuals, the measurements were made with fine callipers. This gives a slight positive error, which is, of course, relatively larger in smaller specimens. Accordingly in these (up to about 9 mm. carapace length) the size of the parts to be measured was indicated on white paper by means of a camera lucida and a dissecting microscope, measured with a ruler, and the absolute size calculated from the known magnification.

Carapace length was measured in the mid-dorsal line. Abdomen-breadth refers to the breadth at the joint between the 5th and 6th abdominal segments.

Results.

The number of crabs accurately measured was 678. Most of them came from Plymouth, at various seasons of the year. In order to obtain some specially large animals, 53 large crabs were procured from Essex : as these came from another locality, their measurements are recorded separately. The distribution of the crabs was as follows :—

Plymouth crabs : unsexable (externally), 74 ; males, 270 ; females, 281. Essex crabs : males, 22 ; females, 31. The results of the measurements are shown in the subjoined Tables I and II. The individual measurements are not given, but the means for classes according to carapace-length.

Graphic presentation of the results is given in Figures 1 and 2, where the relative abdomen breadth (percentage of carapace length) is plotted for each sex.

It was not considered worth while calculating the standard deviation for each of these means. To give some idea of the range of variability, however, the extreme variants in either direction have been given (Table II).

It will be noted that in almost every class, the range of variation shown by the females is considerably greater than that of the males ; in the one exception, they are nearly equal. This is to be expected, since slight differences in the onset of the rate of differential female abdomen-growth would make a considerable difference in the ratios.

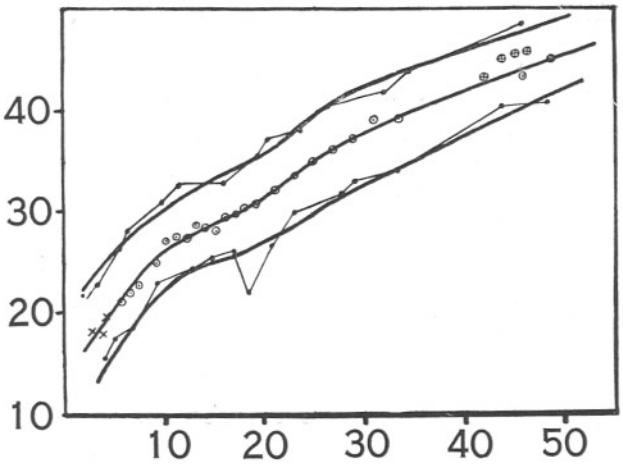

FIG. 1.

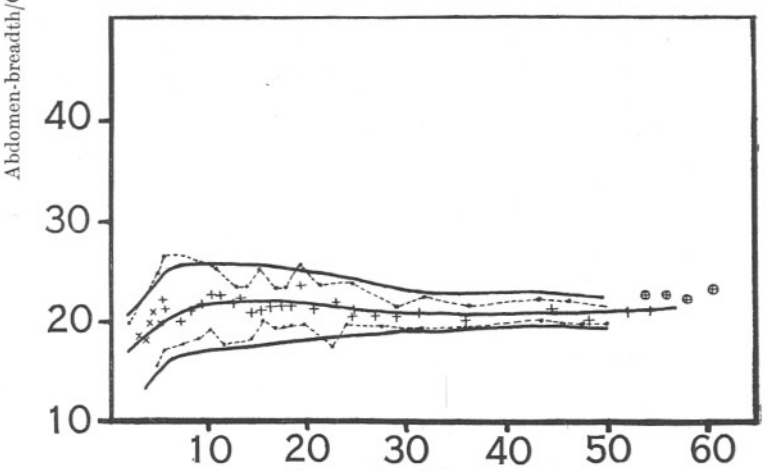

FIG. 2.

FIGS. 1 and 2.—The relative abdomen-breadth of female and male *Carcinus maenas*, against carapace-length.

× unsexable (in both figures).

⊙ Plymouth females. ⊗ Essex females.

\+ ,, males. ⊕ ,, males.

The extreme variants are also given, together with smoothed curves for the probable range of variation.

TABLE I.

ABDOMEN-BREADTH RELATIVE TO CARAPACE-LENGTH IN CARCINUS MAENAS.

(*a*) UNSEXABLE (74 specimens).

Class :— Carapace-l. (mm.)	Σ	Mean car.-l. (mm.)	Mean abd.-br. (mm.)	Mean $\frac{\text{abd.-br.}}{\text{car.-l.}}$ %
2·4–3·4	13	3·09	0·578	18·7
3·5–3·9	22	3·80	0·680	17·9
4·0–4·5	20	4·22	0·823	19·5
4·5–4·9	11	4·76	0·979	20·6
5·0–5·5	8	5·19	1·019	19·6

(*b*) MALES (292 specimens).

Plymouth crabs (270 specimens).

4·75– 6·0	11	5·50	1·238	22·5
6·0 – 7·0	6	6·37	1·224	19·2
7·0 – 8·0	16	7·51	1·48	19·7
8·0 – 9·0	14	8·41	1·75	20·8
9·0 –10·0	15	9·37	2·01	21·4
10·0 –11·0	10	10·36	2·31	22·3
11·0 –12·0	26	11·31	2·56	24·4
12·0 –13·0	12	12·63	2·72	21·5
13·0 –14·0	18	13·32	2·93	22·0
14·0 –15·0	15	14·34	2·95	20·6
15·0 –16·0	10	15·43	3·21	20·8
16·0 –17·0	14	16·35	3·47	21·2
17·0 –18·0	16	17·51	3·71	21·2
18·0 –19·0	6	18·34	3·93	21·4
19·0 –20·0	11	19·37	4·43	23·4
20·0 –22·0	13	20·73	4·56	21·0
22·0 –24·0	19	22·93	4·97	21·7
24·0 –26·0	9	24·58	4·95	20·2
26·0 –28·0	4	26·69	5·44	20·4
28·0 –30·0	3	29·03	5·93	20·4
30·0 –31·0	4	31·16	6·48	20·8
35·0 –37·0	4	35·75	7·13	19·9
43·0 –47·0	5	44·54	9·42	21·1
47·0 –51·0	4	48·35	9·63	19·9
52·0 –57·0	5	54·44	11·46	21·0

TABLE I (*continued*).

Essex crabs (22 specimens).

Class :— Carapace-l. (mm.)	Σ	Mean car.-l. (mm.)	Mean abd.-br. (mm.)	Mean $\frac{\text{abd.-br.}}{\text{car.-l.}}$ %
53·0 –55·0	9	53·98	12·09	22·4
55·0 –57·0	6	56·00	12·58	22·4
57·0 –59·0	4	57·87	12·73	22·0
60·0 –62·0	3	60·57	14·00	23·1

In plotting, the first 2 classes of the Plymouth males have been combined (Fig. 2).

(*c*) FEMALES (312 specimens).

(by 1 mm. carapace-length classes, except that the 8 mm. and 9 mm. classes have been combined, as there was only 1 specimen in the 8 mm. class.)

Plymouth crabs (281 specimens).

Σ	Mean Carapace-length mm.	Mean Abdomen-breadth mm.	Mean $\frac{\text{Abdomen-br.}}{\text{Carapace-l.}}$ %
12	5·56	1·16	20·9
16	6·52	1·45	22·2
14	7·41	1·67	22·6
12	9·32	2·30	24·7
15	10·37	2·80	27·0
16	11·35	3·11	27·4
17	12·33	3·37	27·3
23	13·29	3·81	28·6
19	14·35	4·06	28·3
12	15·31	4·29	28·0
19	16·35	4·82	29·4
15	17·36	5·15	29·6
15	18·16	5·48	30·2
7	19·34	5·93	30·6
6	20·33	6·72	32·1
10	21·51	6·82	
12	22·40	7·54	33·6
8	23·34	7·76	
6	24·33	8·33	35·0
5	25·52	9·16	
10	26·45	9·59	35·9
6	27·65	9·79	

TABLE I (*continued*).

Σ	Mean Carapace-length mm.	Mean Abdomen-breadth mm.	Mean $\frac{\text{Abdomen-br.}}{\text{Carapace-l.}}$ %
2	28·45	10·40	37·2
3	29·30	11·03	
4	30·55	11·62	38·8
4	31·49	12·46	
3	32·37	12·75	
5	33·32	12·70	38·9
4	34·33	13·56	
1	43·50	17·50	
2	45·30	19·20	43·2
1	46·30	19·90	
1	50·20	23·70	
	Essex crabs (31 specimens).		
4	42·10	18·15	43·1
7	43·56	19·54	44·8
6	44·38	19·88	44·8
6	45·28	20·50	45·3
4	46·43	21·13	45·5
4	48·75	21·88	44·7

In plotting (Fig. 1), the Plymouth females have been combined into 2 mm. classes from carapace-length 20 to 33 mm., and the last 4 classes combined into one; and the 8 and 9 mm. classes have been combined in the table, since only one crab of the 8 mm. class was found. Of the Essex females, the 43 and 44 mm. classes, and also the 45 and 46 mm. classes, have been combined in plotting.

When the means are plotted on a double logarithmic grid (Fig. 3) further information is acquired. In general, the points lie along good approximations to straight lines, indicating that constant differential growth-ratios are maintained over long periods of the life-history. The curve for the unsexed is prolonged by that for the females up to a carapace-length of between 17 and 20 mm.; during this period the growth-coefficient of the abdomen is about 1·26. From this point onwards, the relative growth of the female abdomen increases, and remains steady at about 1·42 up to the largest specimens found.

From the moment the sexes are distinguishable, the male curve diverges from the female. It also shows two phases; the growth-coefficient for the first is about 1·07, for the second about 0·94. It is more difficult to

distinguish the exact size at which the change in growth-ratio occurs in the males than in the females, since the male points are more irregular. At any rate it takes place at approximately the same phase in the life history, certainly between 14 and 21 mm. carapace-length. If, as would seem probable on *a priori* grounds, the change occurs at sexual maturity, we should expect there to be a considerable variation in the absolute size at onset.

TABLE II.

Maxima and Minima for Abdomen : Carapace Ratio.

Maxima.				Minima.			
Class. Car.-l., mm.	Carapace-length	Abd.-br. / Car.-l. %		Class. Car.-l., mm.	Carapace-length.	Abd.-br. / Car.-l. %	
FEMALES.							
> 40	45·8	48·2		> 40	48·3	40·6	
	44·4	48·1			43·5	40·2	
30–35	31·75	41·75		30–35	33·5	34·0	
	34·5	43·5		25–30	27·5	31·8	
25–30	25·6	38·3		20–25	21·5	28·4	
	26·25	40·4			22·0	26·4	
20–25	20·25	37·0		17–20	17·0	23·6	
	23·5	37·9			18·25	21·9	
17–20	19·5	35·5		15–17	14·75	25·4	
15–17	16·0	32·8		11–13	11·0	24·4	
13–15	14·75	30·5		9–11	9·1	22·8	
11–13	13·0	30·8		5–9	5·8	20·7	
11–13	11·50	32·6					
UNSEXED.							
4·6–5·5	5·5	27·3		4·6–5·5	5·0	17·7	
4·0–4·5	4·1	26·4		4·0–4·5	4·1	15·9	
3·5–3·9	3·6	22·2		3·5–3·9	3·9	15·4	
3·0–3·4	3·4	21·6		3·0–3·4	3·1	16·1	
3·0	2·4	19·4					

Up to the size of 22 mm. carapace-length, the variation-curves for male and female overlap, the least male-type males having broader abdomens than the least female-type females.

