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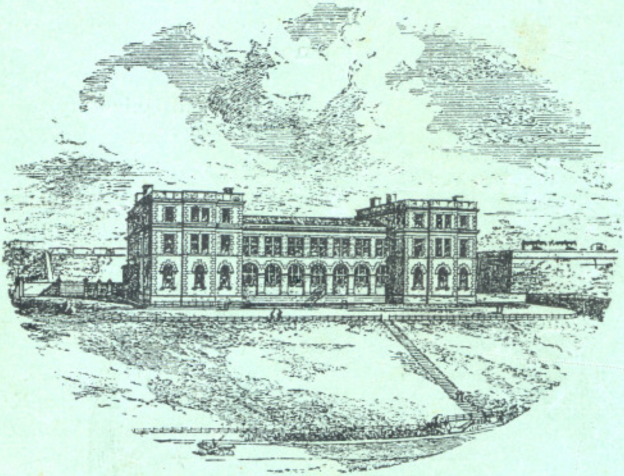

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The Determination of Specific Characters for the Identification of Certain Ascidians.

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INTRODUCTION.

IN the course of a study involving the routine identification of Tunicata the need became apparent of an attempt being made to define more clearly than has been done the diagnostic characters of certain species. The examination of a widely-collected material demonstrates the fact that in certain species considerable variations in structure accompany changes of habitat (depth, latitude, temperature, type of substratum, etc.), while other species vary but slightly. Thus if reference be made to the most recent comprehensive work on British Tunicates (**2**) it is found that in some cases many species—all mere varieties of one definite species (e.g. *Ascidia mentula*)—have been described, while in others (e.g. *Ascidia obliqua*) the features of but one form are given, there being no confusion due to apparent modifications of that form. Hartmeyer (**6**) revised Alder and Hancock's list of species, uniting many closely related forms under specific names not always adhered to in his later work (**7**). In many cases his conclusions were inevitable and have been accepted by more recent workers on the phylum. In connection with certain other cases, however, a distinct tendency has developed to consider that he has subordinated under one name two or more forms sufficiently clearly demarcated to warrant some kind of separate recognition. Thus Ârnbâch

(**15**) and Berrill (**3**) have *inter alia* devoted more special attention to the Family *Molgulidæ*, without, however, leaving the systematic position quite clear. It is a particular merit of the latter author's work that he redirects attention to the importance of developmental characters, concerning which a vast amount of accurate information seems yet to be lacking. At the same time, on practical grounds it is requisite that ontogenetic peculiarities should be correlated with recognisable differences of adult structure, since specific diagnosis must perforce most often be made upon preserved material. Definition of the range of variation of both developmental and adult characters is the desideratum.

Within the limits of the available facilities this paper deals with the type Family *Ascidiidæ* of the phylum, and gives the results of a semi-statistical study of material collected over a wide area (with northern and southern limits of Iceland and the English Channel respectively) wherein the nature of the habitat is sufficiently diversified to give rise to at least a fair amount of structural variation.

With two exceptions the species dealt with here were at various times kept in the live state either on board a research vessel or in the laboratory,* the object being to obtain for study the eggs, larvæ, and early fixed stages. This object was imperfectly attained. Thus species such as *A. mentula*, *virginea*, *conchilega*, and *mammillata*, which are not indigenous in the sea near the laboratory, and which had to be transported thither from a distance, gave rather meagre results. Even on the west Scottish coast, where they are common, and where they were kept on board ship, *A. mentula* and *A. conchilega* did not readily shed the reproductive elements. By contrast *A. aspersa* and *A. scabra*—particularly the latter—displayed enormous reproductive activity whether kept aboard ship or in the laboratory, in the neighbouring waters of which only the latter of these species is indigenous. The shedding of eggs could, in the case of *A. scabra*, usually be induced if necessary by the slight raising of the temperature of the water, but in no case did the other species respond to this stimulus. It is perhaps owing to its great fecundity that *A. scabra* is by far the commonest British Ascidian.

Two or more individuals of each species were kept in large aerated jars. No food was given except that contained naturally in the frequent changes of sea-water supplied. Under these conditions the smaller animals appeared to live quite healthily for months, but large individuals of *A. mentula*, *mammillata*, and *aspersa* could not be kept in condition for more than two or three weeks. No attempt at artificial fertilisation of eggs was made. The latter could be seen being intermittently expelled. In the case of any one individual the shedding of eggs in groups would proceed thus for 24–36 hours during spells of activity occurring every few weeks.

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* Scottish Fishery Board, Aberdeen.

Development of the eggs as far as the larval stage was always easily obtained, but under the conditions the metamorphosing larva almost always died before reaching the fixed stage. Only in the case of *A. scabra* was the fixed stage showing protostigmata obtained. The specific evidence submitted below therefore relates mainly to the production of certain forms of eggs and larvæ by species whose body characters are defined.

Roule (**20**) suggested the establishment of 3 genera within what is now recognised as Fam. *Ascidiidæ*, and these have been accepted (with some reservation) by other authors, partly, we think, since the establishment of the genus Ascidiella segregated a set of troublesome and confusing forms, leaving the genera Ascidia and Phallusia to be devoted to easily distinguishable species. It is to the study of the constancy and the relative specific value of the developmental and anatomical characters of the confusing forms more recently recognised under Genus *Ascidiella* that this paper is chiefly devoted. Collateral work has, however, been done on a scantier material relating to the other species of the Family. For reasons to be given below we incline to the opinion that, in the light of the facts presented here, the retention of the Ascidiella forms in a separate genus is not warranted.

1. Comparative Study of the Forms recently included in Genus Ascidiella (Roule, 1883, modified).

As treated by Hartmeyer (**7**) Gen. *Ascidiella* contains only one species —*A. aspersa* (Müll. 1776). It was that author's considered opinion that the three forms recognised by Herdman (**12**) are mere varieties of this species. The latter author did indeed call attention, as did Roule, to the existence of transitional forms apparently linking up one with another of his types. The first and largest type was named *Ascidiella aspersa ;* the two others—*A. virginea* and *A. scabra*—were much smaller and could be inter-distinguished by their habit, the former being erect, the latter recumbent and attached by the greater length of its side.

Roule's definition of Gen. *Ascidiella* brought in three Ascidian species (*A. virginea*, *obliqua*, *prunum*) which have since been excluded by the alteration of that definition to the following :—

a. Nerve ganglion almost directly above the dorsal tubercle.

b. The branchial papillæ are reduced.

It is chiefly on the constancy of character *b* that Gen. *Ascidiella* is based. All that is, however, implied by the term reduction is that free papillæ, as found in other species (Plate 7, Fig. 3), do not occur, although in certain portions of the branchial sac—e.g. near the mouth—a rudimentary state may persist (Plate 7, Fig. 2). In the latter case irregular bosses arise from the transverse vessels and either remain isolated or become more or less linked up with each other by the outgrowth of longitudinal spurs. In cases where these bosses are numerous they might be mistaken for papillæ. Normally, however, they are completely linked up by longitudinal vessels (Plate 7, Fig. 1) and are seen only as thickened portions of these bars. Instead of growing out into true free papillæ they have the appearance of being repressed back on to the transverse vessels by means of their association with a transverse papillary membrane which links them together laterally. The experienced worker has no difficulty in recognising Gen. *Ascidiella* from this peculiarity of sac structure.

The point to be investigated here is the number of species capable of clear distinction within this genus. Can the reduction from Herdman's three forms to Hartmeyer's one be justified ? The latter author certainly has not submitted a thorough analysis of the forms. Berrill claims that at least two, and possibly three, species are to be distinguished. We may recapitulate the points in which he finds form *aspersa* to differ from form *scabra*.

A. aspersa.—Attached basally ; attains maximum size of 12–13 cm. ; any mantle pigment present is localised near the siphons ; has the renal bodies extensively distributed over the mantle ; has floating egg, with very large outer follicle cells.

A. scabra.—Attached by side ; size restricted to 4 cm. ; has red pigment spread usually over most of the mantle and has the atrial siphon relatively nearer the branchial than is the case in *A. aspersa ;* the renal bodies are less extensively distributed ; the egg is non-floating, with small outer follicle cells and the chorion raised further from the ovum surface than is the case in the egg of *aspersa*.

The third possible form (Herdman's *A. virginea*) is said to differ from form *scabra*, which it most resembles, in possessing a deep, diffusely spread brown pigment, and in forming eggs in which the perivitelline space is narrower.

At the outset of this study an attempt was made to keep forms resembling *scabra* and *virginea* separate, but no justification could be found for so doing. Their eggs and larvæ appear to be identical respectively, and in outward appearance the two extremes of form are linked up by a range of intermediate forms. In addition there is no consistent anatomical difference between them, although in certain habitats the erect, in others the recumbent form may be that more commonly found. The characters of the two forms and their intermediaries are therefore combined here and are submitted under the name *scabra*, thus being contrasted with those of form *aspersa*.

We have had the opportunity of examining the material from over

200 collections of form *scabra* and from 11 collections of form *aspersa*, which is obviously a comparatively rare species in British waters. While dissections were made only on the following specimens selected from this wider material, it is to be emphasised that rougher examination of the remainder served to confirm the conclusions arrived at.

A. aspersa.—22 specimens, length 7–76 mm., taken from shallow water, Plymouth; 11 spec., 30–72 mm., 41 metres, Loch Fyne; 2 spec., 37–50 mm., 40 metres, Loch Duich; 1 spec., 18 mm., 10 metres, Lochmaddy (North Uist); 1 spec., 42 mm., between tide-marks, Olna Firth, Shetland; 25 spec., 8–31 mm., 7–12 metres, Loch Indail, Islay; 2 spec., 37–56 mm., 7–17 metres, Ettrick Bay.

A. scabra.—13 spec., 8–29 mm., Eddystone Grounds; 11 spec., 28–35 mm., 11–20 metres, Luce Bay; 30 spec., 12–43 mm., 48 metres, Firth of Clyde; 7 spec., 27–35 mm., 41–138 metres, Loch Fyne; 5 spec., 20–29 mm., 16–28 metres, Islay; 15 spec., 22–36 mm., 80 metres, between Skye and Mull; 30 spec., 15–38 mm., 103 metres, Hoy, Orkney; 30 spec., 6–34 mm., 123 metres, Scalloway, Shetland; 38 spec., 16–31 mm., 142 metres, E. of Balta, Shetland; 15 spec., 15–37 mm., 107 metres, Northern North Sea; 43 spec., 6–47 mm., 62 metres, Northern Moray Firth; 10 spec., 15–41 mm., 82 metres, 50 miles E.S.E. of Aberdeen; 18 spec., 9–39 mm., 15 metres, Kirkcaldy Bay; 30 spec., 24–73 mm., 36 metres, Dogger Bank (north edge); 30 spec., 19–53 mm., 42 metres, Dogger Bank (Tail End).

The following are the results of the investigations of the characteristic features of these two forms:—

(A) *Geographical and Bathymetrical Distribution.*—If two otherwise closely allied forms have precisely the same distribution the case for considering them the same species is strengthened. Owing to confusion in nomenclature it is not always clear to which form authors have referred, but it can be said that *A. aspersa* is in general found in much shallower water than is *A. scabra.* The former is commonest in harbours, river estuaries, etc., and can succeed in brackish water; it is found coastally from the Mediterranean to the latitude of Shetland, but as far as is known it is absent from the east British coast (except from the Thames estuary). Although it occurs on the south Norwegian coast it is doubtful if it extends much distance northwards along the west coast. The records from Ettrick Bay, Islay, Loch Duich, and Olna Firth are new. North of the English Channel this species is rare. *A. scabra*, however, is taken in great numbers at all points where its congener occurs; it favours deeper water (5–300 metres as compared with

0–50 metres), and is the commonest Ascidian of the North Sea, where *A. aspersa* is lacking. It also extends further north than that species, being found at Faroe and Trondhjem. There is therefore far from complete coincidence between the distribution of the two forms. At the same time they often occur in close association, and were they similar in almost all other respects might be considered as shallow- and deep-water forms of the same species.

(B) *Size.*—In the English Channel where it is fairly common *A. aspersa* can, according to Berrill, attain 13 cm. in size. The average size is, however, probably no more than 6–7 cm. Scottish specimens tend to be smaller even than this. *Scabra* rarely exceeds 2–3 cm. in mean size, and 4–5 cm. in maximum size. On the Dogger Bank, however, a maximum size of 7½ cm., if not more, is reached. Conversely the maximum size in areas in which the recumbent form predominates is seldom more than 3½ cm. (All these measurements, with the exception of Berrill's, refer to the antero-posterior dimension, omitting the length of the siphons, which varies with the extent of their contraction.) *Aspersa* is therefore, on the average, at least twice as large as *scabra*.

(C) *Attachment to Substratum.*—There is by no means uniformity of degree of fixation in either *aspersa* or *scabra* (or, for that matter in most other species). Thus although *A. aspersa* has hitherto been regarded as a basally attached animal, we have obtained in Loch Indail, Islay, a group of specimens (Plate 5, Fig. 2) attached by nearly the whole side. These occurred in the shallow water of a bay exposed to the scouring action of south-westerly swells, and erect, slightly attached individuals would in such a position encounter severe buffeting. The fixation was to a large Cyprina valve which was firmly silted down into the sand. These animals were not dissected since it was desirable to retain them as type specimens, but they resembled *A. aspersa* in size, nature of test, position of apertures, and type of egg. The occurrence of adult individuals so fully attached is doubtless very exceptional. In the Plymouth material 23 individuals were fixed basally and one by half of its side. Twenty of the Loch Fyne animals were attached basally, and two by half the side. It is noteworthy that in the Plymouth material of *Ascidia virginea*, a species hitherto thought always to be erect, a parallel case was encountered (Plate 4, Fig. 6) where an individual was wholly attached by its side to the valve of a Scallop.

Turning now to *A. scabra*, we find that there is no justification for the establishment of two species (*scabra* and *virginea*) on the score that one is attached by the whole or the greater part of the side, the other basally. All Dogger Bank specimens were found to be basally fixed, either to a Lamellibranch valve (Plate 4, Fig. 4) or by means of a conical root-like prolongation of the test substance into the sand. All of the

Firth of Clyde, Orkney, and Islay individuals were also attached by the bases. In the other areas (Plymouth excepted) practically all were so fixed, but a greater or less tendency was displayed for certain individuals to have more extensive attachment (Plate 4, Fig. 1). Only of the Plymouth material could it be said that the predominant tendency was towards complete attachment.

Attachment.	Plymouth.	N. North Sea.	Luce Bay.	Scalloway.	Skye–Mull.	Kirkwall.	Loch Fyne.	Moray Firth.	Balta.	E.S.E. Aberdeen.
Basal	3	10	29	26	12	16	6	39	37	64
One-third of side . .	2	–	3	–	1	–	–	1	–	3
Half of side . . .	7	1	2	2	1	–	1	3	1	6
Two-thirds of side .	7	1	–	–	–	–	–	–	–	–
Three-fourths of side .	3	2	2	1	1	2	–	–	–	–
Whole side . . .	–	1	1	1	–	–	–	–	–	–

It is probable that the recumbent form tends most frequently to be found where stones, shell-valves, seaweed-fronds, etc., occur to afford the basis of attachment, and where, in addition, a large average size is not attained. Thus in the deep water of the northern North Sea, in very soft mud, it is natural to find more than normal use being made of hard objects for means of attachment. Any attempt, however, to establish constant points of anatomical difference as between flat and erect forms has been unsuccessful. On the other hand, as will be shown below, constant points of resemblance are capable of easy demonstration.