It is of considerable interest to find the growth-ratio during the earliest (unsexed) phase apparently identical with that of the first female phase.

It would seem difficult to escape the conclusion that the growth-ratios of the male abdomen change not once but twice, the first time at carapace-length about 5 mm., whereas that of the female only changes once. It

would however be desirable to check this result by measurement of specimens unsexable externally, followed by sexing by means of dissection.

After a large number of measurements had been taken, it was realised that perhaps carapace-breadth would have been a better means of absolute

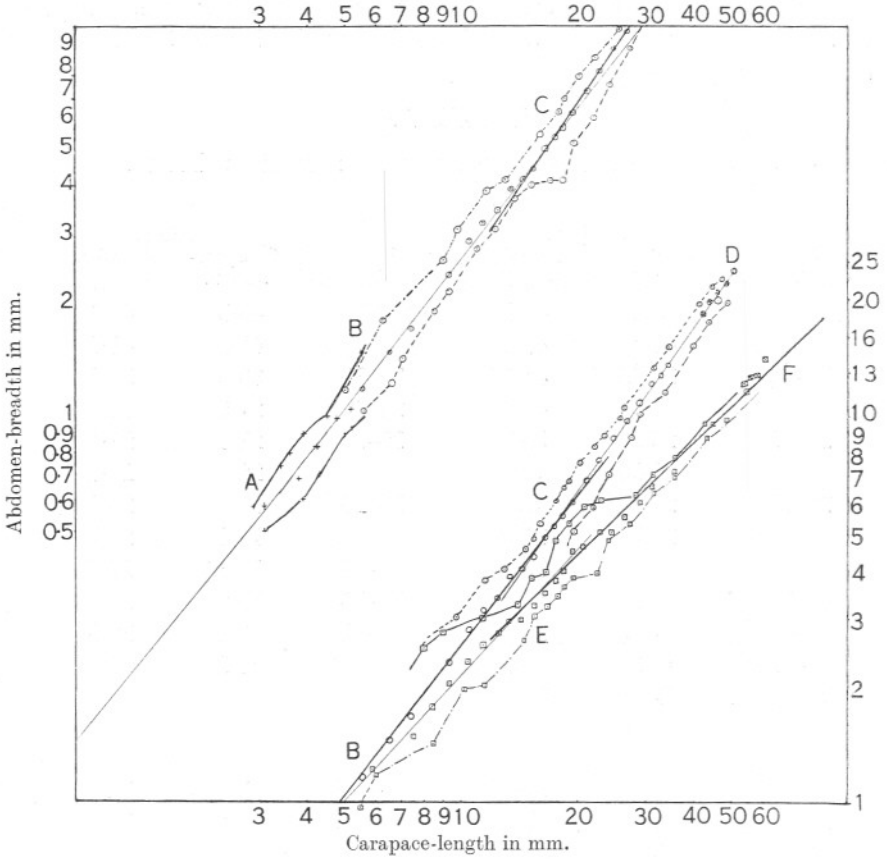

FIG. 3.—Double logarithmic plot of abdomen-breadth against carapace-length in *Carcinus maenas*. Above (abdomen-breadthscale to left) the curve for unsexable crabs (+) and the first part of that for females (⊙). Below (abdomen-breadth scale to right) the curves for females (⊙) and males (⊡).

A–B, unsexable period.
B–C, 1st female period.
C–D, 2nd female period.
B–E, 1st male period.
E–F, 2nd male period.

In addition to the means, the extreme variants are also given.

size than carapace-length, since in that case one would be comparing two breadths, instead of a breadth with a length. Accordingly, in the case of the last 201 animals measured, the greatest carapace-breadth was taken in addition to the other two measurements. The following results were found.

TABLE III.

THE RELATION OF CARAPACE-LENGTH TO CARAPACE-BREADTH IN 201 SPECIMENS FROM 2 TO 52 MM. CARAPACE-LENGTH.

Class; car.-l., mm.	Σ	car.-l.	car.-br.	car.-br. / car.-l. % mean	range.	Σ	car.-l.	car.-br.	car.-br. / car.-l. % mean	range.
	Unsexed (50 specimens).									
2–4	18	3·54	4·13	116·7	(103–136)					
4–6	32	4·69	5·56	118·5	(110–125)					
	Males ♂ (66 specimens).					Females ♀ (85 specimens).				
5–10	24	7·35	8·88	121·0	(112–127)	37	6·88	8·37	121·6	(116–132)
10–15	12	13·80	17·19	124·6	(121–130)	10	12·80	15·97	124·8	(120–130)
15–20	12	17·13	21·96	128·2	(126–130)	21	17·90	23·37	130·0	(125–135)
20–25	8	22·40	29·33	130·5	(128–133)	9	22·19	28·98	130·6	(129–132)
25–30	5	26·60	34·34	129·8	(128–133)	3	26·77	35·07	131·0	(130–133)
30–35	1	31·6	41·1	130·1		3	32·0	31·3	129·1	(127–133)
35–40	2	36·4	48·2	132·5		—	—	—	—	
45–55	2	49·7	66·8	134·5		2	51·7	67·8	131·1	

These results have been plotted in two ways: (*a*), (Fig. 4) the relative carapace-length against absolute carapace-length; (*b*) absolute carapace-breadth against absolute length, on a double logarithmic grid. The mean percentage (relative) carapace-breadth increases from 116·7 to nearly 135, an increase of about 15%. The means for the females are at first slightly above those for the males, but much greater numbers would be needed to establish this point significantly. (The numbers for the last points, from class 25–30 mm. onwards, are too certainly small to warrant attaching any importance to sexual differences.)

The range of variation in percentage carapace-breadth is considerable,

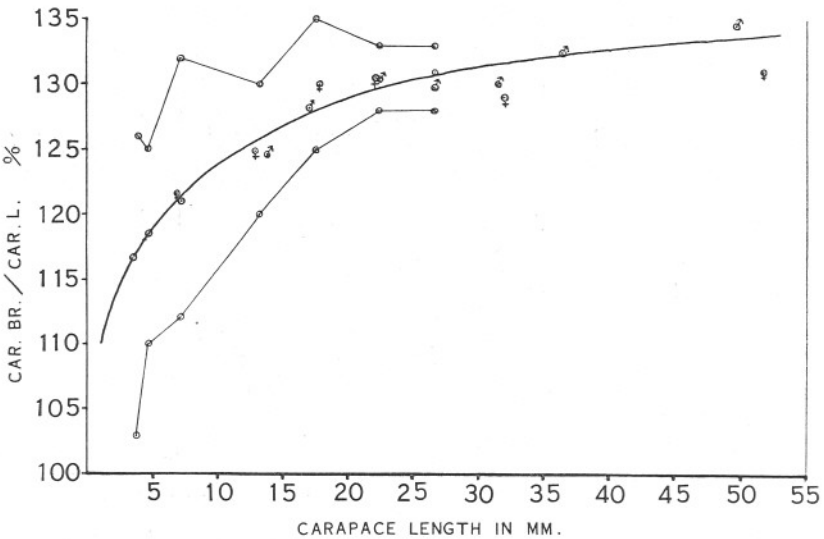

FIG. 4.—The alteration in relative carapace-breadth with absolute size. The mean values are given for unsexed, ⊙; females, ♀; and males, ♂. In addition the extreme variants, irrespective of sex, are given up to 28 mm. carapace-length.

being 23 for the smallest specimens, and diminishing to 10, in spite of increased numbers, by the 15–20 mm. class.

On the double logarithmic plot (not reproduced) the points fall on to a very close approximation to a straight line, whose inclination gives a value of 1·06 or just below, for the growth-coefficient of carapace-breadth relative to carapace-length. The points for the last three classes fall slightly below the line, giving a growth-coefficient of unity or slightly over; but they comprise too few specimens to enable us to say for certain that there is any real change in the growth-ratio. Extrapolation of the curve downwards enables us to say that at carapace-length 1 mm., the carapace-breadth should be 1·1. This is indicated on the graph for percentage values.

By using the ratios thus obtained as a correction coefficient, it was possible to prepare a graph (not here reproduced) of the relation between abdomen-breadth and carapace-breadth. As was to be expected from the regularity of the relation between carapace-breadth and carapace-length, this graph was essentially similar to those constructed with carapace-length as the standard.

Discussion.

Extended discussion of these results need not be undertaken here, as the theoretical bearings have been discussed elsewhere (Huxley 1927, etc.).

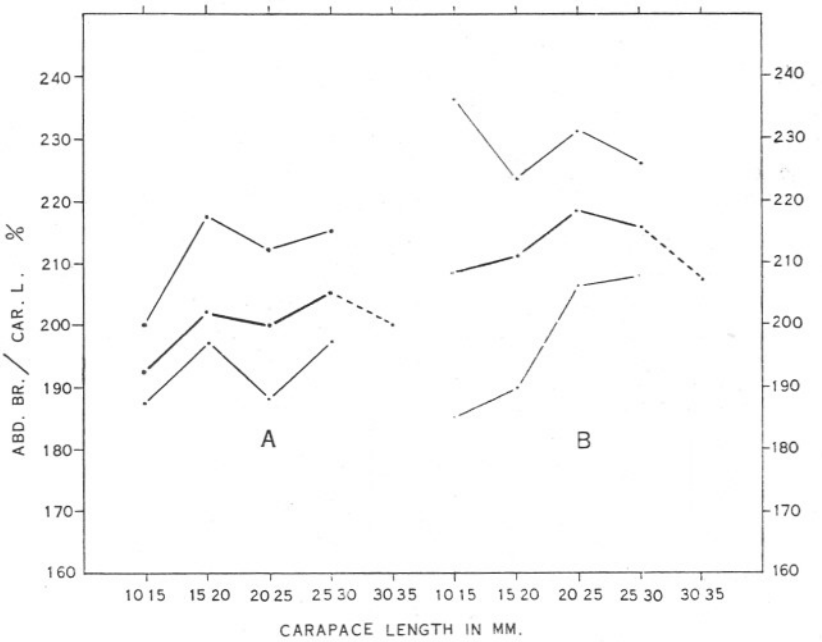

Fig. 5.—Seasonal variation in abdominal-breadth. Relative abdomen-breadth of male crabs from Plymouth (mean and range), A, in June, on left; B, in October, on right.

We need only stress the fact that in regard both to abdomen-breadth and carapace proportions, Carcinus has no fixed proportions in either sex, although the changes are more obvious in regard to the female abdomen. Since these animals show unlimited growth, there is not even any set of proportions which we can regard as adult or in any sense definitive. All that is fixed about the proportions of the shore-crab is their rate of change, as given by the growth-coefficients of the various organs.

One point deserves mention. In the Fiddler crab, Uca, the female abdomen grows heterogonically through all the early periods of life,

but after a certain time approaches the isogonic type (Morgan, 1923, and Huxley, 1924). The difference between this species and Carcinus is presumably correlated with the fact that in Uca the abdomen of the large females touches the bases of the legs on either side, whereas in Carcinus in the largest specimens I have seen there is still a considerable gap between lateral margin of abdomen and leg-bases—but by what means the abdomen growth is slowed down at the correct moment we do not know.