(D) *Colour.*—*A. aspersa* has been stated to differ from *A. scabra* in being practically colourless, whereas in adult individuals of the latter the mantle is usually more or less reddish-brown. This distinction can be said to hold in most cases, but it frequently breaks down. Our material has provided no pigmented forms of *aspersa*, but Alder and Hancock have illustrated their description of *Ascidia Normani* (=*A. aspersa*) by means of a figure showing a brilliantly carmine-pigmented mantle, such as is often found in *A. scabra*. This does not agree with their description of the mantle as being of a pale buff flesh-colour or almost colourless. We conclude that the specimen figured is one of the exceptional pigmented forms, called by these authors *A. Normani* (var. *resplendens*).

On the other hand, almost or quite colourless forms of *A. scabra* are frequently found. For example, the large Dogger Bank individuals have at most the pale buff colour referred to above, while the beautifully transparent specimens from the inner Moray Firth (Plate 4, Fig. 3) are virtually free from pigment. Even the flat forms have their colourless variety (*A. scabra* var. *albida* of A. and H.).

The above distinction therefore applies only to the majority of cases and is not strictly specific.

(E) *Nature of Test.*—Here we deal with a character which falls just short of being absolutely specific. In *A. aspersa*, as the name signifies, the test of the young animals is more or less covered with fine papillæ. In cases where no pigment develops (e.g. in the west Highland sea lochs) the specimens present, at size 2–4 cm., an attractive frosted appearance. In larger animals, however, the test becomes more or less coarsely pustulose (Plate 5, Fig. 1) and is cartilaginous in consistency, rather than gelatinous or coriaceous as in *A. scabra*, in which it is usually smooth or at most wrinkled, with occasionally a few papillæ round the siphons. The test in the neighbourhood of the siphons may indeed be strongly echinated (as in A. and H's *A. scabra* var. *lævis*), but it is possible that the var. *echinata* (Lamlash Bay, Arran) of these authors is a young stage of *A. aspersa*, since the papillæ extended over the test generally.

(F) *Position of the Apertures.*—It has been held to be a distinguishing feature of *A. aspersa* that the atrial aperture is separated from the branchial by a distance equivalent to rather less than one-half of the body-length ; whereas in *A. scabra* the distance is only one-quarter (and rather less than one-quarter in the recumbent forms). If we express the distance between the mid-points of the siphons as a fraction of the body-length we find that out of 65 specimens of *aspersa* 32 gave one-third, 7 rather less than one-third, and 26 rather more than one-third. That is, the mean distance is in these cases rather greater than one-third, and the range of variation is from about one-fourth to just less than one-half.

In the case of *A. scabra*, out of 446 specimens 71 gave a ratio of one-fifth, 311 of one-fourth, 58 of one-third, and 6 of one-half. The tendency towards the larger interval existed in areas in which the recumbent form was most numerous. The mean interval between the apertures was therefore about one-fourth of the body-length, and the variation on either side of that ratio was approximately balanced as between one-third and one-fifth.

Where it is desired to distinguish the species without dissection the distinction (between the mean ratios of one-third and one-fourth respectively) is of accessory value, but as has been shown some overlapping of the respective ratios occurs.

A note may be made here of the very rare occurrence of the persistence of an early post-larval character in *A. scabra*. From the Doghole, off Aberdeen, a specimen was taken with two atrial siphons (Plate 8). Herdman (**10**) records a similar case from Llandudno.

(G) *Numbers of Branchial Stigmata per Mesh.*—A mesh of the branchial sac may be defined as the rectangular area enclosed by the intersection of two adjacent longitudinal with two adjacent transverse vessels. Herdman

(**12**) gave it as a distinction of *A. aspersa* that from 4–6 stigmata are formed in each mesh, as compared with from 7–12 in the recumbent form of *A. scabra*. Now were this the case there would be, in the number of stigmata, a specific point of difference between the two species.

The main features of a count of the stigmata in 29 specimens of *A. aspersa* and 316 specimens of *A. scabra* are shown in the following table, in which size 5 includes specimens ranging in size from 3–7 mm., size 10 those ranging from 8–12 mm., and so on. If it be remembered that *A. aspersa* is, age for age, much larger than *A. scabra*, it is probably the best interpretation of the results to deduce that, stage for stage, though not of course size for size, both forms have approximately the same number of stigmata per mesh, and that this number increases with age to a rather definite maximum average number (6–8). Now this maximum is attained by *A. scabra* at a smaller size than by *A. aspersa* (witness the attainment of the maximum range—4 to 9—at size 20 mm. in the case of the former, and, in that of the latter, the maximum of 6 to 8 at size 40 mm.).

No. of Stigmata per Mesh.

Size (mm.).	*A. aspersa.*			*A. scabra.*		
	No. of Specimens.	Range.	Mean.	Mean.	Mean Range.	No. of Specimens.
5	–	–	–	**3·3**	3–4	2
10	1	2	**2·0**	**4·0**	3–6	7
15	6	3–4	**3·7**	**4·7**	3–7	16
20	2	4–5	**4·3**	**5·2**	4–9	57
25	4	4	**4·0**	**6·0**	4–9	68
30	3	5	**5·0**	**6·5**	4–9	85
35	–	–	–	**6·9**	4–9	44
40	13	6–8	**7·0**	**7·3**	5–9	18
45				**7·3**	6–8	4
50–75				**6·8**	6–8	15

The similarity of the figures for both species at sizes 40–75 is probably due to the fact that in the case of *A. scabra* we are at this stage dealing only with the fast-growing Dogger Bank specimens which, age for age, must approach in size the specimens of *A. aspersa* which have been examined. Neither species can be said to increase its average number of stigmata after a size of about 40 mm. is attained. Unfortunately the table does not show features brought about by differences in growth rate in one area as compared with another. It is informative, for example, to take separately the results for those areas where a small maximum size (35 mm.) is attained by *A. scabra*. In Luce Bay and Loch Fyne individuals 7 stigmata per mesh are found at a size of only 15 mm., whereas from all areas the average is below 5. Again, at size 20 mm., the average number is nearly 7½ as against an all-over average of just over 5. Not only is full stigmatic development reached in these areas at a relatively small size, but the high maximum number of stigmata of 9 is formed. This number is equalled elsewhere only in the northern Moray Firth, but is attained at the relatively larger size of 30 mm. In the material examined the highest individual number of stigmata found was 10 (the figure 9 in the upper limits of the ranges of the above table indicating ranges of 8–10). For all the areas other than Luce Bay, Loch Fyne, and the Moray Firth the maximum number of stigmata found was slightly less—8 or 9—and was attained in each area at a size roughly proportional to the ultimate maximum size attained in that area. The effect of combining the Luce Bay, etc., figures with those from other areas has therefore been slightly to raise the mean number of stigmata attained at the lesser sizes, and may for comparative purposes be ignored since the numbers of individuals examined from the latter areas were by far the greater.

In the case of *A. scabra* we have probably dealt with collections including some specimens which had reached the maximum size attainable by this species. In that of *A. aspersa*, however, the largest animal was 76 mm. in size, so that individuals up to fully half as large again remain to be examined. Whether the latter will exhibit a larger mean number of stigmata than 9 (the highest encountered in our material) seems doubtful. In justifying this opinion we may add information not revealed in the above table, which is a summary. At mean sizes of 40, 45–75 mm. the following were the ranges in the number of stigmata in the individual cases (in ascending order of size) : 7–8, 5–7, 6–8, 7–9, 5–9, 5–9, 7–9, 7–9. Thus the range as well as the mean number of stigmata remained practically stationary although the size of the animal increased to almost double.

The general inference from these results is that size for size (up to a size of about 35 mm.) *A. aspersa* has, on the average, from 1–2 fewer stigmata per mesh than has *A. scabra*, and that in certain areas (e.g. Loch Fyne) where both species occur the difference may be rather more (3 or at most 4). In the general routine of distinguishing the species, however, little aid will be obtained from counting the stigmata.

(H and J) *Number of Tentacles and of Internal Longitudinal Bars.*—These two characters are taken together since a relationship of specific value can be shown to exist between them. Little has hitherto been done with regard to enumerating the number of bars, and estimates of the number of tentacles have varied considerably, part of the variation being due to inaccurate observation, to which Herdman (**12**) calls attention. The method here adopted was to discard individuals which had been indifferently preserved (in the sense that the branchial aperture was closed by the sphincter muscles and the dissected-out tentacular collar so contracted that the tentacles could not be counted with at least 95% accuracy). The tentacles stain very well with very dilute hæmatoxylin so that even the most rudimentary ones can be easily seen and enumeration be made by turning each filament over with the needle under the binocular microscope. In certain cases (small individuals of *A. scabra*) it was necessary in order to secure a non-convolute piece of tissue to cut the collar into about 4 equal portions, and to make the count in each of the latter separately. Repeat counts should correspond to within the degree of accuracy stated above. In well-preserved material discards need seldom be made. The longitudinal bars were enumerated in a transverse direction in the right half of the branchial sac, immediately above the mouth.

The results of the counts made on the two species are plotted against size (Fig. 1). In *A. aspersa the number of bars always outnumbers that of the tentacles* (B. and T., Fig. 1). This, at least, is the case in specimens of 10 mm. or more in size. Individuals from Islay and of size less than 10 mm. showed a reversal of this relationship. (A series of size 5–9 mm. gave an average of 31 tentacles as against 28 bars.) Variation in locality has some effect in causing variation in the number of tentacles, since, size for size, Islay specimens were found to have formed more tentacles than those from Plymouth. The results from the Islay form are not included in Fig. 1, but in animals ranging in size from 10–20 mm. there occurred from 29–34 tentacles (av. 31–32), while at the higher size of 20–30 mm. from 28–43 tentacles (av. 34–35) were found. Thus the Islay form agrees in this character with the forms from Lochmaddy and Shetland (represented in Fig. 1), the number of tentacles being greater than that developed in the forms from Plymouth, Loch Fyne, and Ettrick Bay. (One specimen of size 56 mm. from the last-named locality had 36 tentacles and 50 bars, ostensibly classing it with the Loch Fyne type.)

With regard to the number of bars, it was found that Loch Fyne and Ettrick Bay specimens had a slightly greater number than those of Plymouth, and a much greater number than those of Islay, Lochmaddy, and Shetland. The figures for the Islay forms may be given here since they are not represented in Fig. 1. From sizes 10–20 mm. there were from 32–39 bars (av. 36–37), and from sizes 20–30 mm. from 36–42 bars (av. 40). In every case the number of bars exceeded that of the tentacles but not by so large a margin as in the other areas, which, it may be noted, agree in being less directly exposed to oceanic conditions. In another sheltered area—Loch Duich—one specimen of 37 mm. was found with 54 bars (the tentacles could not be counted), and would apparently fall into the Loch Fyne class.

In the case of *A. scabra* (I–VI in Fig. 1) *the number of tentacles is always greater than that of the bars*—thus reversing the relationship found to hold for *A. aspersa*. For reasons of economy of space the results for the different areas have been grouped where similar. Thus I represents those for the North edge of the Dogger Bank as well as those for the Tail End of the Bank ; II those for Luce Bay alone ; III those for the area E.S.E. of

Aberdeen, as well as for Orkney and Shetland (Balta); IV those for the Firths of Clyde and Forth, for Islay, and for the area between Skye and Mull; V those for the Moray Firth alone; and VI those for the northern North Sea, for Scalloway (Shetland), for Loch Fyne and for Plymouth. The large dots represent the number of tentacles (T), the small dots the number of bars (B), both plotted against size of animal. As was the case in connection with *A. aspersa* both the number of tentacles and of bars appear to increase with size of individual—this as a general rule—but, as was the case in the Islay, etc., forms of that species, the increase in number of tentacles is at most slight in I, II, and IV (in II also there is no obvious increase in the number of bars). The apparently fortuitous way in which areas (in some cases widely separated) gave sufficiently similar results to admit of the grouping of the latter in Figure 1 admits of no obvious explanation. Neighbouring areas, in which similarity of type might be expected to occur, as often as not exhibited dissimilarity of type. For example, the specimens from the two Dogger Bank areas, although agreeing in the size-number of bars relationship, disagreed to some extent in their respective number of tentacles, fewer being developed in those from the north edge. Again, in some areas the progressive increase (with size) in the number of bars or tentacles is much more rapid than in others. The fact of value to this investigation is, however, that a line can in every case be drawn to effect separation of the points representing the numbers of bars and tentacles respectively. *The determination of the relative number of bars and tentacles therefore affords information of diagnostic value with regard to the two species.* As these numbers appear usually to vary with size of individual no specific figures can be defined. The number of bars is much the same in both species (varying from 20–60 in *A. aspersa* and from 25–50 in *A. scabra*); but the number of tentacles varies from 10–40 in the former species and from 30–110 in the latter.

A second distinction lies in the fact that, owing to their comparatively great numbers, the tentacles are in the latter species very much crowded at the base, whereas those of *A. aspersa* are set at intervals and appear to be slightly flattened to a broader base than those of *A. scabra* (Plate 6, Figs. 27, 28).

(K) *The Shape of the Dorsal Tubercle* (Plate 6).—The shape of the opening of the duct from the neural gland affords a further means of distinguishing *A. aspersa* from *A. scabra*. In the former species this opening is transversely oval or elliptical (broader than high); in the latter it is practically always higher than broad. In very small specimens of both species the opening is in the form of a more or less crescentic or incomplete loop (Figs. 1, 15, 16), although in *A. aspersa* the typically broadly-oval contour is often attained even in very young animals. Size

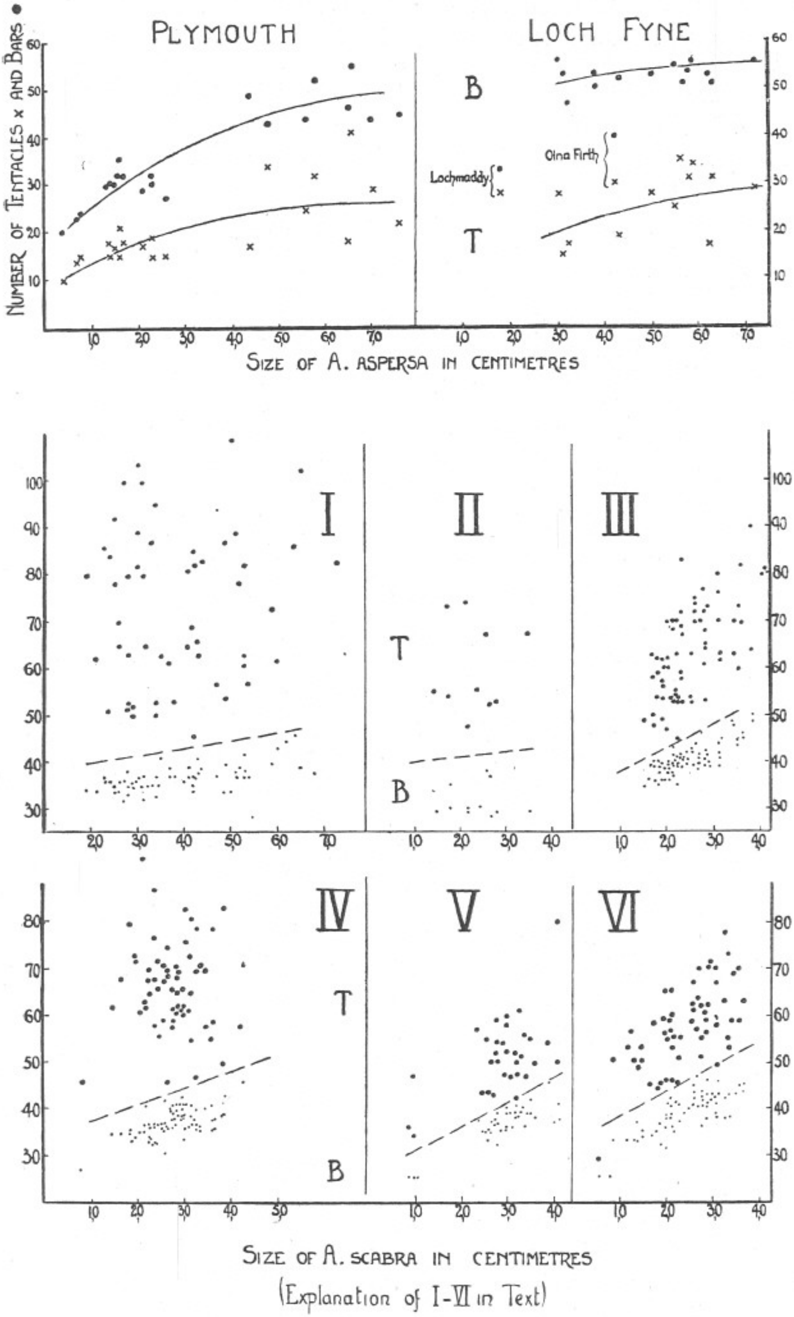
PLYMOUTH
LOCH FYNE
NUMBER OF TENTACLES × AND BARS ●
B
T
Lochmaddy
Olna Firth
10
20
30
40
50
60
1,0
2,0
3,0
4,0
5,0
6,0
7,0
SIZE OF A. ASPERSA IN CENTIMETRES
I
II
III
IV
V
VI
T
B
30
40
50
60
70
80
90
100
SIZE OF A. SCABRA IN CENTIMETRES
(Explanation of I-VI in Text)

FIG. 1.

for size of individual, the tubercle of this species is larger than that of *A. scabra*, and examination of 60 specimens showed :—

a. 46 cases with transversely oval tubercle with both horns incurved (Figs. 2, 3).
b. 4 cases with transversely oval tubercle with both horns turned right (Fig. 5).
c. 7 cases with cordate tubercle (about equally as broad as high), and both horns incurved (Fig. 4).
d. 3 cases with cordate tubercle, with the right horn only incoiled.