The matter is complicated, however, by the fact that in Pinnotheres, the pea-crab, the female abdomen continues to increase in relative size throughout life, even though it comes to overlap the bases of the legs very considerably (see the illustrations in Atkins, 1926 ; and Huxley, 1931).

A minor point is the apparent seasonal variation in the relative size of the male abdomen. The following table gives the results for 73 of the male crabs measured late in the investigation, all of which were taken at Plymouth, but 23 in early June, 50 in October.

The results are set forth in Table IV and Figure 5.

It will be seen that the October males have a consistently higher relative abdomen-breadth. As possible explanation of this, it may be suggested that after the breeding season a non-breeding phase sets in in which the male characteristics tend somewhat in the direction of the female ; this is known to occur in regard to certain species of Inachus as regards the male chela (G. W. Smith, 1906, and Shaw, 1928).

TABLE IV.

Relative abdomen br. $\left(\frac{\text{abd. br.}}{\text{car-l.}}\right)$ %, males.

Classes (mm. car. l.)	June. No.	Mean.	Max.	Min.	October. No.	Mean.	Max.	Min.
10–15	6	19·4	20·0	18·8	21	20·8	23·6	18·6
15–20	6	20·2	21·7	19·7	13	21·0	22·3	19·0
20–25	5	20·0	21·2	18·9	11	21·8	23·2	20·6
25–30	5	20·6	21·5	19·7	4	21·6	22·6	20·8
30–35	1	20·1			1	20·7		

Feeding Experiments.

With regard to the feeding experiments, mentioned in the introduction, a few comments may be made in spite of the results being wholly negative.

Table V gives the percentage increases at the moults for the three classes of the thyroid-fed, the pituitary-fed, and the control animals.

At first sight it may seem surprising that crabs fed exclusively for periods of 6 to 12 months and over on fresh ox-thyroid or ox-pituitary should exhibit no changes in growth or other characteristics as compared with controls fed on fresh fish. As regards the thyroid, however, the work of

Romeis (1925) has since shown that we should not expect any results of an endocrine nature to be obtained from feeding experiments with crustacea. He found that in the crayfish the active principle of the thyroid hormone was destroyed by the digestive enzymes, instead of being absorbed unchanged as in vertebrates, and we may presume that the same holds true for other Decapoda. Any experiments on the effect of thyroid upon crustacea should therefore be made by means of injection of extracts.

TABLE V.

GROWTH MADE BY CRABS FED ON FRESH FISH, FRESH OX-THYROID AND FRESH OX-PITUITARY, OVER PERIODS OF 1 OR 2 MOULTS.

		Initial carapace-length. mm.	1st moult, % increase.	2nd moult, % increase.
CONTROL		9·0	23·4	27·0
		10·9	20·2	19·8
		11·6	24·4	25·2
		14·1	26·2	23·6
		15·2	22·9	21·3
		14·0	18·6	—
	Mean		22·6	23·4
THYROID		9·1	27·6	24·1
		14·4	21·5	20·6
		15·5	25·8	23·6
		16·2	27·6	10·6
		17·2	26·8	17·0
		14·1	20·6	
		15·7	20·4	
		16·1	26·1	
		18·5	18·8	
		19·2	18·7	
	Mean		23·4	19·2
PITUITARY		13·7	23·5	25·4
		15·0	23·4	20·6
		15·4	25·4	21·2
		18·4	23·4	20·7
		13·8	24·4	
		14·6	24·4	
		15·0	25·3	
		16·9	23·6	
		17·9	24·6	
	Mean		24·2	22·0

The mean increase in carapace-length for all first moults is 23·5%; for all second moults, 21·5%; for all moults taken together, 22·8%.

Przibram has contended that arthropods in general tend to double in weight (bulk) at each moult. For an animal remaining constant in all its proportions, the percentage increase in a linear dimension needed to fulfil this condition is almost exactly 26%: ($\sqrt[3]{2}$=1·26). In Carcinus, we have already seen that carapace-breadth is increasing a little faster than carapace-length; it is also certain from analogy with other crustacea that the growth of at least the larger limbs will be at a slightly higher rate than that of the carapace. The increase of carapace-length at each moult needed to give a doubling in weight should therefore be slightly less than 26%. The figures actually found thus support Przibram's contention.

SUMMARY.

1. In regard to relative abdomen-breadth and relative carapace-breadth, the common shore-crab *Carcinus maenas* in both sexes exhibits a continuous change of proportions throughout life, from small animals of 2 mm. carapace-length to the largest obtainable (over 50 mm. carapace-length).

2. The parts measured exhibit constant differential growth-ratios (growth-coefficients) relative to carapace-length taken as standard, over long periods of the life-history.

3. The approximate growth-coefficients are as follows, relative to carapace-length:

Carapace-breadth, 1·06. This appears to be constant throughout the range of size measured, with a possible decline to nearly unity at large sizes.

Abdomen-breadth.

Crabs unsexable externally (2–6 mm. carapace-length), 1·26.
Females: early phase, 1·26; late phase, 1·42.
Males: early phase, 1·07; late phase, 0·94.

The early phase begins as soon as the sexes can be distinguished. The onset of the late phase may be presumed to be correlated with sexual maturity. In females it occurs certainly between 17 and 20 mm. carapace-length, in males between 14 and 29 mm.

4. There are indications of seasonal and local differences in relative abdomen size.

5. Feeding crabs of 9 to 22 mm. carapace-length solely on fresh ox-thyroid or fresh ox-pituitary for periods up to a year produces no change in growth-rate or in secondary sexual characters as against controls fed on fresh fish.

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Apparatus for the Photo-Electric Measurement of Submarine Illumination assembled for the U.S.A. Research Ship *Atlantis.*

By

D. C. Gall and W. R. G. Atkins.

With 4 Figures in the Text.

Introduction.

Shelford and Gail (1922) first used photo-electric cells for submarine photometry in the Puget Sound. Poole (1925) produced an apparatus which was suitable for use on small ships in the open sea. This apparatus was used near Plymouth by Poole and Atkins (1926, 1928, 1929) with various minor alterations in design which rendered it more reliable and less subject to errors due to electrical leakage. The object of these researches was to study illumination in relation to photosynthesis, but Russell perceived their bearing on his own work on the phototropic movements of the zooplankton. When considering the research programme of the *Atlantis*, Dr. George L. Clarke decided that it would be of value to carry out photo-electric measurements of submarine illuminations in connection with his work on vertical distribution of the plankton. A request was accordingly made by Dr. H. B. Bigelow, Director of the Wood's Hole Oceanographic Institute, that such an apparatus should be assembled under our direction. The apparatus here described has been constructed closely upon the lines of H. H. Poole's original apparatus as modified in 1928. Special attention, however, has been given to the elimination of electrical leakage. Furthermore, J. H. J. Poole (1928) devised an apparatus in which rate of flash of a neon lamp was used to measure light. This rate of flash method is one of integration and not an instantaneous measurement as is that of H. H. Poole. The value of the neon lamp method lies in the fact that light under the water is extremely variable near the surface owing to the motion of the waves. This method of measuring under-water illumination was used in Lough Bray, Co. Dublin, by J. H. J. and H. H. Poole (1930), and has since been used at sea by Poole and Atkins (1931). It seemed advisable to include a neon lamp photometer in the outfit so that errors in determining the loss of light on entering the water might be minimised.

The Potentiometer Apparatus.

This equipment is a functional copy of that in use at Plymouth. The original apparatus had been assembled from various parts, and in reproducing this the opportunity was taken of making the constructional improvement possible in apparatus being designed for a specific purpose. One of the chief difficulties is that of insulation, because photo-electric measurements are essentially measurements of very high resistance. During sea fog, surface leakage becomes a serious matter, and in designing the present apparatus this was one of the principal problems to be overcome. The measuring apparatus shown in Figure 1 consists of a potentiometer with associated circuits to measure the current passing through the photo-electric cells under different degrees of illumination. The potentiometer has two dials, the main dial consisting of 18 steps of 0·1 volts, and the slide-wire subdivided into calibrated divisions of 0·001 volts, readable by estimation to 0·0001 volts. A reducing ratio extends the range to one-tenth of the above values, so that the total range of measurement covered is from 1·9 volts to 10 micro-volts. The current passing through the photo-electric cell is measured by observing the volt drop upon a standard resistance in series with it. This resistance consists of 10 steps of 10,000 ohms each, giving a total of 100,000 ohms. With this combination photo-electric currents from $1{\cdot}9\times10^{-4}$ down to 10^{-9} ampere can be measured. To prevent surface leakage at the potentiometer this instrument is totally enclosed in an air-tight metal box. The spindles operating the dials are brought out through glands of a type which has been found successful in somewhat similar instruments for field use. The terminals are all of a special " petticoat " type, hermetically sealed into the metal case with a special high insulating compound. The advantage of this petticoat type of terminal is that the surface leakage path, besides being very long, is shielded from light, and constructed so that condensation from the atmosphere cannot easily form upon the inside surface of the petticoat. The metal top of this instrument is sealed to the case with a rubber gasket between the two metal surfaces. A drying chamber containing calcium chloride is provided to remove the residual moisture inside the instrument. This same type of sealed construction is used for the 100,000 ohms subdivided standard resistance, by means of which the photo-electric currents are measured. A further advantage resulting from this form of metallic construction is that no direct leakage can take place between terminals should the insulation at any time be lowered, but must first leak to the metal case. This allows of employing a " guard " circuit to deflect such leakage away from the measuring circuit. To provide for this, each metal case is highly insulated from the metal lining to the sea-chest containing