In *A. scabra* great variation of the fundamentally U- or longitudinally-elliptical form occurs. Of 310 specimens :—

a. 75 had tubercle simple U- or staple-shaped (Figs. 11, 18, 22, 25).
b. 56 had tubercle U- or flask-shaped with both horns outrolled (Figs. 7, 23, 24).
c. 53 had tubercle U-shaped with both horns turned right (Figs. 10, 17).
d. 38 had tubercle U-shaped with only the right horn outrolled (Fig. 14).
e. 25 had tubercle broadly U-shaped with prolonged horns (Figs. 12, 20, 21).
f. 23 had tubercle U-shaped with left horn inrolled (Figs. 6, 13).
g. 14 had tubercle U-shaped with right horn inrolled (Fig. 19).
h. 13 had tubercle U-shaped with both horns inrolled (Fig. 8).
j. 9 had tubercle almost cordate in shape (Fig. 4).
k. 4 had tubercle U-shaped with left horn outrolled (Fig. 9).

Thus only in a relatively insignificant number of specimens (j) was the cordate type of tubercle to be found, and to this extent slight confusion with two of the minority forms (c and d) found in *A. aspersa* is possible, although in the latter species the size of tubercle is greater. In *A. scabra* the U- or modified U-shaped tubercle is clearly predominant, and in each area there is a particular tendency towards some two or three of the forms. The most striking departure from the fundamental shape was exhibited (e) by many of the Dogger Bank specimens, in which the tubercle was larger than usual and had the horns elongated much as is the case in another species, *A. obliqua*.

(L) *Distribution of the Renal Bodies.*—In both of the species under comparison these bodies are large (as seen in Plate 8, Fig. 2) and, besides being distributed over the mantle on the left side of the gut, extend also *well beyond* that region, whereas in other species of the Family *Ascidiidæ* they are usually said to be confined to the visceral region. This distinction between *A. aspersa*+*scabra* and the other species is probably specific if the phrase " well beyond " be used. (In *A. prunum* we have occasionally found the renal cells to extend *slightly* beyond the region of the viscera, and Herdman (**12**) has found this to be the case also in *A. conchilega*). Berrill has claimed it as a distinction between *A. aspersa* and *A. scabra* that the renal cells are more widely dispersed in the mantle of the former. In our material there has been little to choose in this respect between the two species. At times the cells are difficult to detect owing to their transparency, and the extent of their distribution might then be overlooked. This was the case particularly in the Loch Fyne material of both species. In the Plymouth material, on the other hand, the cells were particularly obvious. The degree of clearness with which the renal cells are seen probably depends upon the amount and colour of the concretions they contain.

(M) *Size and Nature of the Eggs and Larvæ* :—

a. *The Eggs.*—Except in the case of two species the eggs of the members of the Family *Ascidiidæ* were obtained in the aquarium, and are depicted in Plate 1. In the cases of *A. obliqua* and *A. prunum*, however, living animals could not be obtained, and the size of the living egg was estimated from that of the ova in the terminal portion of the oviduct. (It was computed that the mean diameter of the living egg, one hour or so after expulsion, is on the average half as large again as that of the vitellus in the oviduct, most of the increase of size being due to the further withdrawal of the chorion from the vitelline surface.) Figures 7 and 9 are therefore included as showing, for comparative purposes, the probable sizes of the chorion in *A. prunum* and *A. obliqua* respectively.

It is important that the diameter of the recently expelled egg be that which is used for purposes of comparison, since some increase in diameter usually accompanies the development of the larva in the egg (Plate 2, Figs. 2, 3). The mean measurement of a number of eggs should, where possible, be used as a criterion, since at any one shedding period the eggs expelled are not of exactly the same sizes. Some difference in size may also be found if eggs from different regions, or eggs shed at different times of the year, are compared. It is of interest to note, however, that animals sent to Aberdeen from Plymouth, and kept in water from the sea off Aberdeen, yielded eggs differing in no way from those obtained from the same species in English Channel water. Slight differences of temperatures and salinity have therefore little or no effect on the structure of the egg. Certain species (*A. scabra, Dendrodoa grossularia, Ciona intestinalis*) which were kept in the aquarium over the winter season were found to yield eggs and larvæ even in March, although reproductive activity was in winter on a much reduced scale as compared with that in summer and autumn, when, incidentally, the largest eggs appear to be liberated.

The egg of *A. aspersa* differs from those of the other species of Family *Ascidiidæ* in possessing, at the time of liberation, an investing layer of very large follicle cells (Plate 2, Fig. 1). There are from 28–32 of these seen in optical section. The chorion is not at this stage obvious, whereas it can be seen surrounding the ovum even in the oviduct of *A. scabra*. In the newly-liberated egg of the latter species the outer follicle cells are much smaller, resembling those of the eggs of the other species so far examined. From 70–80 of them are seen in optical section and they form a layer over the chorion, which is quite clearly seen. The difference in the nature of the follicle cells can even be seen in groups of eggs dissected out from the terminal portion of the oviduct of each species (Plate 1, Figs. 10, 11). The difference in the size of the follicle cells, as Berrill states, is specific. Otherwise the eggs of these two species appear to agree in regard to diameter of vitellus and the nature of the cells which come to lie upon the surface of the latter.

Some time after the eggs of *A. aspersa* are set free the follicle cells separate to a greater distance from the ovum surface and are clearly seen to surround the chorion (Plate 2, Fig. 2). The result is that instead of being compressed owing to contiguity so as to present, in optical section, the appearance of a hexagonal network (Plate 2, Fig. 1), these large cells come to lie more or less free of each other (Fig. 2) so that they appear to be circular in optical section. Figure 1 represents an average size of egg of ·22–·24 mm. and Figure 2 of from ·28–·31 mm. The latter size persists unchanged for at least several hours, and may be taken as typical. The fertilised and developing egg (Plate 2, Fig. 3) may, however, be up to ·36 mm. in diameter. It is interesting to note that the average diameter of eggs obtained from Plymouth and West Scottish specimens of *A. aspersa* was found to be identical (from ·27–·32 mm.). As Berrill states the egg floats —in fact most of the eggs cluster together subjacently to the surface film of the water, and none is found further than one inch from the surface. This is not, however, the only species of Ascidian forming eggs displaying this character. Specimens of *Corella parallelogramma* taken in the Firth of Clyde and kept under observation on board ship yielded within a few hours similar but slightly smaller eggs (Plate 1, Fig. 8). These had a diameter of about ·18 mm. at the time of liberation, and of from ·24–·26 mm. one hour later. The eggs of *A. scabra*, however, do not rise to the water surface, remaining at or near the bottom of a jar containing them. At liberation they have the diameter and form which is maintained for many hours afterwards (Plate 1, Fig. 5; Plate 2, Fig. 4). It cannot be said that the chorion diameter differs materially from that of the eggs of *A. aspersa*, but this statement is made with reservation, since we have found that variation apparently arises if observations be continued from season to season and upon individuals from different localities. The following variation in diameter has been found :—

Off Aberdeen, June. Size ·32–·36 mm. *Average* ·33 mm.
Off Aberdeen, Oct. Size ·27–·31 mm. *Average* ·29 mm.
Off Peterhead, June. Size ·34–·37 mm. *Average* ·345 mm.
Off Plymouth, June. Size ·30–·33 mm. *Average* ·32 mm.
Off Skye, August. Size ·28–·30 mm. *Average* ·29 mm.
Off N. Scottish Coast, Sept. Size ·29–·30 mm. *Average* ·295 mm.
Firth of Clyde, Aug. Size ·31–·32 mm. *Average* ·315 mm.

As Berrill figures an egg of only *ca.* 0·25 mm. diameter from the Swedish coast and one of *ca.* 0·40 mm. from the English Channel, it appears that even greater variation is possible. We have not, however, found any distinction in this character between erect and recumbent forms from the same area.

The conclusion is that *A. aspersa* may be distinguished from *A. scabra* and from all other species of Family *Ascidiidæ* by the nature of the outer follicle cells of the egg, and that this distinction may be effected even by dissection of the oviduct of the preserved mature animal. (In our material Scottish specimens of 29 and 31 mm. in length were found to be mature, while those in the region of size 24 mm. were immature. Berrill gives the size at first maturity as being not less than 40 mm. in the case of English Channel specimens.)

At the lower limit of its size-range the egg of *A. scabra* is not clearly to be differentiated from the eggs of *A. mentula* and *A. mammillata*. The two later species along with *A. conchilega* form relatively small eggs, viz :—

A. conchilega (Plate 1, Fig. 3). Diameter of egg *ca.* 0·22 mm.
A. mammillata (Plate 1, Fig. 4). Diameter of egg *ca.* 0·23–0·25 mm.
A. mentula (Plate 1, Fig. 1). Diameter of egg *ca.* 0·24–0·27 mm.

Again at the middle or upper portion of its size-range the egg of *A. scabra* might be confused with those of

A. prunum (Plate 1, Fig. 7). Diameter *ca.* 0·31–0·32 mm. (estimated), and

A. virginea (Plate 1, Fig. 2). Diameter *ca.* 0·34–0·35 mm.

All these species form eggs with relatively small outer follicle cells. The largest egg is evidently that yielded by *A. obliqua*, and, judging from the size of the ovum in the duct, must reach ·50 mm. in diameter (Plate 1, Fig. 9). In this case also the outer follicle cells are small, but the size alone would apparently be a feature of diagnostic value.

In view of the new scheme for the classification of Family *Ascidiidæ* suggested below, notice may be directed here to the fact that the eggs of

A. mentula, conchilega, and *mammillata* are very alike, and are the smallest formed in the Family. Examination of further material is, however, desirable to determine the precise limits of variation in the diameter of the eggs of these species, none of which, either on board ship or in the aquarium, freely shed their ova.

In passing it may be mentioned that, as is shown in Plate 2 (Figs, 5, 6), the rupture of the chorion by the larva appears, in this Family, to occur at a point opposite the anterior portion of the tail of the larva, this portion serving as a fulcrum for the stressing convulsive movements of trunk and tail.

b. *The larvæ.*—From *A. aspersa* and *A. scabra* from various regions larvæ were easily and repeatedly obtained. Only a few were, however, secured from *A. mentula* and *A. mammillata*, and none from *A. conchilega* and *A. virginea*. Two or more adult individuals of a species were maintained in the same jar. No attempt was made to obtain larvæ by means of artificial fertilisation. In Plate 3 there are represented the larvæ of the first four of the above-mentioned species. Save in Figures 1 and 3a the hyaline ectodermic mantle is omitted. The view of the subjects is such that only in Figure 3a are all three anterior adhesive papillæ shown, while Figures 2 and 5 show larvæ not long after the escape of the latter from the egg, so that the papillæ are more or less repressed, as they appear in the egg (Plate 2, Figs. 3, 5, 6). It is however obvious that the papillæ are, in all four species, of a short, truncated cone-like form. Allowing for the fact that in Figures 3, 4, and 5 the larvæ are viewed from the right side, while in Figures 1, 2, and 3a they are seen from the left (in Fig. 1 rather obliquely), it seems that there is no essential difference in any one species, as compared with another, in the relative positions of otocyst and eye in the cerebral vesicle. In some of the figures of Plates 2 and 3, however, different stages of notochordal development are shown. In the case of *A. scabra* (Figs. 3 and 3a of Plate 3, and Fig. 5 of Plate 2) the sheath of the notochord surrounds a hyaline core, and this is the only stage which we have observed in the larvæ of this species. In *A. aspersa* (Plate 2, Fig. 3), however, both in the developing larva in the egg and in the newly-hatched larva, the hyaline substance is restricted to an ordered series of biconvex discs. The latter are formed originally, according to Kupffer (**13**), from " refringent particles " appearing in the plasma of the cells of the notochord, and increase in size, finally uniting (in Fam. *Ascidiidæ*) to form a more of less elastic hyaline axis. In *A. aspersa, A. mentula*, and *A. mammillata*, so far as we have observed, the latter stage is not attained until some time after the larva has been free, whereas in *A. scabra* it occurs even prior to hatching, although the hyaline axis may be discontinuous in places—i.e. broken up into several rod-like portions, this probably being an intermediate stage to complete fusion.

There is thus no readily to be observed essential difference in the structure of the larvæ, save perhaps with regard to stage of notochordal development at hatching, and this point is worthy of further investigation. There remains to be considered the question of larval size. Here again, as in the case of the eggs, there is apparently some slight seasonal as well as regional variation.

Length (μ). Means in brackets.

Larva.	Head (excluding papillæ).	Tail.	Head and Tail.	No. of Specimens.
A. aspersa	270–310 (284)	575–675 (620)	845-985 (904)	8
A. scabra (Aug.)	250–275 (262)	700–750 (725)	950–1020 (987)	9 Plymouth North Sea North Scottish Coast
A. scabra (Aug.)	230–250 (238)	575–620 (597)	805–870 (835)	3 (Islay)
A. scabra (Oct.)	175	525	700	1 North Sea
A. mentula	175–250 (204) *(133)	450–650 (544)	625–900 (748)	4
A. mammillata	180–190 (185) *(208)	520–550 (535) *(522)	700–740 (720) *(730)	2

* According to Lohmann (**16**).

From these data it is obvious that the dimensions of the larvæ of *A. scabra* vary sufficiently to cover almost completely the range of variation in size of larva in the other three species. Probably the only safe deduction is that the larvæ of *A. mentula* and *A. mammillata* are rather smaller than those of *A. aspersa* and *A. scabra*.

Conclusion.