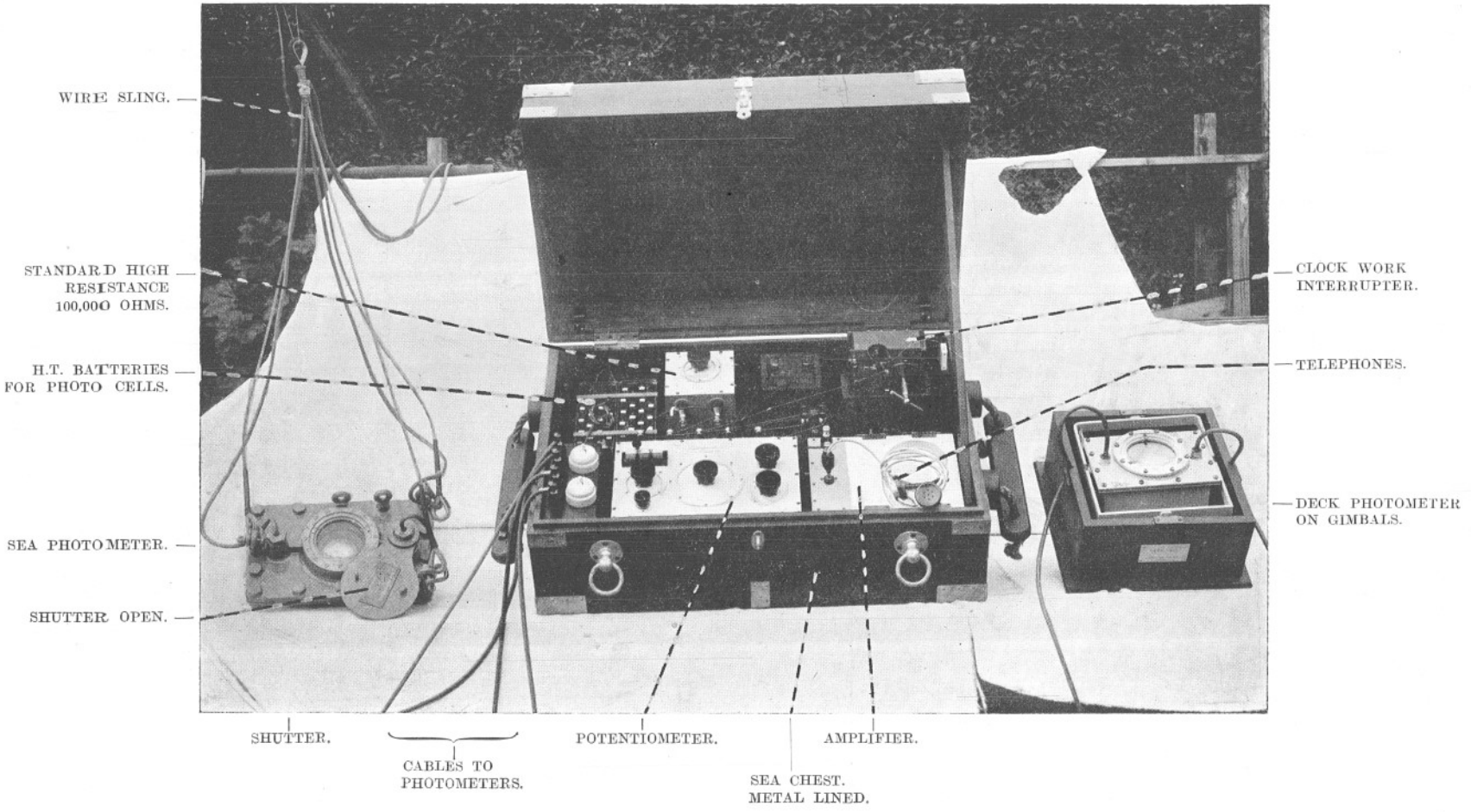
WIRE SLING.
STANDARD HIGH RESISTANCE 100,000 OHMS.
H.T. BATTERIES FOR PHOTO CELLS.
SEA PHOTOMETER.
SHUTTER OPEN.
CLOCK WORK INTERRUPTER.
TELEPHONES.
DECK PHOTOMETER ON GIMBALS.
SHUTTER.
CABLES TO PHOTOMETERS.
POTENTIOMETER.
SEA CHEST. METAL LINED.
AMPLIFIER.

FIG. 1.

the complete potentiometer and accessories. The instruments have no direct connexion between their metal cases, but are all mounted upon the common metal lining, so that all leakage must be localised to this. By raising the potential of any one of the cases to an appropriate value, any tendency to leakage can be neutralised. When finally tested the insulation was so perfect that it was found unnecessary to make use of the guard circuit facilities, but during fog and other bad conditions need might arise and they would then be available. The insulation of the finished apparatus was tested in a steam-saturated chamber for half an hour without any observable effect upon the insulation.

The potentiometer sea-chest contains all the apparatus required for the measurements. This consists of the high-tension battery, potentiometer, high resistance, standards cells, accumulator for the potentiometer, clockwork interrupter, and valve amplifier and telephone which takes the place of a very sensitive galvonometer in this equipment. Electric heating of the chest is provided for drying out in bad weather. This is intended for use with the ship's electric supply current, 110 volts D.C.

In the original instrument the clockwork interrupter was made of " Meccano " parts at very small cost. Although this has given wonderfully reliable service it was felt that something better should be provided in a finished design. A Morse telegraph clockwork movement was chosen on account of the known reliability of these for continual service. The interrupter is constructed upon fundamentally the same principles as that described by Poole and Atkins (1928), and consists of a ratchet-toothed wheel in rolling contact with a smooth jockey wheel. Mechanical refinements in adjustment for wear are introduced, and manganin is employed to reduce thermo-electric effects in the contact itself as these appear directly in the measuring circuit. Parasitic E.M.F.'s in the contact maker are further reduced by shunting a small condenser across the contact. The complete explanation of these parasitic E.M.F.'s is not fully clear, but they have been eliminated by these means. With the high amplification employed in the valve amplifier (about 30 decibels) any stray potential entering into the circuit becomes of importance. The clockwork drive is necessary because a motor is too liable to give stray electrical effects. The chief sources of these in the present instrument were found to be thermo-electric and frictional electrical effects in the mechanical contact maker and induction from external lighting and power circuits. The former were overcome by the use of manganin against brass, and the condenser as mentioned above, while the latter were completely eliminated by metal screening the whole circuit. This was rendered easy by the all-metal construction adopted for all the components of the circuit. A certain amount of experiment was

necessary to find the best points at which to connect the screens, but the final results fully justify the precautions. A very perfect silence can be obtained in the telephones, and the photo-electric currents balance with ample precision. The amplifier has three stages and is operated by dry cells contained in its own metal case, so that no leakage paths are anywhere provided, and further, the screening is rendered complete. The telephone leads also are screened and arranged to be at " earth " potential, so that the balance is quite unaffected by the operator's body. This also guards against insulation troubles from this part of the circuit. The precaution has one drawback, in that it definitely fixes the potential of the operator, so that when the high-tension battery is accidentally touched the full 50 to 100 volts is felt. This causes some surprise to the unsuspecting, but is a necessary price to pay for perfection of balance.

The Photo-electric Photometers.

The deck photometer and the sea photometer, although considerably larger, are constructed upon lines identical with the originals at the Marine Biological Association Laboratory. The cells themselves were specially made by the General Electric Company at Wembley and are much larger than those in use at Plymouth. This necessitates much more massive construction for the gun-metal casting in which the sea cells are contained.

The general appearance of the deck and submarine photometers is shown in Figure 1. In the latter the photo-electric cell is supported resiliantly from the lid on highly insulating ebonite supports. The bottom casting is sealed to the lid with a rubber gasket between the two machined faces and clamped by massive bolts. The glass windows are 3·2 cm. thick, and sealed between rubber washers by means of a clamping ring. A close-fitting sliding shutter closes this window when necessary to measure the " dark currents." This shutter is operated by cords from the surface, suitable fairleads being provided on the lid and wire cable upon which the submarine photometer is suspended. The two heavily rubbered cables to the terminals of the photo-electric cell enter the lid through glands, arranged to contract conical rubber stoppers on to the rubber covering of the cables. This type of joint has been found to be perfectly satisfactory. Drying chambers are provided inside the photometers to remove any residual moisture. When assembled, the insulation at the ends of the cables was more than a million megohms.

One submarine photometer is provided with cable sufficient for measurements down to 200 metres and the other for depths of 100 metres. Each is arranged for vertical suspension as well as horizontal. For vertical suspension the single wire cable shown in the extreme left of Figure 1 is

undone and fixed through a shackle hole in a fin on the bottom of the case midway between the two shackle eyelet bolts on right of case.

In the case of the photometer for use down to 200 metres, the photo-electric cell is a gas-filled one, but for use down to 100 metres, and for the deck photometer, vacuum cells were used. All three were potassium cells of approximately 7·6 cm. diameter and aperture, as figured in Type B by Campbell and Ritchie (1929).

The deck cell is contained in a light metal case, arranged for gimbal mounting, the gimbal ring remaining in a housing upon the deck, while the metal cell case can be removed to safety when not in use.

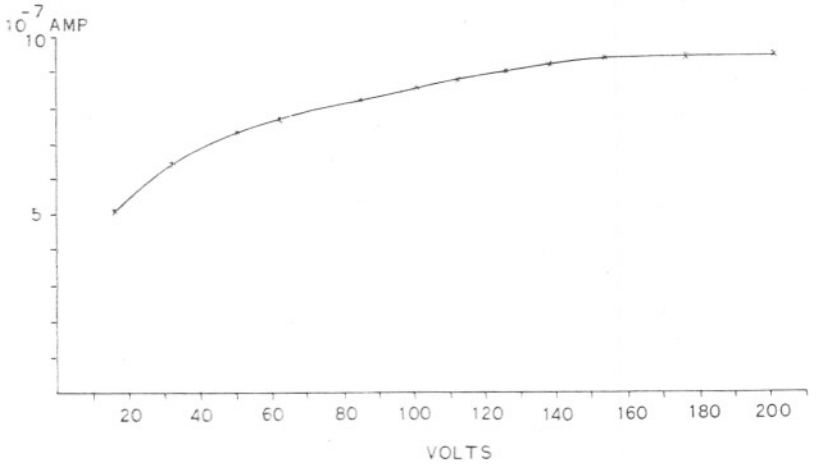

FIG. 2.

Over the window of the photo-electric cells discs of double surface flashed opalised glass are placed. These are held in position by three screw clips. It was found that owing to the great sensitivity of the cells, it is necessary at times to make use of diaphragms. These are of brass, 0·8 mm. thick, with central apertures 3·8 and 0·6 cm. in diameter. Figure 2 shows the voltage sensitivity curve for the vacuum cell housed in submarine photometer No. 1. From this it may be seen that at 140 to 150 volts saturation has been obtained. It is, however, quite permissible to operate the cell at 60 volts, at which point the sensitivity change amounts only to 0·33 per cent per volt. It seems safe to assume that the voltage sensitivity coefficient for the similar vacuum cell housed in the deck photometer is approximately the same.

Figure 3 shows the voltage sensitivity curve for the gas-filled cell housed in submarine photometer No. 2. The curve on the right was obtained with the large aperture diaphragm in position. The curve on the left was obtained subsequently without diaphragm. The point

marked F shows the reading obtained with the diaphragm in position at 16 volts after the first curve had been obtained. The sensitivity has much increased since the cell had been raised to a high voltage. For this reason in practice measurements are made after the cell has been caused to glow, by momentarily connecting it with a high voltage. In this cell the necessary voltage is 201 in the absence of light. It is inadvisable to work

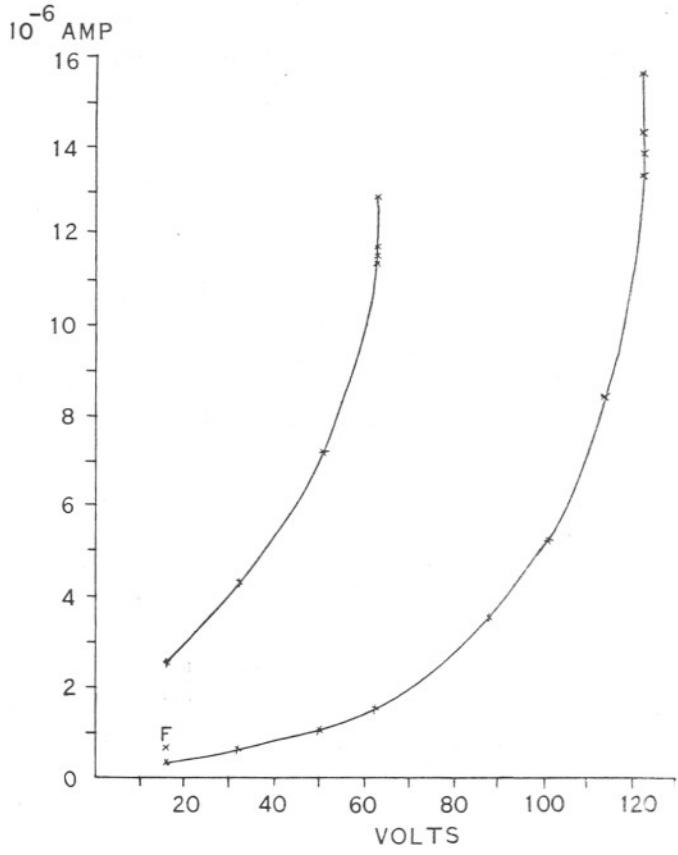

FIG. 3.

this cell under conditions leading to the production of a current greater than 50 μa (micro-amperes) owing to the steep rise in the curve at this reading. The deck photometer was standardised in diffused daylight against a similar vacuum potassium cell, which had been standardised by Poole and Atkins against an open carbon arc lamp (1928). This photometer had been in use for several years and was tested with a special lamp from time to time. It was shown that it had changed only slightly, if at all. The sensitivity is such that a current of 10^{-9} ampere is produced by a

vertical illumination of 40 metre candles or 42·4 for uniformly diffused light. When compared in diffused daylight, the new deck photometer was found to be 109 times as sensitive as the standard. Accordingly the *Atlantis* photometer at 60 volts anode potential gives one micro-ampere for 370 m.c. vertical illumination, or with uniformly diffused light for an illumination of 390 metre candles. The diaphragm reduces the illumination approximately to one-sixth, actually it is reduced 5·95 times. Consequently with diaphragm in position the vertical illumination necessary to produce one micro-ampere is 2200 metre candles vertical illumination or 2320 m.c. for diffuse light.