The foregoing investigation of the features of *A. aspersa* and *A. scabra* clearly establishes the fact that, by means of certain of these features, these two forms can always be distinguished from each other. The specific points of difference are found in (1) the relationship holding between number of tentacles and longitudinal vessels and (2) the nature of the egg. Almost, but not absolutely specific, are the differences in the following characters: (3) shape of the dorsal tubercle; (4) average size; (5) nature of test, and (6) position of the atrial aperture relative to the branchial aperture. The following are features of less specific value: (7) geographical and bathymetric distribution and (8) extent of area of attachment to the substratum. Little or no specific value can be attached to (9) colour; (10) number of stigmata per mesh of the branchial sac; (11) distribution of the renal cells, and (12) size and structure of larva (if the possible more rapid notochordal development in *A. scabra* be excepted).

Characters which did not in this case appear to call for special investigation were the nature of the musculature in the mantle and the details in connection with the alimentary tract, the dorsal lamina and the gonads.

Any or all of these characters might, however, be of specific importance where other species are concerned.

2. Variation in other Species of Family Ascidiidæ.

A less extensive material relating to these well-defined species was examined.

(1) Ascidia mentula.

From 35 collections of this species 53 individuals were selected for dissection. This material was obtained from various parts of the Scottish coast between the Moray Firth and Loch Fyne, over a general depth range of 17–60 metres. No justification was found for differentiating the results according to area, and they are here presented in combination.

A. mentula, along with the remaining species of the Family, is distinguished from *A. aspersa* and *A. scabra* by the possession of typical free papillæ on the branchial sac. This is a constant feature, and need not be further dealt with. Along with *A. conchilega* and *A. mammillata* this species can be distinguished from *A. virginea*, *A. obliqua*, and *A. prunum* by having the branchial sac prolonged behind the viscera. This feature also is constant. From *A. conchilega* it has been distinguished on account of having the nerve ganglion situated on the mantle at a point distant from the dorsal tubercle by about one-fourth (as compared with one-sixth) of the body-length, by possessing small instead of large renal cells, and a smooth as compared with a papillate test surface. Secondary branchial papillæ have been stated constantly to occur, whereas in *A. conchilega* they may occasionally be absent. These points of distinction therefore require special investigation. From *A. mammillata* the species is sufficiently distinguished by the occurrence in the latter of a recurved branchial sac and a peculiar modification of the dorsal tubercle.

(A) *Distribution.*—*A. mentula* resembles *A. aspersa* in that while it extends northwards along the west Scottish coast (being found even in the northern part of the Moray Firth), it is generally absent from the east coast of the British Isles.

(B) *Size.*—From 5–18 cm. in length.

(C) *Attachment.*—This is usually effected by means of a small area at the left posterior part of the body. There are however all variations from this slight attachment to complete fixation by the side or even, in a crevice, by a portion of both sides. In our material 3 specimens were attached by almost the whole side, 8 by from two-thirds to three-fourths, 12 by rather more than one-half, 9 by one-half, 4 by rather less than one-half, and 17 by about one-third of the side. (Two of the latter were attached not basally, but by a section of the mid-portion of the side.) As has been the case with regard to other species, differences in mode of attachment have in the past been made part of the basis for splitting this clearly-defined species into several species (see, e.g. Alder and Hancock's monograph, in which 8 species and 1 variety, all referable to *A. mentula*, were described).

(D) *Colour.*—This varies from a horn-coloured or milky white tint in young specimens to a much darker tint in older specimens, which range in colour from greenish white through red to dark brown.

(E) *Test.*—This is thick, cartilaginous, and smooth in young individuals, but becomes more or less wrinkled or roughly furrowed (though not tuberculated) in older animals.

(F) *Position of Apertures.*—The atrial aperture is usually described as lying at a point distant from the branchial by from one-half to two-thirds of the body-length. In the specimens dealt with here, however, the interval was rather less than one-half in a minority of 9 cases. Of the remainder 10 showed an interval of one-half, 32 of rather more than one-half and only 2 of two-thirds.

The results in the case of *A. conchilega*, which rather resembles *A. mentula* in this character, may be given here. Out of 16 specimens, 4 showed an interval of rather less than two-thirds, 7 of rather more than one-half, 3 of one-half, and 2 of rather less than one-half. These two species therefore agree with regard to this feature, and may by its means be distinguished from all the other common species of Family *Ascidiidæ* except *A. mammillata.*

(G) *Branchial Stigmata.*—The number of stigmata per mesh of the branchial sac of *A. mentula* is usually given as being 6 or 7. Counts made on the above material showed that specimens from the region N. Moray Firth–Orkney possessed from 4–7 stigmata between sizes 4–8 cm., and from 5–8 between sizes 8–18 cm. There was thus an increase of only one slit in the larger as compared with the smaller sizes. Individuals from the N.W. and W. Scottish coasts possessed from 4–6 and 4–7 slits in the smaller- and larger-sized animals respectively. That is, accompanying increase of size, there was practically no increase in number of stigmata. In this species therefore it seems that the number is fairly constant (4–8) and that there is little increase with increasing size of individual. Slight differences may arise with change of area since the individuals of the Orkney region appear consistently to form about one more slit per mesh than do those of the west coast.

(H and J) *Number of Tentacles and Longitudinal Vessels.*—*A. mentula* is generally recognised as having from 20–80 (mostly about 40) tentacles. In our material the number was found to vary from 33–100 in individuals ranging in size from 4–18 cm. The average number was about 65. All rudimentary tentacles were as usual included in the counts. The number of tentacles did not obviously increase with increasing size of animal. The number of bars did, however, so increase. Thus if number be plotted against size as in Figure 1 the loci fall in the neighbourhood of a curve rising gently from a point representing about 64 bars (at size 4 cm.) to one representing about 90 bars (at size 18 cm.). The entire range of number of bars is from 60–105.

(K) *Shape of Dorsal Tubercle.*—In descriptions of this species the tubercle is usually said to be irregularly rounded or horse-shoe shaped. Of the specimens dissected 47 out of 51 could be said to possess U-shaped tubercles. Of these 15 had the left horn and 11 both horns incoiled. These are evidently the usual shapes formed in Scottish waters. Of the remainder 8 were simply U-shaped, 7 had the right horn incoiled, 3 the left horn turned outwards, 2 both horns turned left, and one both turned out. It is noteworthy that a minority of 4 tubercles were (as is typically the case in *A. aspersa*) broadly ovate, with both horns incoiled.

(L) *Distribution of the Renal Bodies.*—These cells are of moderate size and form a coating over the viscera.

(M) *The size and nature of the eggs and larvæ* were discussed under *A. aspersa* and *A. scabra*.

Reference remains to be made to two characters which are used to form part of the means of distinguishing *A. mentula* from *A. conchilega*.

(N)—Although in the first-named species there are almost always, and in the latter rarely, secondary papillæ lying between the primary papillæ of the branchial sac, the distinction is liable to fail unless a large tract of the sac be examined.

(O)—On the other hand, the relative distance of the dorsal tubercle from the ganglion (this distance being expressed as a fraction of body-length) may definitely be used as a specific point of difference between these species. For *A. mentula* the fraction is usually stated to be one-fourth, and in the 51 specimens examined an average of 0·26 was obtained. The lower and upper limits were, however, 0·17 and 0·37. In *A. conchilega* the variation was found to be from 0·10–0·18 (average 0·14, or one-seventh, as compared with one-sixth found by previous workers). There is thus practically no overlap into the range of variation found for *A. mentula*.

(2) ASCIDIA CONCHILEGA.

Out of 25 separate collections of this species 16 specimens only were taken for dissection. The latter were obtained from the northern North Sea, the Faroe–Shetland Channel, the Minch and Eddystone, being taken in depths ranging from 98–229 metres.

(A) *Distribution.*—This is not yet very fully known, but appears to resemble that of *A. mentula*, though with a rather more northerly bias. Although the lower depth limit has hitherto been regarded as being

360 metres, this species has occurred in a recent Scottish Collection from a depth of 1104 metres in the Faroe–Shetland Channel, whence it has not hitherto been obtained.

(B) *Size.*—The specimens here dealt with ranged in size from 10–45 mm., but a size of 55 mm. has been recorded. The species may therefore readily be distinguished from *A. mentula*, which is seldom taken at a size of less than 55 mm.

(C) *Attachment.*—In 14 of these specimens the attachment was by almost the complete side, and in one individual by the complete side. In the remaining case, however, less than half of the side was fixed. This species is described as being fixed by the whole length of the left side, and this is probably usually, though not invariably, the case.

(D) *Colour.*—There is no obvious pigmentation. The animals have a more or less pale greenish tint.

(E) *Test.*—This is rather thin and cartilaginous, and has numerous minute tubercles on the free surface.

(F) *Position of Apertures.*—This has been dealt with under *A. mentula.*

(G) *Number of Stigmata in a Mesh of the Branchial Sac.*—In animals of size 10–13 mm. this number was from 2–3, but rose to from 3–4 at size 15–28 mm. and to from 5–7 at size 34–46 mm. The number therefore tends to increase as the individual grows.

(H, J) *Relative Number of Tentacles and Longitudinal Vessels.*—The number of tentacles was found to vary from 44–125, and did not appear to be dependent on the size of the animal. There are in these species three distinct rows of tentacles of different size—a feature absent from or not so clearly seen in the other species of the Family.

On the other hand, the number of bars was found to increase steadily with the size—from about 34 at a size of 10 mm. to about 54 at a size of 45 mm.

(K) *Shape of Dorsal Tubercle.*—In this species the tubercle is almost always horse-shoe shaped. Modifications of this simple fundamental shape are practically absent. In one individual, however, the right-hand horn of the tubercle was found to be incoiled, and in another the horns were prolonged.

(L) *Renal Bodies.*—These are particularly large and obvious, though of varying degrees of transparency. They are practically confined to the region of the viscera. Their arrangement over the stomach often imparts a ridged appearance to that organ.

(M) *Eggs and Larvæ.*—The egg of this species was described under *A. aspersa.* The larva was not obtained.

It is seen that *A. conchilega* may easily be distinguished from *A. mentula* by determination of the nature of the following characters : Bathymetric distribution, test, distance of dorsal tubercle from nerve ganglion, size of renal cells, frequency of occurrence of intermediate papillæ in the branchial sac, and number of longitudinal bars (in the former species only about 54 occur at a size of 45 mm.; in the latter 64 at a size of 40 mm.).

Differences in the shape and course of the gut are not discussed here, since the latter is often obscured by the overgrowth of renal bodies and gonads. Features of little or no specific use in separating these species are the nature of the attachment, the colour, the relative distance apart of the apertures, the number of gill-slits and tentacles, the shape of the dorsal tubercle, and the size and structure of the egg. In cases, however, in which the number of tentacles exceeds 100 the probability will be that a specimen of *A. conchilega* is being examined.

(3) ASCIDIA MAMMILLATA.

This species is easily identified. It has been recorded from as far north as the Clyde Estuary but has not recently been found there. With the exception that its northerly limit is probably the region Irish Sea–Firth of Clyde, this species is distributed over much the same area as is *A. mentula*. Three specimens from Plymouth were dissected. The surface of the test is mammillated, and this feature, added to those of the reflexed branchial sac and the peculiar structure of the dorsal tubercle, sufficiently distinguishes the species. The dorsal tubercle proper is a scarcely to be discerned gutter-shaped opening, very far distant from the nerve ganglion. More prominent, however, are the very numerous bright orange secondary openings situated all along the course of the neural canal.

The following are other features of the species, with the relative observations (in brackets) made upon the three specimens: Size from 5–13 cm. (5, 5½, 8). *Attachment* diagonally by the base (by more than one-third, by one-half, and by more than one-half of the length of the side). *Colour* of test opaline white or yellow, of mantle dark pink to blue. *Apertures* (atrial nearly one-half of the body-length distant from the branchial). *Number of stigmata per mesh* (from 5–7 in these medium-sized specimens). *Branchial papillæ* (as in *A. mentula*). *Tentacles*—of three sizes, and about 48–60 in number (56, 74, and at least 65 were counted in these specimens); the number of *longitudinal bars* was 78, 87, and 102 respectively, and appears therefore to increase with size of animal; the egg and larva have already been referred to; the renal cells are abundant but confined to the visceral region.

Of these features only one—the colour of the mantle—can be said to distinguish this species from *A. mentula*, which is the only form likely to be confused with it.

There remain to be considered three boreal species of Family *Ascidiidæ*. These are distinguished from (1), (2), and (3) by having no prolongation of the branchial sac beyond the viscera ; further, the dorsal tubercle lies close to the ganglion, and the apertures are not more than one-third of the body-length apart. In all three of these characters they resemble *A. aspersa* and *A. scabra*, from which they differ in having real free papillæ in the branchial sac.

(4) Ascidia obliqua.

From 18 separate collections of this northerly deep-water species 33 specimens were taken for dissection. Of these 8 were from the Faroe–Shetland Channel and 25 from Faroe.

(A) *Distribution.*—Like *A. prunum*, this species is limited to Arctic and north Boreal regions, but may extend its range slightly into northern British waters by way of the deep channels whose water is partly of Arctic origin. The record given by Herdman (**8**) from Lamlash Bay, Firth of Clyde, should probably have been referred to another species. (We have found in a collection from Ettrick Bay an individual of *A. conchilega* which rather resembled *A. obliqua* outwardly.) Both *A. prunum* and *A. obliqua* extend their range into deep water, the former to nearly 400 metres' depth, and the latter (according to a new Scottish record from the Faroe–Shetland Channel) to 1250 metres. *A. obliqua* may in fact be said to be the northern deep-water counterpart of *A. scabra*, being quite the commonest Ascidian species in, e.g., that Channel. *A. virginea* is distinguished from these two more northerly species by having a south-Boreal distribution (from the Mediterranean to Faroe). That is, it is commoner in the south, and solitary specimens only are to be taken from the northern North Sea and the coastal waters of west Scotland.

(B) Size of *A. obliqua.*—From 25–75 mm. The individuals dealt with here ranged in size from 30–73 mm.

(C) *Attachment.*—*A. obliqua* is attached rather diagonally by a large circular area which includes the base and part of the left side. When removed from the water the animal, which has a flaccid body, sags down around this base. This is a distinguishing feature of the species.

(D) There is no pronounced pigmentation, the test being merely horn-coloured, though occasionally somewhat rugose in older individuals.

(E) *The test* is fairly thin and soft, with smooth or wrinkled surface. The species often adheres loosely to other Ascidians.

(F) *The apertures* are set not far apart upon conical and rather deeply lobed tubes. In the specimens examined their distance apart was one-third of the body-length in 19 cases, rather more than one-third in 10 cases, and rather less than one-third in 4 cases.

(G) *The number of stigmata* per mesh of the branchial sac is usually stated to be from 3–6. In the above material the number was from

3–5 in the smaller and from 4–6 in the larger specimens. There are no intermediate papillæ in the sac of this species.

(H, J) *The number of tentacles* varied from about 30–75, and apparently rises for some time with increasing size of individual, but becomes more or less constant after a size of about 50 mm. is attained.

The number of longitudinal bars increased gradually with the size of the animal from a minimum of about 65 (at size 30–50 mm.) to a maximum of about 104 (at a size of from 40–70 mm.).

(K) *The dorsal tubercle* is very large for the size of the animal and was found always to be elongate—U-shaped. The horns are prolonged but never coiled to any great extent. This is one of the species in which the size and shape of the tubercle are distinctive.

(L) *The renal cells* are not large. They are finely felted over but not beyond the visceral region.

(M) *The egg* of the species is, as has been stated above, probably the largest of any formed by the species of Family *Ascidiidæ*.

The larva has not been obtained.

(5) ASCIDIA PRUNUM.