The No. 1 vacuum sea photometer at 60 volts anode potential requires 870 metre candles to produce one μa, or with uniformly diffused light 920 m.c. With diaphragm in position the values are respectively 5300 and 5600 metre candles. The gas-filled cell must not be regarded as quite constant in its behaviour, but the values given are those obtained immediately after the instantaneous glow when it is in its most constant and highly sensitive condition, according to the Research Staff of the General Electric Company (see also Atkins, 1931). With diaphragm in position and at 63 volts anode potential the gas-filled cell requires 1380 metre candles to give one μa, or 900 m.c. vertical illumination at 85 volts.

Without diaphragm at 63 volts 232 metre candles produce one μa, and at 85 volts 151 metre candles give one μa. It may be seen therefore that under these conditions the cell will measure down to less than one-sixth of a metre candle. For low illuminations the voltage may be increased very considerably and still smaller illuminations can then be measured.

The Neon Discharge Tube Photometer.

In addition to the potentiometer for measuring the photo-electric currents, one of Dr. J. H. J. Poole's neon lamp devices was provided. This is an extremely convenient means of measuring photo-electric currents, by counting the flashes of the neon lamp, the speed of which depends upon the amount of current flowing into a condenser, and therefore upon the rate at which the condenser builds up to sufficient voltage to discharge through the neon lamp. This instrument is illustrated in Figure 4. Its extreme simplicity is very attractive, and its application may be extended much beyond the present purpose. One feature worthy of note is that a given number of flashes can be regarded as proportional to a definite quantity of light, irrespective of the time taken. Thus the photographer can calibrate any emulsion in terms of the number of flashes necessary to give correct exposure, irrespective of the intensity of illumination.

The neon discharge tube photometer was assembled exactly as figured

by J. H. J. and H. H. Poole (1930), with the exception that the paraffin wax was extended to cover all the internal wiring in the housing instead of being placed around the neon discharge tube only. The petticoat type of terminal was used on the outer side of the casing, as shown in Figure 4.

The apparatus contains four condensers of capacity 0·5 to 0·0005 μF. Even with 0·5 μF. the current given by the highly sensitive photo-electric cells supplied with this outfit was so great that the flashing in bright daylight was too rapid to count, even with the diaphragm necessary for use with the potentiometer apparatus. Accordingly a smaller

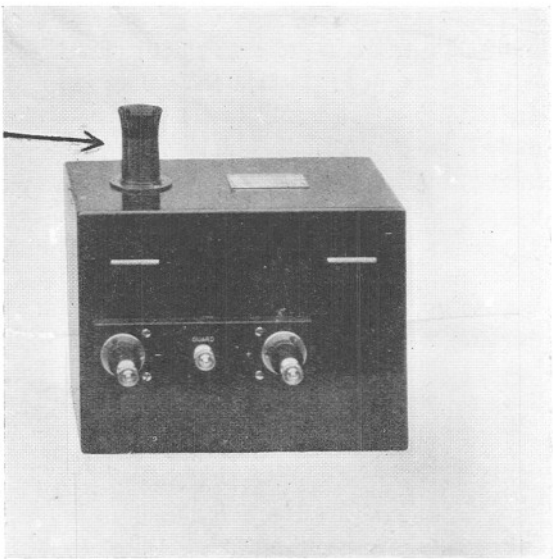

FIG. 4.

diaphragm, 0·6 cm. aperture, was obtained for use with the neon discharge tube.

The time before the ship sailed was too short to permit of a complete standardisation of the sensitivity of the neon discharge tube photometer with the various condensers. It was, however, ascertained that when one of the photo-electric cells was almost closed and placed in diffused light in a room so that it gave a current of 30×10^{-9} ampere, the neon lamp just maintained a slow rate of flash. Its sensitivity, therefore, appears to be ample for use down to a considerable depth, though its sphere of usefulness is most pronounced in that region, immediately under the surface and at small depths, at which the light varies very rapidly owing to the motion of the waves.

The high-tension batteries for use with the neon discharge tube are

housed in a suitable box with a small volt-meter attached to its lid. Flashing in the lamp began at a voltage of 236 and did not take place at lower voltages however great the illumination. For use it is advisable to have a voltage considerably—say, about 60 volts—above this, so that there may remain an adequate voltage for the working of the photo-electric cell at all times in the cycle of charge and discharge of the tube. The whole apparatus was taken on board the *Atlantis* and a trial was made at sea in the neighbourhood of the Eddystone Lighthouse, off Plymouth. It was not possible to test the submarine photometers down to a depth of more than about 40 metres, but at such depth they showed no sign of leakage.

As regards the depth to which it is possible to measure illumination, it may be said the gas-filled cell is provided with cable to go to 200 metres. The illumination at that depth is probably quite measurable though small. Poole and Atkins (1929) arrived at an approximate formula connecting the depth at which it was possible to see the Secchi disc and the vertical absorbtion coefficient. The latter is roughly equal to 1·7 divided by the depth in metres. It is on record that in the open ocean the disc has been seen to as great a depth as 66 metres. From this a vertical absorbtion coefficient 0·026 is derived ; such a value would lead one to expect a quite measurable amount of light at 200 metres. The results obtained on board the *Atlantis* are, however, to be awaited with great interest. They should offer an interesting comparison with visual observations made by Beebe in the bathysphere.

All the apparatus described in this paper was manufactured and assembled at the works of Messrs. H. Tinsley and Company, except the photo-electric cells and neon discharge tube, which were supplied by the General Electric Company, Wembley, Middlesex.

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Abstracts of Memoirs

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY.

The Photo-electric Recording of Daylight.

By W. R. G. Atkins and H. H. Poole.

Nature, 1930, **125**, 305.

A Burt vacuum sodium photo-electric cell was mounted in a heavy gun-metal case, such as used in submarine photometry. A sheet of opal glass was placed above the window. This acts as an efficient diffusing surface and is set horizontally so as to measure vertical illumination. High-tension ignition cables lead from this to the laboratory where the high-tension batteries are stored together with a Cambridge Instrument Co. "thread-recorder." In this manner continuous records of daylight have been obtained.

W. R. G. A.

Some Geochemical Applications of Measurements of Hydrogen Ion Concentration.

By W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1930, **19**, 455–460.

The reaction of natural waters may vary between pH 1·5 and pH 10·0. Obviously the reaction has an important influence upon the solution of rock and upon precipitation of metallic hydroxides already in solution. It is found that ferric salts are precipitated when the solution is still markedly acid. Ferrous salts remain in solution at a much lesser degree of acidity. The presence of organic matter, owing to its reducing action, favours the solution of iron ore. The problem of the formation of dolomite may also be regarded from this point of view. There are certain marked differences between the behaviour of the carbonates, bicarbonates and hydroxides of calcium and magnesium. The weathering of basalt has also been studied. Strongly weathered basalt is acid in reaction. Basalt which has only been slightly weathered gives a reaction which is neutral or only slightly acid, whereas a freshly exposed basaltic surface may be quite alkaline. It is obvious that considerations such as these must enter into a large number of geological problems.

W. R. G. A.

On the Photo-electric Measurement of Daylight.

By W. R. G. Atkins and H. H. Poole.

In the Photo-electric Cells and their Applications, published by the Physical and Optical Societies. Discussion on June 4th and 5th, 1930, 128–137.

Previous work on daylight and submarine photometry is reviewed. Details are given of the standardisation of the photo-electric photometers against a carbon arc. Measurements are described with the General Electric Co. new cæsium monatomic vacuum cell, type CMV 6. This is sensitive throughout the whole spectrum. A method was evolved for comparing light of different colours by obtaining the ratio of the blue to red, blue to yellow and blue to green readings, using colour filters. These are obtained in white light, and again in light of different composition. The method has been described at greater length in a subsequent paper.

W. R. G. A.

Photo-electric Measurements of Illumination in Relation to Plant Distribution. Part 3. Certain Spruce, Larch, Oak and Holm Oak Woods.

By W. R. G. Atkins and Florence A. Stanbury.

Sci. Proc. Roy. Dublin Soc., 1930, **19**, 517–531.

A portable photo-electric outfit with micro-ammeters for measuring current has been found serviceable over rough ground. Under shade from *Picea excelsa* the daylight factor was reduced to 1–2 per cent. There was little or no growth on the ground save occasional seedlings of *Hedera helix*. Under shade from a narrow wood of *Larix europæa* the value of the daylight factor was about 15 per cent. There was a good undergrowth of *Rubus fruticosus*, a belt of *Pteris aquilinum* and a woodland flora.

In a wood of *Quercus ilex* on level ground the daylight factor was found to be 1–2 or 3 per cent. In many sites there were pure carpets of Hedera. The deepest shade found was under *Ilex aquifolium* where the daylight factor was only 0·6 per cent.

W. R. G. A.

The Distribution of Pasture Plants in Relation to Soil Acidity and other Factors.

By W. R. G. Atkins and E. Wyllie Fenton.

Sci. Proc. Roy. Dublin Soc., 1930, **19**, 533–547.

Many British grasses are distributed over pastures varying from the most alkaline to almost the most acid found. Some have a range which is limited on the acid side, viz. *Cynosurus cristatus*, *Lolium perenne* and

Dactylis glomerata, but *Nardus stricta*, *Aira flexuosa* and *A. cæspitosa* are only found on acid soil. Of leguminous plants *Ulex europæa* extends throughout the whole range. *Trifolium repens* is the most important leguminous constituent of acid pastures, in which, however, it is not found in soil more acid than pH 5. *Trifolium pratense* is rare beyond pH 6, as are most of the other leguminous plants. In a well-drained alkaline soil *Medicago sativa* was found to persist, when sown, for six years. It was found that when allowed to roam freely sheep and cows grazed closely on herbage growing in soil at pH 6 and on most sites less acid than pH 5; in more acid sites grazing did not take place, or if it did, only slightly. The use of a neutral solution of potassium chloride in making soil extracts leads to large errors through base exchange.

W. R. G. A.

Photo-electric Measurements of Illumination in Relation to Plant Distribution. Part 4. Changes in the Colour Composition of Daylight in the open and in shaded situations.