This species is at best rare even in north British waters. It has been taken by Scottish research vessels only off the coast of Iceland. From the collections from that coast 3 specimens only were examined for the purposes of this investigation. These were from 10–45 mm. in length, but a size of 70 mm. can be attained by this species. The attachment was by almost one-half of the left side in two of the cases and by the whole side in one. The apertures were separated by a distance equal to rather less than one-third of the body-length in two individuals, and rather greater than one-third in one individual. The test, as in *A. obliqua*, is usually thin and semi-translucent, but is never flaccid, and may become moderately thick. In young individuals the surface is smooth, but later it becomes a little wrinkled. Minute papillæ may be present. In the branchial sac intermediate papillæ are almost always present. There are stated to be from 3–5 stigmata per mesh of the sac in smaller and from 6–7 in older animals. (In these three specimens rather more were found, viz., from 5–6 at a size of 10 mm. and of 35 mm., and from 7–8 at a size of 45 mm.) The number of tentacles is usually given as being about 50, of three sizes. (In these specimens the number varied from 17 in the smallest to approximately 95 in the largest individual, and probably increases with size of animal, at least for some time.) The number of longitudinal bars rose similarly from 19–73 (from 40–70 is the range of variation given in the descriptions by other workers). The dorsal tubercle in its simplest form is merely a crescent-shaped slit, but it may also be half-moon or horse-shoe shaped. In the latter case one or both horns may be bent inwards. Large renal bodies are distributed over the region of the viscera and may even extend slightly beyond the latter.

A. prunum therefore differs from *A. obliqua* in being more completely attached, and in the nature of the test and habit. The renal cells are larger, but the egg is probably smaller than in the latter species. The dorsal tubercle is smaller and of different shape. There are fewer longitudinal bars in the branchial sac, in which, however, intermediate papillæ are present.

Features of little or no distinctive value are the geographical distribution, the size, the colour, the distance apart of the apertures, and the number of stigmata and of tentacles.

(6) ASCIDIA VIRGINEA.

This species is rather rare. Out of 12 collections containing it we have taken only 8 specimens for dissection. Three of these were obtained from Plymouth and 5 from points on the west Scottish coast between the Clyde and Shetland. The total size-range was from 27–58 mm., but this species can reach a size of 75 mm. In shape the body is elongate—quadrilateral, tapering slightly towards the anterior end. In one specimen from Shetland the test was produced into a stalk, with the result that the animal was pear-shaped. One Plymouth specimen was attached by the entire side to a shell. This modification of the usual basal form of attachment has not, as far as we are aware, been hitherto observed, and forms an analogy with the depressed forms of *A. aspersa*, *A. scabra*, and *A. mentula*. Of the other specimens 6 were attached basally and one by two-thirds of the left side. This species is usually capable of being identified by the nature of the test, which is glabrous, rather gelatinous in texture, semi-transparent, and of a delicate pinkish hue. The apertures are quite sessile, the atrial aperture lying at a distance of rather less than one-third of the body-length from the branchial. (In 5 cases the interval was less than one-third, in 2 it was one-third, and in one—the depressed form—rather more than one-third.) In the meshes of the branchial sac the number of stigmata is stated as varying from 6–8. In our specimens the number ranged from 4–6 in the smaller and from 6–9 in the larger individuals. The crowded tentacles are often extremely difficult to count, especially since there are many minute ones. The number found exceeded that usually quoted, there being about 60 of the first order and probably about an equal number of a lesser size, some of which are mere papillæ on the tentacular collar. The minimum number of tentacles is probably about 60, and the maximum upwards of 120, but there is no obvious increase in the number as the size of the animal increases. As is more usual, however, the number of longitudinal bars does so increase, regularly in the case of this species from about 35 at a size of 27 mm. to about 54 at a size of 58 mm. The dorsal tubercle is simply U-shaped (in two cases, however, the left horn was incoiled and in one the horns were prolonged after the fashion of those of the tubercles of *A. obliqua* and the Dogger Bank specimens of *A. scabra*). The renal bodies are not prominently seen. Secondary papillæ are rare or rudimentary in the branchial sac. The egg is moderately large.

The chief features distinguishing *A. virginea* from *A. obliqua* and *A. prunum* are therefore the nature of the distribution, of the test, and of the shape of the body. The number of longitudinal bars is more restricted. An additional distinction lies in the shape of the gut, since in this species the anal portion runs directly forwards so that the anus is considerably higher than the uppermost portion of the loop of the intestine (Plate 7, Fig. 4). In the other two species the anus is at approximately the same height as, or is actually lower than, that portion of the intestine.

A. TRITONIS (Herdman, 1883), the remaining Boreal species of Family *Ascidiidæ*, has been recorded from various parts of the slope of the N.W. European continental shelf, viz., to the south-west of Ireland and of Faroe and to the south of the Wyville–Thomson Ridge, at depths ranging from 840 to 1210 metres. It has not occurred in recent Scottish collections from either slope of the latter Ridge, and appears to be confined to very deep water in a limited area. As described by Herdman (**9**) and by Hartmeyer (**7**), this form would appear to have many features in common with *A. conchilega*. It reaches a much greater size, however, the range being from 5–17 cm. It is noteworthy that our new record of *A. conchilega* from a depth of 1104 metres does away with any absolute bathymetric distinction being made between the two species. This record was made, however, in the Faroe–Shetland Channel, on the north (or cold-water) side of the Ridge, where the temperature is below zero, whereas the temperature was found to vary from $5\frac{1}{2}$–$8\frac{1}{2}$ °C. on the south side of the Ridge whence *A. tritonis* has been obtained. It is suggested here, nevertheless, that proof is required that the latter species is not merely a large form of *A. conchilega*. Hartmeyer, from a study of about 50 specimens of the former species, revised Herdman's description. The outstanding features appear to agree in most details with those of the latter species. The branchial sac extends beyond the gut, the course and appearance of which, judging by Herdman's illustration, agree with those found in *A. conchilega*. The ganglion is separated from the dorsal tubercle by a distance equal to approximately one-sixth of the body-length. There are small papillæ on the test, which is cartilaginous in texture. The attachment is by from one-half to two-thirds of the left side, and the atrial aperture is separated from the branchial by a distance equivalent to from rather less than one-half to two-thirds of the body-length. There are about 3 stigmata in a mesh of the branchial sac of smaller, and 5 in the sac of larger individuals. (The number in *A. conchilega* rises to a maximum of from 5–7, so that here there may be a point of difference.) Branchial papillæ are present but secondary papillæ are absent. (In *A. conchilega* the latter are occasionally present, but we have found that this is not quite a specific feature, since the formation of secondary papillæ is—in some species at least—the prelude to the formation of transverse vessels between them, with the result that the original mesh is divided transversely into two meshes. In other words, the more fully developed the branchial sac is—e.g. in *A. mentula*, whose sac may or may not show secondary papillæ of a lesser size than primary—the less chance there is of finding in it intermediate papillæ.) The tentacles are very numerous—from 80–100 or more. The number of longitudinal bars exceeds 100. In *A. conchilega* the number rose steadily with size of animal to about 54 at a size of from 4–5 cm., and might conceivably be much greater in individuals of double or treble this size. In this species, as in *A. tritonis*, the dorsal tubercle is simply horse-shoe shaped, with rare modifications.

We found that in *A. conchilega*, while the number of tentacles did not appear to be dependent on the size of the animal, the number of bars did so. This would account for the agreement in the number of tentacles of the two species and the disagreement in the number of bars. The presence or lack of intermediate papillæ in the sac may prove to be a constant and specific feature whereby these species may be distinguished. Beyond this and the slight difference in number of branchial stigmata per mesh there seems to be little to go upon other than the difference in the maximum size which the animals may attain. It would apparently be very difficult to state to which species individuals of, e.g., 5 cm. in length belonged.

From the Key to the Boreal *Ascidiidæ* given below *A. tritonis* has been omitted for these reasons and since the form is not likely to be encountered in water of moderate depth.

3. A Suggested Key to the Boreal Species of Family Ascidiidæ.

It is hoped that the foregoing does something to bring into clearer prominence those features which may reliably be used in the classification of the species of this Family. Our experience has been that in nearly every case the species can be recognised from its external appearance. That is, the number of possibilities is first of all narrowed down by such a character as the distance apart of the apertures (the corollary of which in internal structure is the distance apart of nerve ganglion and dorsal tubercle); it is further narrowed down by consideration of the nature of the test and the habit. The size of the animal and its mode of attachment to the substratum are of less importance, and little reliance need be placed on the colour. The ability to identify a species from its external appearance is, however, and must remain, the outcome of knowledge gained by dissection of most if not all of its forms of variation—including variation in size, which may or may not entail variation in such characters as the number of tentacles and longitudinal bars, of the stigmata in a mesh in the branchial sac, and even in the presence or absence of secondary branchial papillæ. Internal evidence of first importance is afforded by the presence or absence of a prolongation of the branchial sac behind the region of the viscera, and of true papillæ in the sac. The shape and position of the dorsal tubercle are of importance in certain cases, but variation in the former character often occurs. Importance can seldom be attached to pigmentation of the mantle. The shape of the gut is often largely obscured by overgrowth of gonads and renal cells, but the terminal portion of the intestine can easily be seen, and its course and relative position afford in certain cases evidence of specific value. The size and distribution of the renal cells, while aiding an identification to be confirmed, are not of primary importance, and in this Family a study of the nature of the gonads—organs whose appearance is subject to change with season and with size of animal—is unnecessary for purposes of identification. Much information still remains to be gathered with reference to the precise limits of geographical and bathymetric distribution of certain of the species. In addition the developmental characters require further study ere full use can be made of them for systematic purposes.

It is suggested that the three existing genera of Family *Ascidiidæ* may be combined without entailing increased difficulty in the identification of the species or failure to give due weight to the known structural or developmental characters. The Family is not crowded with species, and the present division into genera is not a natural one. Genus *Phallusia* has been established to include a species to be distinguished from the others of the Family by having a modified type of dorsal tubercle and a reflexed portion of the branchial sac. But, as has been shown, this species resembles *A. mentula* and *A. conchilega*, and differs from the other species of the Family in having the branchial sac produced behind the gut and the dorsal tubercle placed at a considerable distance from the nerve ganglion. In addition, as far as we know them, both the eggs and the larvæ of these three species seem very similar. These deep-rooted resemblances would appear to warrant the formation of a genus (Gen. *Phallusia*) were it desirable that a separate genus be formed, and seem far to outweigh the rather trivial differences upon which the existing definition of Gen. *Phallusia* rests. In all three species the typical form is attached diagonally to the substratum, the apertures are very widely separated, and with the possible exception of *A. conchilega*, the upper limit of whose size requires confirmation, a very large maximum size is attained. The diagonal attachment is necessary if the atrial aperture is to be kept clear of the substratum (Plate 7, Figs. 5–6), whereas, in the remaining species the typical form can well be erect since the apertures are rather closely approximated and anterior (Plate 7, Fig. 4). Only in *A. obliqua* is there a tendency to oblique attachment, and only *A. aspersa* reaches a size of over 10 cm., with an average size much smaller than that figure. Tubercle and ganglion are closely approximated and the branchial sac does not extend beyond the gut. These species therefore appear to form a natural group from which it is difficult to justify the separation of genus *Ascidiella* by reason of the lack of real branchial papillæ in the latter and the excessive straying of renal vesicles over the mantle surface. As has been said, the absence of papillæ is only a matter of degree (the appearance of the bars at certain stages of development and from certain angles, has led numerous observers to state that papillæ are to be seen, but on further study all have agreed that real free papillæ, projecting abruptly from the surface of the longitudinal vessels and not being mere thickenings of these vessels, are absent). The extension of the distribution of the renal cells beyond the viscera is simulated in a lesser degree in *A. prunum*. These points of difference are, by comparison, scarcely of generic value when balanced against the more deeply-set features of resemblance with *A. obliqua*, *A. virginea*, and *A. prunum*. Also, the implied diminutive in the term *Ascidiella* is misleading. While there might be considered grounds for the separation of these smaller forms into a genus apart from that which would contain the larger forms, the simpler course is suggested here of bringing together into one genus all the Boreal forms of the Family. To this procedure there appears to be no obstacle arising from the study of developmental characters, at least as far as this study has gone.

KEY TO GENUS ASCIDIA.

1.	Nerve ganglion adjacent to dorsal tubercle ; apertures not more than one-third of the body-length apart ; sac not prolonged beyond the viscera..................................	**2**
	Ganglion at a considerable distance from the tubercle ; apertures much more than one-third of the body-length apart ; sac prolonged beyond the viscera	**6**
2.	Typical free papillæ absent from the sac	**3**
	Typical free papillæ present in the sac	**4**

3.	With more longitudinal vessels than tentacles; test papillate or pustolose; dorsal tubercle transversely ovate; ova with large follicle cells	*A. aspersa.*
	With fewer longitudinal vessels than tentacles; test smooth or wrinkled, with papillæ absent or confined to the region of the siphons; dorsal tubercle U-shaped	*A. scabra.*
4.	Anal portion of gut running directly forwards; anus considerably higher than upper bend of the intestine; body of elongated quadrilateral shape, tapering slightly anteriorly	*A. virginea.*
	Anus at approximately the same height as, or lower than, the upper bend of the intestine; body more or less roundish	**5**
5.	Intermediate papillæ absent from sac; gut of limited size; egg large	*A. obliqua.*
	Intermediate papillæ almost always present; gut extensive	*A. prunum.*
6.	Dorsal tubercle-proper small and irregular, but a great number of secondary openings are studded along the course of the duct from the neural gland; sac recurved upon itself	*A. mammillata.*
	Dorsal tubercle without secondary openings; sac not recurved	**7**
7.	Ganglion distant about one-sixth of the body-length from the dorsal tubercle; intermediate papillæ of the sac absent in places; renal cells large; test papillate	*A. conchilega.*
	Ganglion distant about one-fourth of the body-length from the dorsal tubercle; intermediate papillæ almost always present in the sac; renal cells small	*A. mentula.*

4. SYNONYMY.

(With chief reference to recent British Works).

ASCIDIA ASPERSA (Müll. 1776).

=*A. aspersa*+*A. truncata* (Herdman, 1881).

=*A. aculeata* (part)+*A. canina* (non. Müll.)+*A. Normani*+do. (var. *resplendens*)+*A. affinis*+*A. pustulosa*+*A. scabra* (var, *echinata*) (Alder & Hancock, 1905).

This species was described by Risso (**18**) as *Phallusia cristata* and later by others—including Roule (**20**)—as *Ascidiella cristata*. If, as Alder and Hancock thought probable, Müller's *A. aspersa* was a young stage of *A. scabra*, the specific name should probably be *A. cristata*. However, the present name has been much used, is expressive, and will probably be allowed to stand.

ASCIDIA SCABRA (Müll. 1776).

=*A. virginea*+*A. scabra*+*A. triangularis* (Herdman, 1881).

=*A. sordida*+*A. morei*+*A. scabra*+do. (vars. *albida*+*lævis*)+ *A. elliptica*+*A. pellucida*+ ? *A. orbicularis*+ ? *A. vitrea* (Alder & Hancock, 1905).

=*Ascidiella scabra* (Roule, 1884).

Ascidia mentula (Müll. 1776).

=*A. lata*+*A. fusiformis* (Herdman, 1881).

=*A. mentula*+*A. robusta*+*A. rubicunda*+*A. rubrotincta*+*A. crassa*+*A. mollis*+do. (var. *carnosa*)+*A. plana*+*A. Alderi*+*A. rudis* (Alder & Hancock, 1905).

Ascidia conchilega (Müll. 1776).

=*A. depressa*+*A. plebeia*+*A. exigua* (Herdman, 1881).

=*A. depressa*+*A. Roulei* (part)+do. (var. *petricola*)+*A. Herdmanni* (Garstang, 1891).

=*A. producta*+ ? *A. inornata*+*A. depressa*+*A. elongata*+*A. aculeata* (part)+*A. amœna*+*A. plebeia* (Alder & Hancock, 1905).

Ascidia prunum (Kupff., 1875).

=*A. callosa* (Stimpson, 1854).

=*Phallusia prunum* (Kupff., 1875).

=*A. glacialis*+*A. prunum* (part)+*A. complanata* (Herdman, 1891).

Ascidia mammillata (Cuv., 1815).

=*A. mammillata* (Cuv., 1815).

= Do. (Alder & Hancock, 1905).

Ascidia obliqua (Ald. 1863).

=*A. obliqua*+*A. falcigera*+*A. mollis* (Herdman, 1891).

=*A. obliqua* (Alder & Hancock, 1905).

Ascidia virginea (Müll. 1776).

=*A. patoni* (Herdman, 1881).

=*A. venosa* (Alder & Hancock, 1905).

5. SUMMARY.

1. A detailed investigation is made into the identity of the forms recently grouped under Genus *Ascidiella*. Two species only have been found to be capable of being differentiated, and these have been re-included under Genus *Ascidia*.
2. The relative specific importance of certain developmental and body characters is discussed.
3. A new Key to the Boreal species of Family *Ascidiidæ* is suggested.

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PLATE 1.

Eggs of Fam. *Ascidiidæ*. (×110. Zeiss Camera Lucida.)

FIG. 1.—*Ascidia mentula*.

FIG. 2.—*Ascidia virginea*.

FIG. 3.—*Ascidia conchilega*.

FIG. 4.—*Ascidia mammillata*.

FIG. 5.—*Ascidia scabra* (2 hours after emission).

FIG. 6.—*Ascidia aspersa* (2 hours after emission).

FIG. 7.—*Ascidia prunum* (calculated size of chorion).

FIG. 9.—*Ascidia obliqua* (calculated size of chorion).

FIG. 8.—*Corella parallelogramma*. (Fam. *Rhodosomatidæ*.

FIG. 10.—Egg in oviduct of *A. scabra*.

FIG. 11.—Egg in oviduct of *A. aspersa*.

PLATE 1

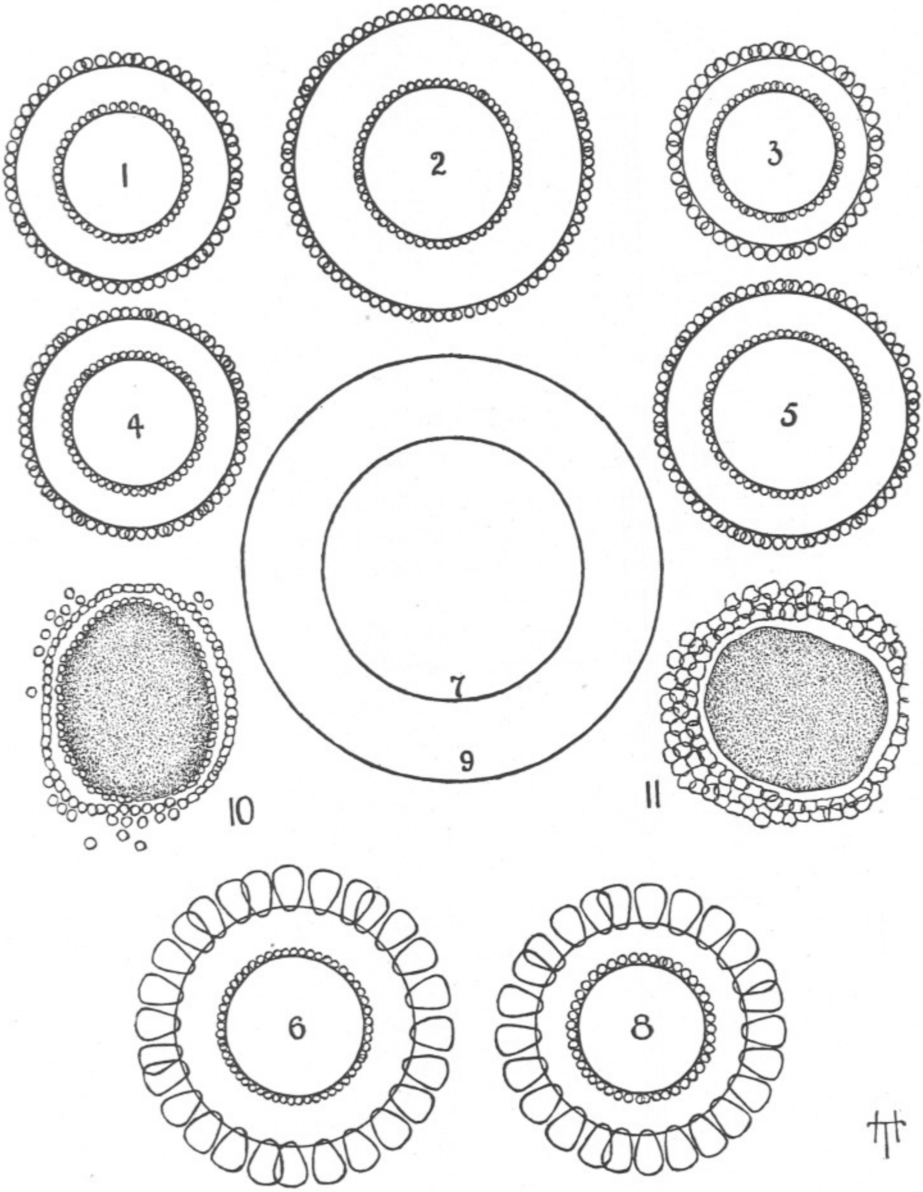


PLATE 2.

Eggs of Fam. *Ascidiidæ*. (× 110. Zeiss Cam. Lucida.)

Fig. 1.—*Ascidia aspersa* (Plymouth). 10 mins. after emission.

Fig. 2.—*Ascidia aspersa* (Plymouth). 2 hours after emission.

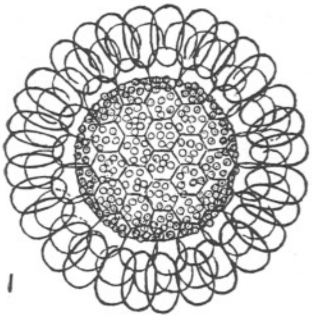
Fig. 3.—*Ascidia aspersa* (Islay). One day after emission.

Fig. 4.—*Ascidia scabra* (Plymouth). May.

Fig. 5.—*Ascidia scabra*, escaping larva (Aberdeenshire coast). August.

Fig. 6.—*Ascidia mammillata*, escaping larva (Plymouth).

PLATE 2.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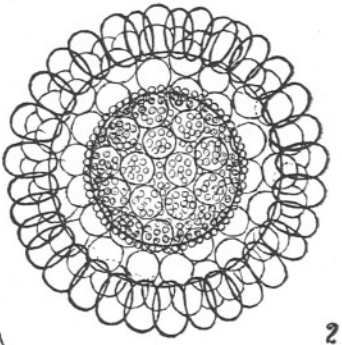
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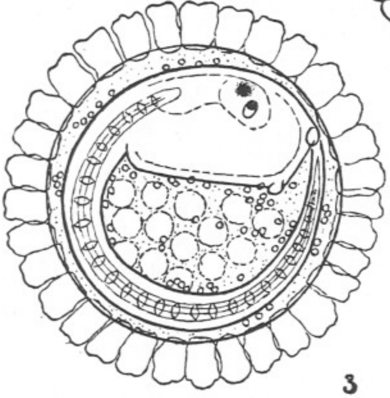
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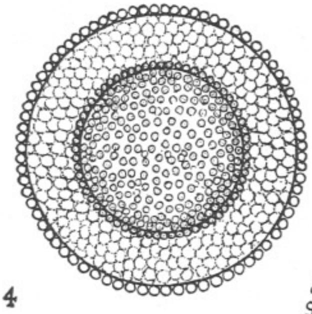
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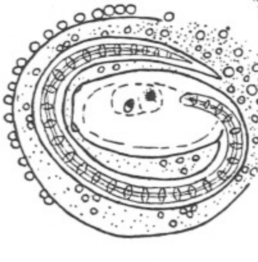
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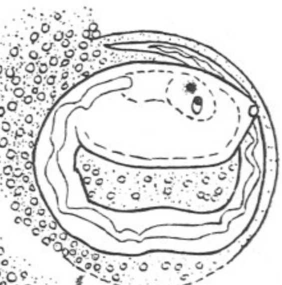
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PLATE 3.

Larvæ of Fam. *Ascidiidæ*. (× 104. Zeiss Cam. Lucida.)

FIG. 1.—*Ascidia aspersa* (Plymouth). Left side, oblique view.

FIG. 2.—*Ascidia aspersa* (Islay). Cf. Fig. 3, Plate 2.

FIG. 3.—*Ascidia scabra* (Plymouth, Aberdeen, Loch Eriboll, etc.). Cf. Fig. 5, Plate 2.

FIG. 3a.—*Ascidia scabra* (North Sea), an example of smaller late season (October) larvæ (cf. Fig. 3).

FIG. 4.—*Ascidia mentula.*

FIG. 5.—*Ascidia mammillata.*

PLATE 3.

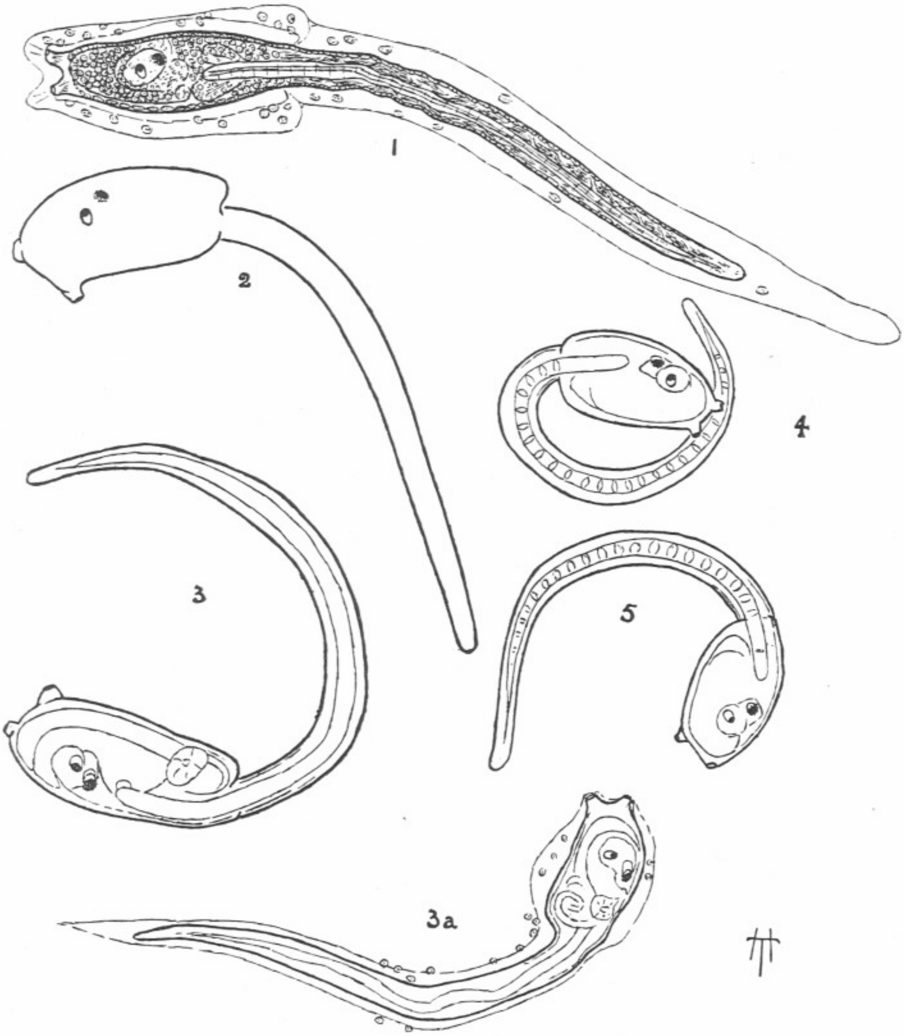

PLATE 4.

Types of Fixation and Habit in Fam. *Ascidiidæ*. (Seven-eighths natural size.)

FIGS. 1–4.—*Ascidia scabra*.

FIG. 1.—Attached by side (Luce Bay).

FIG. 2.—A specimen from Firth of Clyde. The apertures are unusually wide apart.

FIG. 3.—Attached by base. A typically transparent specimen from Moray Firth.

FIG. 4.—Attached by base. Large Dogger Bank form.

FIGS. 5–6.—*Ascidia virginea*.

FIG. 5.—Attached by base (normal method of fixation).

FIG. 6.—Attached by side (abnormal method of fixation).

PLATE 4.


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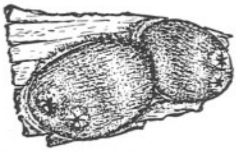
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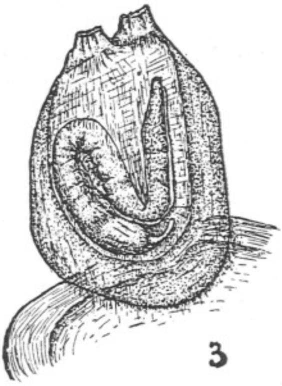
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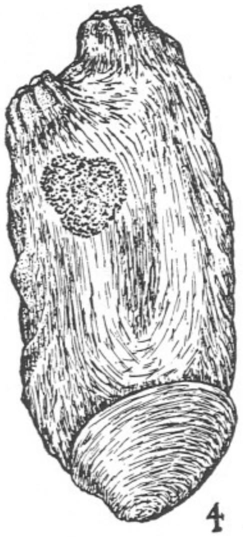
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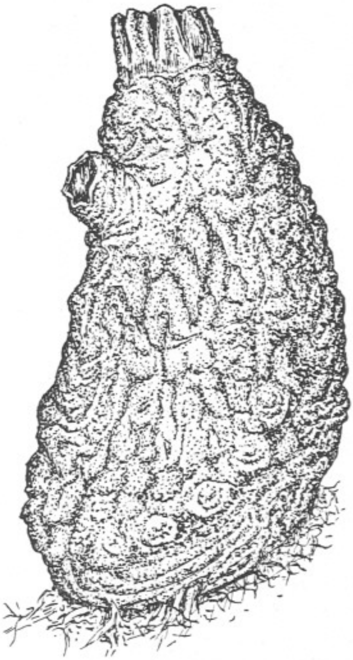
PLATE 5.

Types of fixation (*continued*).

Fig. 1.—*Ascidia aspersa*. Basal attachment (Plymouth).

Fig. 2.—*Ascidia aspersa*. Attached by side (Loch Indail, Islay).
(Both figures natural size.)

PLATE 5.