By W. R. G. Atkins and H. H. Poole.

Sci. Proc. Roy. Dublin Soc., 1931, **20**, 13–48.

Data are presented concerning the transmission of various colour filters. For work in shaded situations J. H. J. Poole's neon lamp device was found to be the most convenient measuring instrument. The cæsium vacuum cell CMV 6 was satisfactory for such work. Its infra-red sensitivity may be suppressed by a Corning heat-absorbing filter so that it gives a wave-length sensitivity curve which is approximately horizontal between 440 and 640 mμ. By means of the above cell with a diffusing opal glass and colour filters it is possible to obtain a measure of the colour of the light under different conditions and in woods, taking daylight of some definite type as standard. In woods the light is very poor in blue, relatively rich in green, is close to sunlight in orange-red, and very much richer than either skylight, daylight or sunlight in the deep red. The source of light in woods is predominantly blue sky or grey sky rather than normal daylight with sunshine. Measurements have been made of the relative intensities of direct sunlight and diffuse skylight. Sunlight being relatively much richer in the light towards the red end of the spectrum, the value of this ratio at any given time depends on the type of photo-electric cell used to measure it, and is greatly altered by the use of colour filters.

W. R. G. A.

Observations on the Photo-electric Measurement of the Radiation from Mercury Vapour Lamps and from the Sun, and on the effects of such Radiation upon the Skin.

By W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1931, **20**, 49–65.

A glass vacuum sodium photo-electric cell was used with a micro-ammeter to show that it is advisable to run a mercury vapour arc continuously, exposure being made six minutes after switching on. After thirty-five minutes it should be switched off to allow of cooling. Five minutes later its initial potency has been recovered ; the loss due to overheating is a real phenomenon. The aluminium reflector used, when adjusted to its position of maximum efficiency, increases the total radiation about 2·7 times and the ultra-violet radiation about 2·0. This more than counter-balances any loss of efficiency in the lamp due to overheating occasioned by the reflector. When the reflector is used the decrease in intensity is considerably less than that calculated according to the inverse square law. J. H. J. Poole's neon lamp is very convenient for the study of the mercury vapour arc. Data are given concerning the times required for the arc to produce slight erythema. These times are compared with those required for sunlight of different intensities reckoned in thousand metre candles. Approximate photo-electric determinations of the ratio of total to diffuse ultra-violet show that even at midsummer noon the sunlight is not very much more potent than the diffuse light from the whole sky and the direct light must be relatively less intense at other times. W. R. G. A.

Some Experiments on the Accuracy obtainable with Gas-filled Photo electric Cells.

By W. R. G. Atkins.

Sci. Proc. Roy. Dublin Soc., 1931, **20**, 67–73.

Gas-filled cells were tested for constancy of emission immediately after the glow-discharge had been passed momentarily. The cæsium hydride cell behaved irregularly. The potassium hydride cell is more constant, and readings could be obtained to within 2 per cent with anode potential 60 volts. No tests were made as to the constancy or otherwise of the cell over prolonged periods. The rate of decrease of sensitivity after the glow amounts to about 2 per cent per minute. It is therefore advisable to make measurements immediately after the discharge which should be of momentary duration only. From this it follows that, if Poole's neon lamp method be used to integrate the current, such integration should be over equal periods of time in each case rather than for an equal number of flashes of the lamp. W. R. G. A.

The Penetration of Light through successive Layers of Tissue-paper.

By W. R. G. Atkins.

Nature, 1931, **128**, 545.

A sodium photo-electric cell was used to measure the light transmitted and it was found, when allowance has been made for the extra loss at the first surface, that the succeeding layers from numbers 2 to 10 transmitted fairly regularly, the transmission factor being 79 per cent. It was found that 8·4 per cent of the original light remained after passing through ten layers of paper. The results bear on previous letters to *Nature*.

W. R. G. A.

The Treatment of Gapes in Chicken.

By W. R. G. Atkins.

Nature, 1931, **128**, 585.

Between February and May fourteen chicken affected with gapes were treated with a dilute solution of carbon tetrachloride in medicinal paraffin. Only one died, whereas all untreated chicken died in the same period. The chicken were about one month or six weeks old. At the end of May, however, the treatment broke down completely when applied to chicken only a fortnight old. None of these recovered. One, however, never contracted gapes though freely exposed. The treatment appears to be worth careful investigation.

W. R. G. A.

The Adductor Mechanism of Pecten.

By L. E. Bayliss, E. Boyland and A. D. Ritchie.

Proc. Roy. Soc., 1930, *B.*, *Vol.* 106, *p.* 363.

A study has been made of physiological behaviour of the adductor muscle of Pecten. The slow part of this muscle can be isolated from the nervous system in a completely relaxed state in *P. magellanicus*. Stimulated electrically, it gives twitches about 100 times as slow as frog's skeletal muscle, which can be fused to form a tetanus. The difference in time scale is determined by the viscosity of the tissue, which in this muscle is about the same in the excited and unexcited states. The tensions developed are large. In *P. maximus* and *P. opercularis*, on the other hand, different nervous connections make it difficult to isolate the muscle without some "contracture"; apart from this, however, the muscles of these animals behave in the same manner as those of *P. magellanicus*.

The state of " contracture " is a result of reflex excitation which survives isolation, but may be partly or completely abolished by direct faradic stimulation. The " contracture " is not accompanied by increased viscosity, and it is uncertain whether it results from a continued state of excitation; the tensions in " contracture " are much less than the maximum tensions obtainable. Reflex movements of intact animals suggest that for the most part the muscle is contracting tetanically and is not in a state of " contracture."

The quick muscle gives a rapid twitch with single induction shocks that resemble the normal reflex contraction (swimming movement or flap). Complete fusion of twitches is not readily obtained, and the maximum number of contractions obtained by stimulation is not large, although varying in different species according to the animal's normal activity.

L. E. B.

Studies in Tunicate Development. Part I. General Physiology of Simple Ascidians.

By N. J. Berrill.

Phil. Trans. Roy. Soc. B., Vol. 218, 1929, *pp.* 37–78.

The following species were investigated: *Tethyum pyriforme, Boltenia hirsuta, Styelopsis grossularia, Phallusia mammillata, Ascidiella aspersa, A. scabra, Ascidia conchilega, A. mentula, A. prunum,* and *Ciona intestinalis.*

In the egg the perivitelline space is due to colloids exerting an osmotic pressure equivalent to 0·8 per cent gum-arabic in sea-water. In the oviduct this is counterbalanced by substances in the oviducal fluid. " Organ-forming " substances similar to those in the egg of *Styela partita* but much more striking occur in the egg of *Boltenia hirsuta.*

In the Ascidiidæ, Cionidæ, and probably in all ascidians with small eggs, the tadpole larva hatches through the digestion of the egg-membrane by a proteolytic enzyme active within the limits pH7–10. An alternative method which is only possible later in development is by rupture of the membrane, usually by ectodermal ampullæ. These ampullæ combine the functions of respiration and fixation.

The onset and rapidity of metamorphosis may be controlled by varying the hydrogen-ion concentration of the water. Hyper-alkalinity tends to inhibit metamorphosis, in particular tail-absorption, altogether; increased acidity tends to induce metamorphosis. The total salt concentration of sea-water has little effect upon development other than that of retardation.

The great variability of eggs and larvæ is due primarily to the length of time an egg has lain within the oviduct and to the degree of toxicity of the ovidical fluid during that time.

N. J. B.

Studies in Tunicate Development. Part. II. Abbreviation of Development in the Molgulidæ.

By N. J. Berrill.

Phil. Trans. Roy. Soc. B., Vol. 219, 1931, *pp.* 281–346.

The development of 16 species of Molgula and 2 of Eugyra is described. Ten are viviparous. Viviparity is due to reduction in adult size (in this family) in turn due to precocious sexual maturity resulting from the colonisation of exposed rocks by sand-adapted types. Increase in egg-size is a result of viviparity. Nine species develop without forming tailed tadpoles. Two species said to be anural were found to produce tadpoles. Cleavage is identical in anural and urodele development. Hatching in anural development is always by membrane rupture and never by digestion. An aggregation of cells is always seen near the larval stomach in both types of development ; in the urodele it is known to be the absorbed tail. Failure of tail development is due to the absence of swelling on the part of the notochord cells, which, however, are present in normal number. Failure to extend on the part of the notochord results in a delay in closure of the blastopore. Imbibition by notochord cells is to some extent dependent upon the alkalinity or acidity of the surrounding medium.

Out of 139 species of the Ascidiacea anural development is confined to 9 molgulids. Within the Molgulidæ the origin of anural development is polyphyletic. The otolith (the only sense organ) is present in all urodele larvæ, absent in all anural larvæ. Anural development is to be correlated with large size, oviparity, and a free, unattached sand life ; urodele more with small, viviparous, attached forms. The first type is considered to be primitive, and to have secondarily colonised the rocks.

It is concluded that anural development is a direct response to the sand-embedded habitat, that the hatching enzyme is lost when tail development is disturbed, and that anural development is compatible with race-survival only when there is an efficient alternative method of hatching.

N. J. B.

Regeneration in *Sabella pavonina* (Sav.) and other Sabellid Worms.

By N. J. Berrill.

Journ. Exp. Zool., Vol. LVIII, 1931, *pp.* 405–523.

The account represents a preliminary investigation into the phenomena of regeneration and metamorphosis typical of this group of annelids. In a normal worm the body is divided into three regions, a head and collar, a thoracic, and an abdominal region. The thoracic and abdominal segments differ in that the setæ and uncini in the first are respectively ventral and

dorsal, while in the second they are dorsal and ventral, as though the anterior part of the worm is twisted through 180 degrees. In development thoracic segments are first formed and then abdominal segments added behind.

In regeneration from anterior cut-surfaces, only a head and collar segment is formed from any segment of the body; from posterior cut surfaces regeneration is continuous as in normal growth. Up to two or three thoracic segments can be formed from the posterior surface of thoracic segments. In isolated abdominal pieces thoracic segments are always formed through the metamorphosis of originally abdominal segments. The usual number is 5–12, but under certain imperfectly known conditions it may be from 0–80. Metamorphosis never extends into abdominal segments newly regenerated posteriorly. There is always a gradient in degree of metamorphosis, the process being completed anteriorly while but just starting posteriorly. Contact with thoracic structure is unnecessary for abdominal metamorphosis, and every abdominal segment in the body is potentially thoracic. Temperature has merely an indirect influence, actual and physiological age being of greater importance in determining the extent of transformation. The reorganizing stimulus resides in the anterior regenerated head and collar segments. A hormonal control is precluded, while there is some evidence that it may be neuroid or electrical.

N. J. B.

Untersuchungen zur Physiologie der Tonusmuskeln.

By E. Bozler.

Zeitschr. f. vergl. Physiol. 12, *pp.* 579–602.

Two preparations of nonstriated muscle, suitable for quantitative experiments, are described, the retractor of the pharynx of the edible snail and the nonstriated part of the adductor muscle of Pecten. They respond easily to electrical stimuli, also to weak single induction shocks. The isometric twitch is very asymmetric, the rise of tension is as rapid as in most striated muscles, the relaxation is relatively slow. The resting muscle behaves like a plastic body; stretching produces tension. This, however, disappears completely, if the length remains constant. The time relations of this process are exactly the same as those of relaxation in an isometric twitch. In the Pecten muscle the quickness of the relaxation may change within wide limits in the same muscle preparation. After stimulating with a series of shocks, the muscle relaxes more quickly than if single shocks be applied in long intervals. In the discussion of the nature of this change it is important that the mechanical properties

of the muscle change at the same time in a definite manner. This change seems to be of great importance for the energetics of the muscle and explains some of the peculiarities of nonstriated muscle. E. B.