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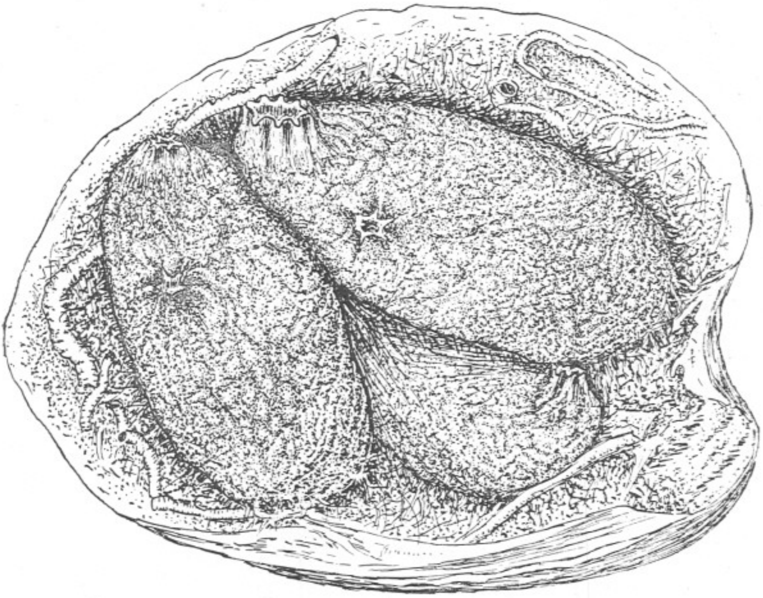

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PLATE 6.

Dorsal Tubercles and Tentacles of *Ascidia aspersa* and *Ascidia scabra*.
(Zeiss Cam. Lucida.)

FIGS. 1–5.—Variation in form of Dorsal Tubercle in *A. aspersa*. Figs. 2 and 4 are the normal form; Fig. 1 (×3½ times ordinary scale) from a very small Plymouth specimen, 6 mm. in size; Figs. 2 and 3 are from Plymouth, and Figs. 4 and 5 from Loch Fyne specimens.

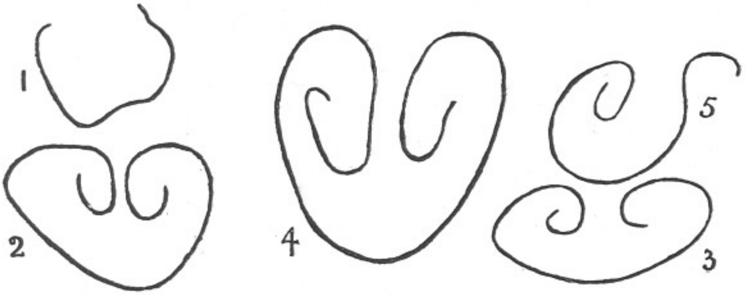
FIGS. 6–26.—Variation in form of Dorsal Tubercle in *A. scabra*. Figs. 6–16 from a random selection of specimens from the northern Moray Firth; Figs. 15 and 16 (×3½ times ordinary scale) from very small specimens (9 and 12 mm.); Fig. 17 from Loch Fyne;

Figs. 18–20 from Luce Bay; Fig. 21 from Dogger Bank; Figs. 22–26 from Plymouth.

FIG. 27.—A group of tentacles from *A. aspersa* (Plymouth), of size 40 mm. (×18).

FIG. 28.—A group of tentacles from *A. scabra* (Dogger Bank), of size 40 mm. (×18).

PLATE 6.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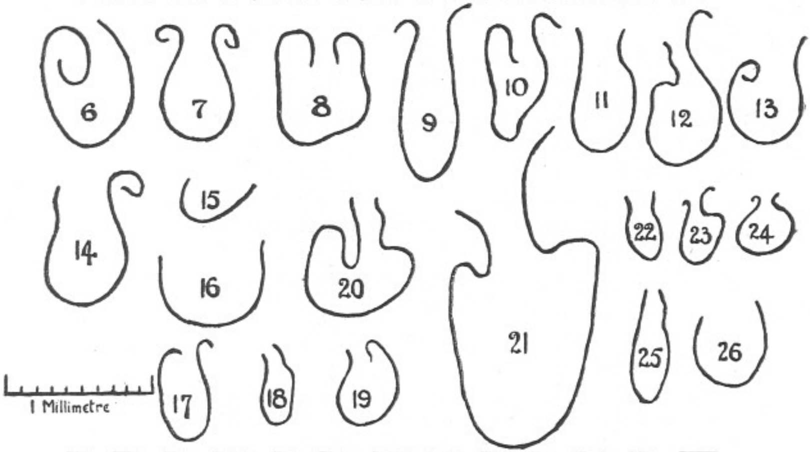
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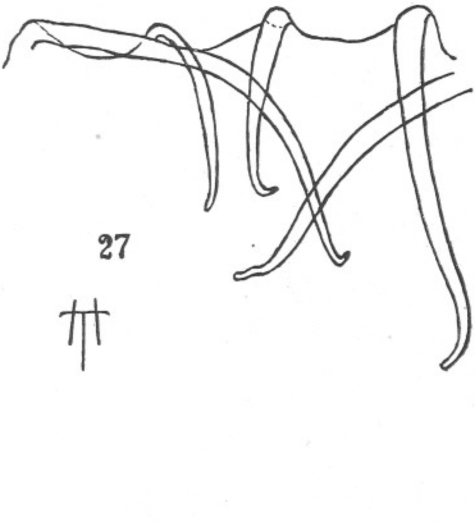
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PLATE 7.

FIGS. 1-3.—Portions of Branchial Sac.

FIG. 1.—*Ascidia aspersa.* Size 30 mm. (from Loch Indail, Islay), pseudo-papillæ on present (× 60, Zeiss C.L.).

FIG. 2.—*Ascidia aspersa.* Size 8 mm. (from L. Indail).

a. = Knob-like vascular processes, simulating papillæ.

b. = A similar process linked up with its neighbour by a longitudinal b (× 110, Zeiss C.L.).

FIG. 3.—*Ascidia mentula.* Showing typical free papillæ (× 60, Zeiss C.L.).

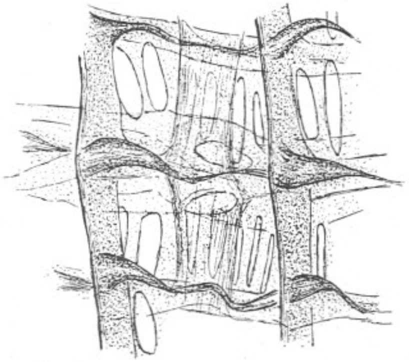
FIGS. 4–6.—Illustrating mode of attachment.

FIG. 4.—*Ascidia virginea.* Basal attachment is normal; apertures are well clear substratum.

FIG. 5.—*Ascidia mentula.* Showing how basal attachment (none occurs in this specie would bring position of atrial aperture near to substratum.

FIG. 6.—*A. mentula.* Normal oblique attachment by side, atrial aperture free substratum.

PLATE 7.



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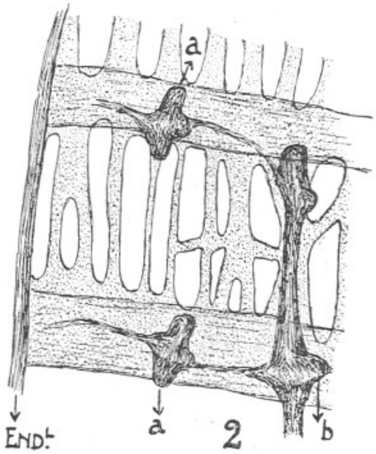

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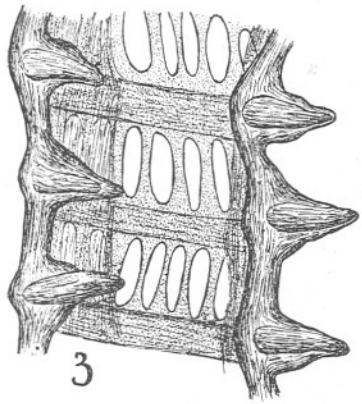

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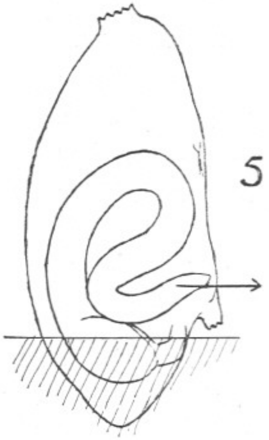

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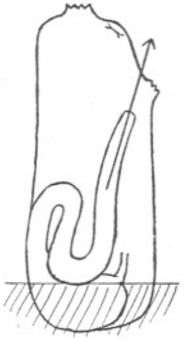

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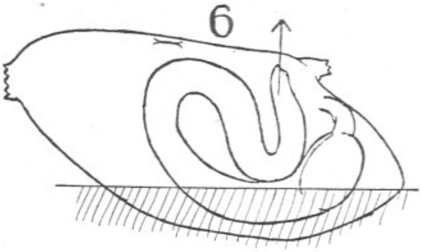


PLATE 8.

A specimen of *A. scabra* showing double atrial siphon (Test removed).

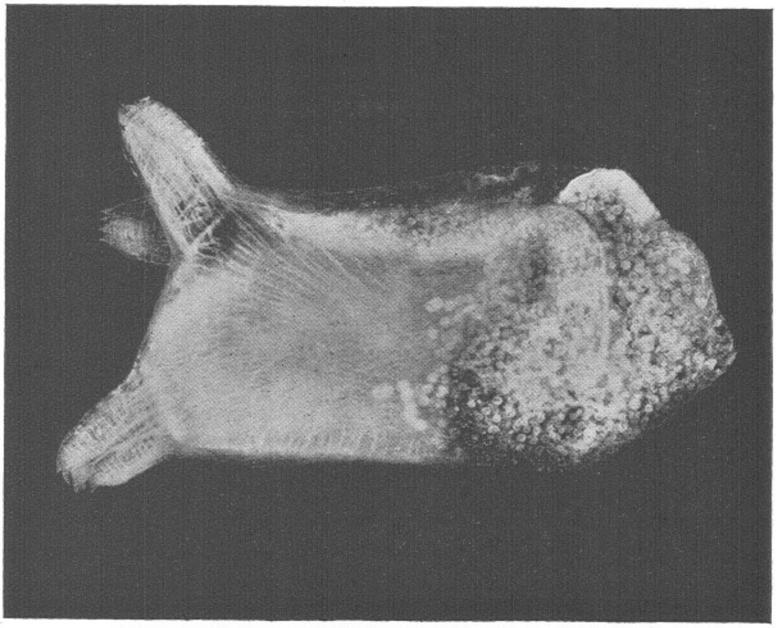
FIG. 1.—From right side, showing musculature of mantle.

FIG. 2.—From left side, showing extension of renal cells beyond the viscera.

Both Figs. about three times natural size.

(Photographs by Mr. John McKenzie, of the Staff of the Fishery Board for Scotland.)

PLATE 8.



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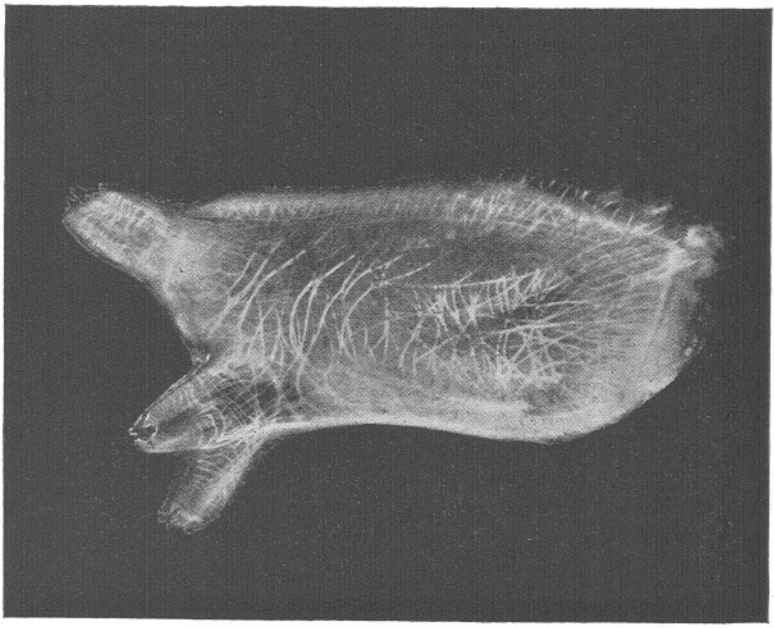

1.

Some Abnormal Fishes Received at the Plymouth Laboratory.

By

E. Ford, A.R.C.Sc.,
Fisheries Naturalist at the Plymouth Laboratory.

With 8 Figures in the Text, and Plates I–V.

Introduction.

The object of this short paper is to describe a number of fishes exhibiting interesting abnormalities. It will be seen from the list given below that several of the specimens to be described were sent to the Laboratory on the personal initiative of gentlemen to whom I express my thanks. I am also greatly indebted to Dr. H. A. Harris and the staff of the X-ray Department of the Institute of Anatomy, University College, London, for the beautiful radiograms they supplied. Mr. C. H. Gill, Press Photographer, of Plymouth, photographed several specimens and also prepared prints for the illustrations.

	List of Specimens Described.	Date Received.	Source.
1.	Cod with Malformed Mouth*	May 10th, 1929	From steam trawler *Stormcock* landing at Plymouth, per P. Hawthorn, Esq., Inspector in the Public Health Department, Plymouth.
2.	A Pug-headed Herring	July 11th, 1927	From River Tamar, among catch of young clupeoids.
3.	A Fan-tailed Pilchard	Oct. 9th, 1928	From Newlyn, Cornwall. The specimen was noticed among salted pilchards being packed, and was forwarded by B. Dunn, Esq.
4.	Coalescence of Vertebræ in a Lemon-Dab (*Pleuronectes microcephalus* Donov.)	April 5th, 1929	From s.s. *Salpa*, trawling off Mewstone.
5.	A Deformed Stickleback (*Spinachia vulgaris* Flem.)	June 14th, 1928	From motor-boat *Gammarus*, trawling in Plymouth Sound.
6.	Abnormal Rays		
	6 A *Raia microcellata* Mont.	Jan. 1st, 1928	From s.s. *Salpa*, trawling on Eddystone Grounds.
	6 B *Raia clavata* L.	Feb. 24th, 1930	Landed at Plymouth market; caught in ray-net set in Bigbury Bay.
	6 C *Raia microcellata* Mont.	Feb. 25th, 1930	From s.s. *Salpa*, trawling in Bigbury Bay.
	6 D *Raia microcellata* Mont.	Feb. 25th, 1930	Ditto.
7.	Double-monster of the Spur-Dogfish (*Acanthias vulgaris* Risso)	Aug. 9th, 1929	From Newlyn, Cornwall, per R. Phillips, Esq., of Plymouth.

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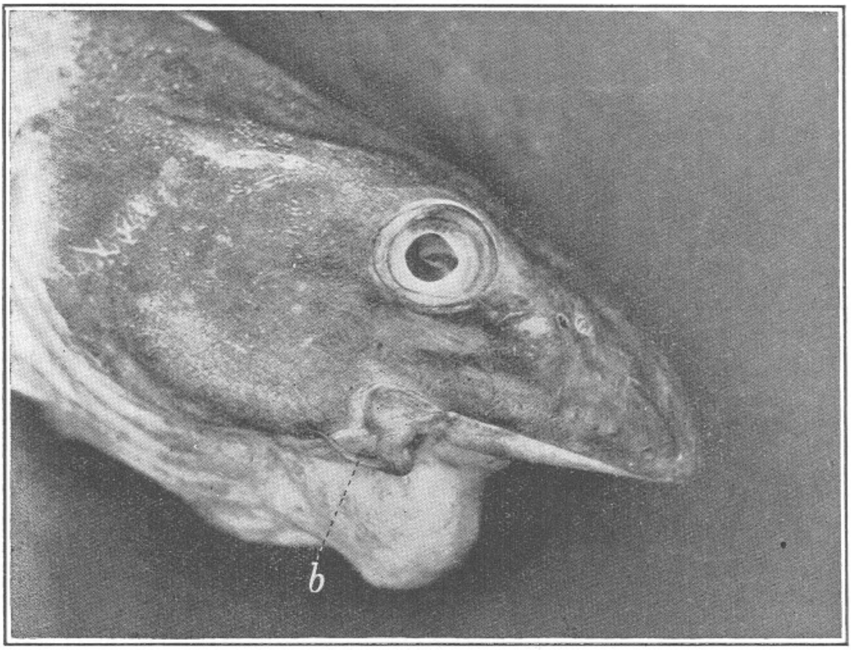
* I am indebted to Dr. R. H. Burne, F.R.S., and the Pathologist at the Royal College of Surgeons for their report on this specimen, and for the half-section of the fish figured in Plate I.