Notes on the Hydrogen Ion Concentration Excess Base and Carbon Dioxide Pressure of Marine Aquarium Waters.

By E. M. Brown.

Proc. Zool. Soc., 1929, *Pt.* 4, *pp.* 601–613.

A comparison of tank-water from the Aquarium of the Zoological Society of London with that of Plymouth showed that, while both deviate from the normal in certain respects, the former shows a greater variation in different tanks and at different times.

Plymouth maintains a nearly constant pH, as a result of liming, but is supersaturated with carbon dioxide. The Zoo Aquarium water shows a relatively low varying pH, low excess base and high carbon dioxide pressure, but a large variety of fish and invertebrates adapt themselves successfully to these conditions.

The diminution of the excess base in untreated Aquarium water was examined and the advantages of liming were discussed. E. M. B.

The Action of Potassium Cyanide and Potassium Ferricyanide on certain Respiratory Pigments.

By S. F. Cook.

Journ. Gen. Physiol., Vol. XI, No. 4, 1928.

Measurements with the Barcroft differential manometer show that different types of respiratory pigments are affected differently by $K_3Fe(CN_6)$ and KCN. The oxygen in hemoglobin is liberated by the former and not the latter, that in hemocyanin by the latter and not the former, that in echinochrome by the former and not the latter, and that in hemerythrin by both. S. F. C.

The Anatomy and the Histology of Bud-Formation in the Serpulid *Filograna implexa*, together with some Cytological Observations on the Nuclei of the Neoblasts.

By G. H. Faulkner.

Journ. Linn. Soc. Zool., Vol. XXXVII, 1930, *pp.* 109–190.

In the anatomy of *Filograna implexa* the chief points of interest are: the nephridia and their homology with other Polychaet nephridia: the

nerve supply to the branchial filaments : the circulatory system and the support this gives to the theory of a blastocoelic origin of the Annelid blood spaces.

During summer Filograna reproduces sexually, and during spring asexually, by a process of transverse fission. Posterior to the future plane of fission a new anterior region consisting of a head and two setigerous segments is inserted, and anterior to it a new growing point for the stock. The position of the abdomen of the plane of fission is variable.

The segments which are destined to be separated as the bud undergo prior to fission a complete histolysis. The old tissues break down, partly independently and partly by phagocytosis and are replaced by new embryonic tissues. A similar rejuvenation of tissues occurs to some extent on the stock. The cells which lay down the new tissue arise by the proliferation of neoblasts in the ventral body wall. These neoblasts are identical with the definitive germ cells of the sexual season. They are distinguishable from other cells by the fact that during resting stages their chromosomes persist as condensed bodies lying in pairs in a clear nuclear cavity.

G. H. F.

A Spectrographic Analysis of Animal Tissues.

By H. M. Fox and H. Ramage.

Proc. Roy. Soc., B., Vol. 108, 1931.

The present paper is the first report on a quantitative spectrographic analysis of animal tissues. It deals largely, but not exclusively, with annelids and molluscs. Iron and copper were present in all tissues analysed. Manganese was widely distributed. The manganese content of tissues varies with locality. Its function is discussed. Nickel and cobalt occurred spasmodically, the former being more frequent. Except in one case, all high concentrations of nickel were accompanied by cobalt. In one tissue only did cobalt occur without detectable nickel. Lead and silver both exhibit an irregular distribution. Certain tissues have a disposition to accumulate one or other of these elements. One man had silver in all organs, two others had none. Lead accumulates in different tissues of different individual men. Cadmium occurred in the livers of *Pecten maximus* from different situations. Lithium is very widespread in animal tissues, rubidium is much less so, while cæsium was not found. Strontium was found in numerous cases. Barium was not detected. Calcium fluoride was found in one case only, namely, the body-wall of *Archidoris tuberculata*.

H. M. F. AND H. R.

Notes on Protodrilus.

By E. S. Goodrich.

Quart. Journ. Micr. Sci., Vol. LXXIV, 1931, *pp.* 303–319.

The nephridium of *Protodrilus flavocapitatus* is described in detail. With its long-coiled canal and small projecting nephridiostome it is shown to be more complicated than hitherto supposed.

The sperm-duct of the male has a ridged ciliated cœlomostome and represents a cœlomoduct or possibly a nephromixium. It is argued that the "brachynephridia" and sperm-ducts of all Protodrilids are of the same morphological nature.

The fate of the cœlomoduct is related to the mode of emission of the genital products. In the female of *Pr. flavocapitatus*, which sheds the ripe ova by dropping off posterior segments, the cœlomoducts have been lost in all the segments, and in the male in all the segments excepting the eleventh. Remains of the cœlomostomes are perhaps represented by the ciliation of the cœlomic epithelium in the genital segments of the female.

It is maintained that Protodrilus is dicœcious, that the female may be early inseminated by the male, that copulation must take place, and that the dorsal glands are perhaps concerned in the process. Ripe spermatozoa only are found in the female, and the so-called stages in "cystospermatogenesis" are probably stages in the phagocytosis of superfluous spermatozoa.

E. S. G.

On the Morphology, Feeding Mechanisms, and Digestion of *Ensis siliqua* (Schumacher).

By A. Graham.

Trans. Roy. Soc. Edinburgh, Vol. LVI, pp. 725–752, 1931.

The structure of the razor shellfish *Ensis siliqua* is briefly described. A description of the byssus gland, which is only found in very young specimens, is given, while the structure of the nervous system is described in detail. The four principal ganglion pairs of the Lamellibranch are present, the cerebral and pleural ganglia on each side being fused, while the two pedal ganglia have fused to form a median ganglion; the two visceral ganglia lie closely approximated. The peripheral portions of the nervous system are remarkable for the large number of pallial anastomoses, there being four main circumpallial loops in each mantle fold in addition to minor connections. An asymmetrical stomatogastric system

supplying the anterior parts of the alimentary canal and in connection with vestiges of the buccal ganglia, is represented.

An account is given of the pallial ciliary currents : these appear to be in essentials similar to those described for other genera, save that the rejection tracts on the mantle are more powerful. The mode of functioning of the selective mechanisms on the palps is discussed.

The place of secretion of the style is described as two longitudinal tracts in the style sac of granular, darkly staining (iron hæmatoxylin) cells ; these are held to be homologous with the major and minor typhlosoles of those forms where the style sac and the mid gut are confluent.

The style diastase has an optimum temperature of 35° C. at pH 6·0 and an optimum pH of 6·0 at 22° C. The style also contains an oxidase.

The protease of the digestive diverticula has an optimum temperature of 32° C. and optimum pH values of 4·2 and 8·2 at 30° C. The diverticula also contain a lipase, a diastase and a glycogenase.

A. G.

On the Optimum Hydrogen Ion Concentration and Temperature of the Style Enzyme of *Pecten maximus*.

By A. Graham.

Proc. Roy. Soc., B., Vol. 108, *pp.* 84–95, 1931.

The diastase of the crystalline style of *Pecten maximus* was studied in order to investigate :—

(*a*) The effect of time on the pH optimum.
(*b*) The effect of pH on the temperature optimum.
(*c*) The effect of time and temperature on the pH optimum.

The principal results were as follows :—

(*a*) There is no variation in the pH optimum with variation in the duration of the experiment.

(*b*) There is a fall in the optimum temperature accompanying a fall in the pH of the medium.

(*c*) When two out of the three factors under the control of the animal —time, pH, and temperature—are made equal to those found in natural conditions, and the optimum for the third is determined, it also is found to be the actual condition encountered in the living animal.

A. G.

On the Correlation of the Life-history of the Acephaline Gregarine, Gonospora, with the Sexual Cycle of its Host.

II. *Gonospora* (*Kalpidorhynchus*) *arenicolae*.

By C. C. Hentschel.

Parasitology, XXII, 4, 505–509, *November*, 1930.

It is shown that there is a correlation between the life-history of the acephaline gregarine, *Gonospora arenicolae*, and the sexual cycle of its host, *Arenicola ecaudata*. This correlation exhibits certain points of similarity with that between the allied species *G. varia* and its host *Audouinia* (*Cirratulus*) *tentaculata*, described in a previous paper. The correlation is, however, not so definite, for the life-history of a generation of parasites does not necessarily coincide with the sexual cycle of the host. The ejection of the sporocysts together with the worm's gametes was observed. A brief description of the spawning behaviour of *Arenicola ecaudata* is also given.

C. C. H.

Regeneration of the Spines in Sea-Urchins.

By A. D. Hobson.

Nature, Vol. 125, *p.* 168, 1930.

Specimens of *Psammechinus miliaris* exposed to direct sunlight in the laboratory threw off all their spines except those on the oral surface. Regenerated spines were visible in a week and were fully developed in two months.

A. D. H.

Carbohydrates of Crab Nerve.

By E. G. Holmes.

Biochem. Journ., Vol. XXIII, 1929, pp. 1182–1186.

The peripheral nerves and nerve ganglia of Maia and Cancer are extremely rich in carbohydrate, which is present as glycogen and as "free carbohydrate." In the case of the ganglia, some, at least, of the carbohydrate is present as di- or poly-saccharide, soluble in 60 per cent alcohol, and in Schenk's reagent. In nitrogen there is hydrolysis of glycogen, and in the case of the ganglion, of the soluble di- or poly-saccharide ; there is also formation of lactic acid. In oxygen, the formation of lactic acid is inhibited ; the breakdown of glycogen is less than occurs in nitrogen.

E. G. H.

Observations on Dicystid Gregarines from Marine Worms.

By D. L. Mackinnon and H. N. Ray.

Q.J.M.S., Vol. LXXIV, 1931, *pp.* 439–466.

The detailed classification of dicystid gregarines is in a very confused state, and some attempt was made to correlate and correct the observations by earlier workers.

Dicystids in polychæte worms were studied, and notes made on the structure of two species of Polyrhabdina, occurring in *Scololepis fuliginosa* and in *Polydora flava* respectively.

Two new dicystids, for which the generic names Hentschelis and Lecythion were proposed by us, were described from the intestine of the echiurid worm, *Thalassema neptuni*. Spore-formation, after evacuation of the associated gametocytes into sea-water, was observed, and flagellated male gametes were seen to develop; but it was not possible to decide certainly to which species of gregarine in Thalassema these should be referred.

D. L. M.

A New Protozoon, *Hyperidion thalassemae* n. gen., n. sp., from the Intestine of *Thalassema neptuni* Gaertner.

By D. L. Mackinnon and H. N. Ray.

Q.J.M.S., Vol. LXXIV, 1931, *pp.* 467–475.

A new sporozoan, for which we propose the name *Hyperidion thalassemae*, was observed in the gut of *Thalassema neptuni*. This is an acephaline, pestle-shaped gregarine, which lives within modified epithelial cells while it is young; but which later on protrudes a contractile, club-like portion of its body into the lumen of the intestine. Its possible relationship with *Zygosoma gibbosum* (Greeff) from *Echiurus pallassii* were considered.

D. L. M.

The Feeding Mechanism, Formation of the Tube and Physiology of Digestion in *Sabella pavonina*.

By E. A. T. Nicol.

Trans. Roy. Soc. Edin. III, LVI, pp. 537–598, 1930.

The branchial crown of *Sabella pavonina* is a specialised ciliary filtering organ which collects small particles of detritus, diatoms, flagellates and similar organisms, as well as fine sand, from the water. The ciliation of the pinnules causes water to flow between the filaments into the branchial funnel. Particles in suspension are caught by cilia and carried down the filaments to the basal folds, where they are sorted into three grades, the

criterion being size not weight. The largest particles are rejected, the medium are stored in the ventral sacs (to be used later for tube building), while the smallest are carried to the mouth. The distribution of mucus cells on the branchial crown shows clearly that they are associated with the rejecting, and not with the collecting tracts of the ciliary apparatus.

The enzymes present in the gut are an amylase, protease and lipase. The optimum hydrogen ion concentrations at which these enzymes work are 6·8, 7·8, and 7·4 respectively, all of which fall within the limits of the hydrogen ion concentration of the gut, 6·0–8·4.

E. A. T. N.

Giant English Oysters.

By J. H. Orton.

Nature, Vol. CXXVI, August 30, 1930.

Details are given of size, weight and sex of two giant oysters, *O. edulis*, taken by E. A. T. Nicol and W. Searle near the Salstone, Salcombe Estuary, September 20th, 1929. It is of some economic importance that both the oysters were females, one mature which extruded a few ripe ova, and one maturing. Evidence is thus obtained that old oysters breed as females. From the volume of the gonad in the larger specimen (the shell of which was 17·6 cm. long by 19·8 cm. broad and 5·9 cm. wide) it is estimated that this individual had the capacity to produce 10 to 20 cm. of eggs—the equivalent of three to six million larvae—in one batch; hence the value of such oysters for repopulating old or new beds may be inferred.

J. H. O.

On the Oyster Drills in the Essex Estuaries.

By J. H. Orton.

Essex Naturalist, Vol. XXII, 1930.

Three oyster drills are recorded from the oyster beds of the Essex Estuaries, namely, *Ocenebra erinacea* (L.), *Nucella* (=*Purpura*) *lapillus* (L.) and *Urosalpinx cinerea* (Say). Figures of the shells and egg-capsules of each species are shown and their habits discussed. Experiments are cited showing that Urosalpinx and Ocenebra eat small (brood) oysters in about three days, and larger (half-ware) oysters in five or six days. It is shown that the habits of Ocenebra and Nucella vary in different habitats. Nucella attacks oysters, but probably much less frequently than the two other tingles. The introduction of the American oyster tingle, Urosalpiux, into English waters is discussed; the earliest record of its occurrence is 1920, though the date of introduction is undoubtedly much earlier.

Incidentally a record is given of an observation on the introduction of living Crepidula and Anomia into English waters on American oysters in 1908. The importance of the suppression of the tingle pests for successful oyster-culture is emphasised, as well as the economic value of knowledge of the habits of these animals.

J. H. O.

Oysters and Oyster Culture.

By J. H. Orton.

Encyclopædia Britannica, 14th Edition, 1929.

The article consists of a much condensed account of oysters and oyster culture. The chief economic species are noted. The incubatory and external modes of development are described briefly, with paragraphs on food and mode of feeding, oyster beds, fattening, shell growth, enemies and parasites, diseases, the oyster industry, oyster culture and breeding. In the latter paragraph are brought together the records published to that date of the spawning seasons of *O. edulis* and *O. virginica*. The arrangement of the records in localities of increasing latitude, as follows, shows earlier spawning in the warmer situations.

Species.	*Locality.*	*Range of spawning period.*	*Reference.*
O. edulis	Taranto Gulf (Italy)	March – April to October	Proprietors (Dean)
	Arcachon (France)	May to September	De Bon
	Thames Estuary (England)	End of May to September	Anson and Willett
	Fal Estuary (England)	End of June to September–October	Orton
	Norway (fattening ponds)	August to September	Helland-Hansen
	Norway (offshore)	Little or rare	Do.
O. virginica	Chesapeake Bay* (Md.)	May – June to August	Winslow-Brooks
	Barnegat Bay (N.J.)	End of June to ?	J. Nelson
	Malpeque (Canada)	June–July to ?	Stafford

J. H. O.

* Recently Hopkins (*Bull. Bur. of Fisheries*, U.S. Dept. of Commerce, Bull. No. 3, 1931, Washington) records spawning in Galveston Bay (Gulf of Mexico) from end of March to at least August in 1929.—J. H. O.

The Adaptation of *Gunda ulvae* to Salinity. I. The Environment.

By C. F. A. Pantin.

Journ. Exp. Biol., Vol. VIII, 1931, *pp.* 63–72.

The environment of the triclad *Gunda ulvæ* has been studied. This organism lives on the seashore in the estuaries of very small streams. The components of the external medium are (*a*) stream water, which is rich in Ca and CO_3, and (*b*) Atlantic sea-water. These are mixed in different proportions in different parts of the estuary. An analysis of the stream-water is given. The habitat of the organism is described. This extends roughly from high-water neap tides to low-water neap tides. A faunistic survey is given. The conditions which control the limits of the habitat of Gunda are discussed. Between the upper limit of occurrence of Gunda and the place of occurrence of fresh-water forms there is a region devoid of fauna. This region corresponds roughly with the span between high-water neap tides and high-water spring tides. Salinity determinations have been made on samples taken from the actual places where Gunda occurred. It is shown that Gunda has to withstand changes from completely fresh to undiluted sea-water. It may normally be exposed to either extreme for several hours. Salinity determinations made continually throughout the range of Gunda show that its environment may vary from one in which it is subjected to the action of sea-water for only about one hour at high tide to one in which the sea-water is only diluted to about 10 per cent of its normal strength for a few hours during low tide.

C. F. A. P.

The Adaptation of *Gunda ulvae* to Salinity. II. The Water Exchange.

By E. Weil and C. F. A. Pantin.

Journ. Exp. Biol., Vol. VIII, 1931, *pp.* 73–81.

The effect of fresh waters and dilute solutions on the behaviour and water exchange of the estuarine flatworm, *Gunda ulvæ*, has been studied. In Plymouth tap-water, which contains little dissolved substances, the majority of the worms die within 48 hours. While immersed in this water the worms swell rapidly during the first hour to about double their volume in sea-water, the volume falling slightly after this. The effect is reversible. In dilute sea-water the worms swell to a greater extent the greater the dilution. At great dilutions the swelling is much less than would be expected if the worm behaved as though it were covered with a perfectly semi-permeable membrane. In water from the stream which normally flows over the Gunda at low tide, the swelling of

the worms is much less than in Plymouth tap-water or in distilled water. This stream-water is rich in $CaCO_3$. The effects of distilled water and of solutions of NaCl, $NaHCO_3$, glycerol, $CaCl_2$ and of Cambridge tap-water are compared with the effects of Plymouth tap-water and the stream-water. It is found that the beneficial effects of the stream-water can be imitated only by the solutions containing calcium. The mode of action of calcium is discussed. It is suggested that it acts primarily by lowering the permeability of the worms to water.

C. F. A. P.

The Adaptation of *Gunda ulvae* to Salinity. III. The Electrolyte Exchange.

By C. F. A. Pantin.

Journ. Exp. Biol., Vol. VIII, 1931, *pp.* 82–94.

The rate of loss of salts by the estuarine worm, *Gunda ulvæ*, on transference from sea-water to various dilute solutions has been studied by measurement of the electric conductivity of the surrounding solution. Salts are lost by the worms from the moment of immersion in dilute solutions. Conditions affecting the rate of loss of salts are discussed. The relation between the amount of salts lost and the total electrolyte content of the worm was determined. It is shown that the worms only lose 25 per cent of their salts during the time that they imbibe a volume of water from the dilute solution equal to their initial volume. The limiting internal salt concentration of worms surviving in waters containing calcium is about 6–10 per cent of the normal concentration in sea-water. No such limiting value can be found for distilled water, since salts are lost continuously till cytolysis occurs. The significance of the limiting concentration is discussed. The effect of osmotic pressure, pH, dilute solutions of NaCl, $NaHCO_3$, glycerol, $CaCl_2$ and $CaCO_3$ are studied. The presence of calcium reduces the rate of loss of salts. Other factors do not seem to influence this rate. The relation of calcium to the maintenance of normal permeability to water and salts in the worm, and the significance of this to the problem of migration into fresh water are discussed.

C. F. A. P.

Do Oceanic Plankton Animals lose themselves?

By F. S. Russell.

Nature, January 4th, 1930.

The suggestion is made that there are threshold light intensities below which some plankton animals cease to be stimulated to move upwards. In the open ocean certain plankton animals which live in light of moderate

intensities near the surface may move downwards out of their normal light zone, perhaps at night, and reach layers at which the intensity is below the threshold. There will be no longer any light stimulus to bring them up, and there they may roam until random movement brings them once more into their threshold intensity zone.

F. S. R.

Vitamin Content of Marine Plankton.

By F. S. Russell.

Nature, September 27th, 1930.

Mention is made of the possible connection between the habit of plankton animals in the Plymouth area of living nearer the surface in July and August than in the previous months, and Belloc, Fabre and Simonnet's record that sterols collected from plankton animals in July were found to be biologically active, whereas those collected in April only acquired biological activity after irradiation.

F. S. R.

The Swimming of Cuttlefish.

By F. S. Russell and G. A. Steven.

Nature, June 14th, 1930.

Attention is called to the use made by the cuttlefish of its siphon for slow swimming in all directions, a fact not mentioned in zoological text-books, in which the siphon is only recorded as being used for backward swimming.

F. S. R. AND G. A. S.

Digestive Processes in Marine Invertebrates and Fishes.

By C. M. Yonge.

Jour. du Conseil, VI, 1931, *pp.* 175–212.

This paper contains a summary of recent work on the subject, particular emphasis being laid on the specialization of digestive enzymes characteristic of many groups of Invertebrates, and the gradual development of extracellular digestion in the animal kingdom from the primitive intracellular digestion.

C. M. Y.

The Significance of the Relationship between Corals and Zooxanthellae.

By C. M. Yonge.

Nature, CXXVIII, 1931, *pp.* 309–311.

This is a short summary of the author's papers on this subject published in the Scientific Reports of the Great Barrier Reef Expedition 1928–29 (British Museum (Nat. Hist.)). The conclusion is reached that the association between corals and zooxanthellae is essential to the plants, certainly not to *individual* coral colonies, but probably an indispensable factor in the necessarily exceptional powers of growth and repair possessed by the marine communities known as coral reefs.

C. M. Y.

The Crystalline Style of the Mollusca and a Carnivorous Habit cannot normally co-exist.

By C. M. Yonge.

Nature, Vol. CXXV, 1930, *pp.* 444–445.

Evidence is produced demonstrating that the presence of a crystalline style in any mollusc (Lamellibranch or Gastropod) is a certain indication that the animal in question possesses *no extracellular proteoclastic enzymes* and so cannot digest any but the very minute particles of protein matter which can be digested intracellularly. Such an animal is, therefore, except where a powerful crushing gizzard is present as in the Septibranchs, a specialized herbivore, feeding on phytoplankton or finely divided algal material.

C. M. Y.

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