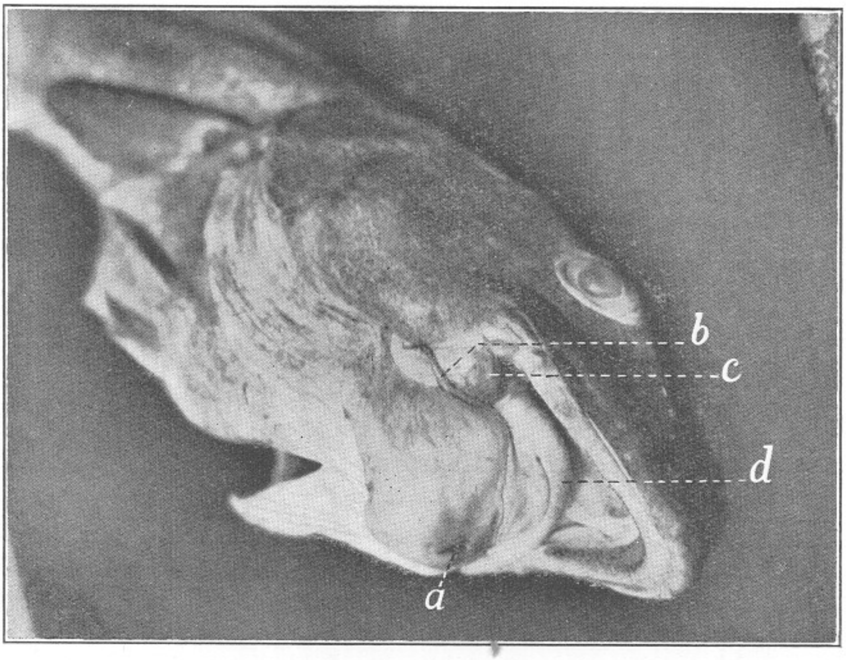
1. A Cod with Malformed Mouth.

The cod showing this abnormality measured 86·5 cm. in length and was in fairly good bodily condition despite its seemingly serious disability. The external features of the head are well shown in Text-Figs. 1 and 2. The snout projects beyond a curiously deformed lower jaw with a bulbous growth beneath, giving the head a most quaint appearance. The barbel (*b*), normally central, lies to the right of the bulbous growth, and what would normally be the left half of the lower jaw (*d*) is symmetrically arched across and beneath the upper jaw, presumably functioning as a whole lower jaw. The representative of the right half of the lower jaw is displaced and doubled back upon itself at a sharp angle with the left half. When first observed, the bulbous growth was ulcerated (Text-Fig. 2.*a*), leading one to suspect that it was pathological in character. The specimen was later sent to the Royal College of Surgeons where sagittal sectioning revealed the true state of affairs. Plate I from a photograph of the cut face of the left half of the head serves to illustrate the conclusions communicated to me by Dr. Burne. The protuberance is not a tumour, but is due to the downward bending of the tongue (Plate I, *t*), pushing the



Text Fig. 1.—Head of Malformed Cod, viewed from right side. (Photo, C. H. Gill.)

intermandibular wall before it. Dr. Burne suggests that the condition is a congenital one; i.e. want of growth of the lower jaw accompanied by full growth of the tongue, and the necessity for the tongue to find room. Instead of growing out of the mouth, the tongue has bent downwards, pushing the sub-mental wall before it. It occurs to me to suggest that the process described by Dr. Burne might have produced the end result if it came into operation subsequent to an injury to the lower jaw of a young normal individual. This fish certainly provides an excellent illustration of the ability to survive and grow under adverse circumstances.



TEXT FIG. 2.—Head of Malformed Cod, viewed obliquely from beneath. (Photo, C. H. Gill.)

a. lesion on ventral protuberance.
b. barbel, normally median in position.
c. original right-half of lower jaw.
d. original left-half of lower jaw, now functioning as whole lower jaw.

2. A PUG-HEADED HERRING.*

This specimen, 8 cm. in length, exhibits the features described by Gemmill (**2**, p. 48) and others under the name of "pug-head." Of this

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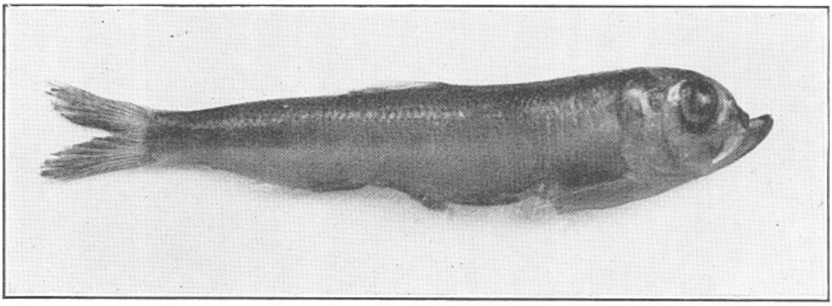
* Dr. E. W. Gudger has recently published an interesting paper entitled "Pug-Headedness in the Striped Sea-Bass, *Roccus lineatus*, and in Other Related Fishes." Bull. Amer. Mus. Nat. Hist., Vol. LXI, March 31, 1930.

condition Gemmill says: "In typical examples the snout is markedly reduced in size, and curved in such a way that the anterior frontal region arches rapidly downwards just in front of the eyes. The latter are lessened in horizontal diameter and become oval in shape, having the long axis vertical. The lower jaw retains its usual size, and accordingly projects a considerable distance in front of the rest of the head." It can be seen from Text-Fig. 3 that the specimen conforms with this type description. In other respects the fish was normal and in healthy condition, its stomach being well-filled with recently-caught mysids. Gemmill refers to the interesting results of Knauthe who allowed breeding between males and females of *Leucaspius delineatus* v. Sieb. and *Cyprinus aphya ?*, which, though apparently normal, were derived from "puggy" parents or grandparents. For instance, he found that a male and female Leucaspius, normal themselves though derived from "puggy" parents, provided in the offspring the large number of 50 out of 180 which "reverted" to the grandparental form. In later experiments with Cyprinus he was able to show that 6 of a total of 168 progeny were "puggy" like their great-great-grandparents although the intervening ancestors were all apparently normal.



Text Fig. 3.—A Pug-headed Herring. Length 8 cm.

3. A Fan-tailed Pilchard.

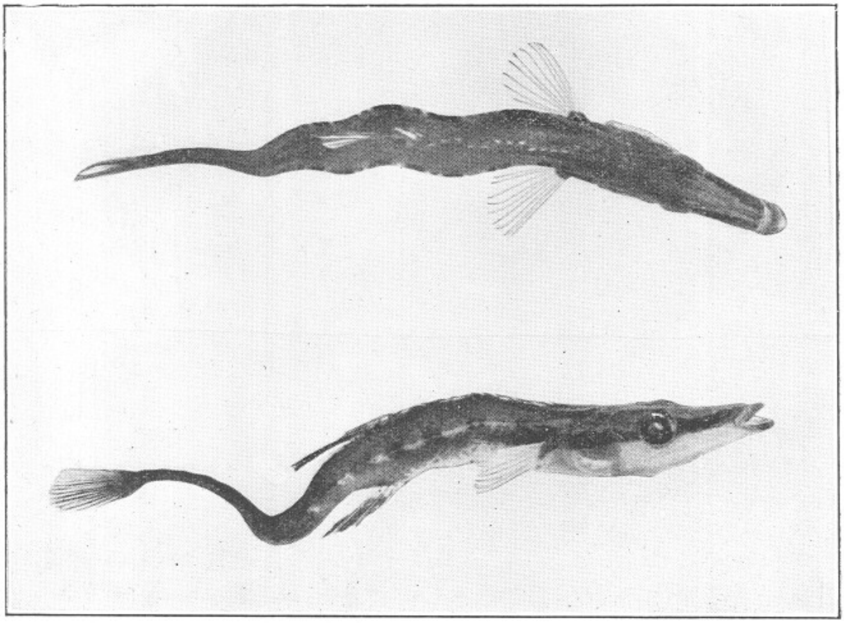
Measurements of this unusual specimen resulted as follows :—

Tip of snout to root of tail	20·8 cm.
Tip of snout to end of mid-caudal ray	22·0 cm.
Tip of snout to end of flukes	26·6 cm.
Greatest width of tail across flukes	6·5 cm.

The relative size of the tail as compared with that of a normal fish of approximately the same length may be gathered from Plate II. Photography by X-rays (Plate II) reveals that the leaf-like expansion of the tail is due to an excessive lateral branching and rebranching of the dermal fin-rays. At their proximal ends the latter retain their rod-like appearance and are in normal association with the endoskeletal elements of the caudal fin.

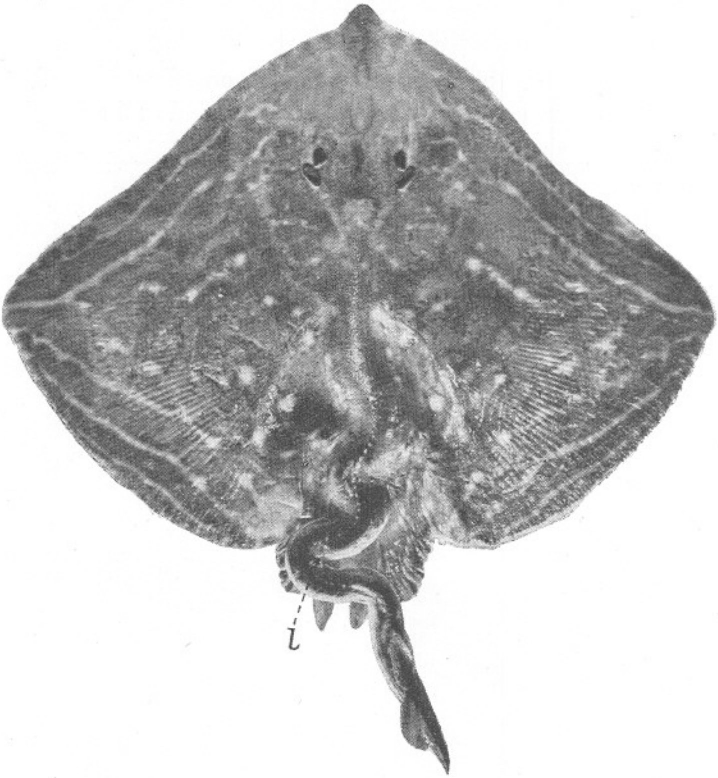
4. COALESCENCE OF VERTEBRÆ IN A LEMON-DAB (*Pleuronectes microcephalus* Donov.)

The small Lemon-Dab in which this abnormality was observed measured 22·5 cm. from the tip of the snout to the end of the middle rays of the caudal fin. It will be seen from the X-ray photograph (Plate III) that as the result of considerable co-ossification of vertebræ in the posterior half of the vertebral column the fish presents the contour of a top-knot rather than of a lemon-dab at the tail-end. The outer edge of the caudal peduncle is thus brought almost into alignment with the bases of the dorsal and anal fins in this region. Photography by X-rays has conveniently revealed the main features of this vertebral abnormality. Anteriorly the vertebræ appear to be normal and it is not until about the 18th vertebræ from the front that anything markedly unusual is



TEXT FIG. 4.—A Deformed Stickleback (*Spinachia vulgaris* Flem.).
Upper: From above. Lower: From side.

noticeable. At this point, however, there are signs of a dorso-lateral displacement of vertebræ, particularly evident in the next half a dozen vertebræ. It is as if these had become forced out of alignment as the result of undue compression along the vertebral column. Behind these obviously displaced vertebræ, the remainder of the series appear to be co-ossified to form several unequal-sized blocks of fused vertebræ. Continuing the use of the "compression" analogy the appearance is as if pressure had been here so great that the centra had been forced to collapse together like the bellows of a camera, rather than being displaced dorso-ventrally. Nevertheless, the identity of the vertebræ still remains apparent in that the neural and hæmal spines are properly paired and normal in number, representing a total of 47 (or 48 ?) vertebræ exclusive of the caudal end-piece.



TEXT FIG. 5.—Abnormal *Raia microcellata* Mont. Specimen 6 C, described in text.

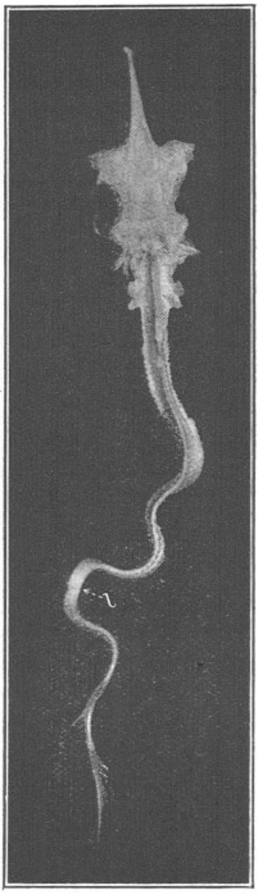
5. A Deformed Sea-Stickleback (*Spinachia vulgaris* Flem.)

This little fish of 8 cm. in length was alive and active when brought to the Laboratory and presented a most odd appearance while swimming in an aquarium. Viewed from the side (Text-Fig. 4) it showed a marked kink in the tail region posterior to the dorsal fin. Seen from above, it exhibited a sinuous formation of the body. Photographs by X-rays show that the vertebral column follows the lines of the kink and waves of the body but that the vertebræ are normal in character. This instance adds another to the long list of references given by Gemmill (**2**, p. 52) to cases of twisted bodies with or without associated coalescence of vertebræ. Gemmill refers to examples of twisting or curvature without coalescence of vertebræ (i.e. of the class to which the present stickleback belongs) in a sole and in a codfish, described by Howes (**4**) and Storrow (**6**) respectively. In both there were five sinuosities.

6. Abnormal Rays.

6 A. A small female of *Raia microcellata* Mont., measuring 26 cm. across the disc, was found to show fin abnormalities on the right side. The pectoral was separated from the head by a deep triangular notch involving two gill-clefts. The posterior lobe of the right ventral fin was also divided into two by a somewhat shallower notch. These features are shown in Plate IV, 6 A.

6 B. A mature male of *Raia clavata* L., measuring 51 cm. across the disc, had the pectorals of both right and left sides separated from the head (Plate IV, 6 B), although in this case the separation did not extend so far back as in specimen 6 A, nor was there any accompanying abnormality of the ventral fin.



Text Fig. 6.
Vertebral skeleton of specimen 6 C, described in text.

There are numerous references in literature to rays in which the pectoral fins are not adherent to the head, more commonly, perhaps, to cases in which both fins are free as in specimen 6 B. Bashford Dean (**1**, p. 620) cites the genera Hieroptera and Propterygia as being originally described as specific forms although now known to be rays of this peculiarly abnormal type. He also credits Gesner (**3**) with the first known account and figure in 1556, and gives a list of references to published accounts in later times. Williamson (**8**, p. 64) advances reasons against the explanation of these abnormalities as the result of cutting by fishermen, pointing out the exactitude of the separation along the dividing-line between the snout and the fin on either side. Johnstone (**5**, p. 188) suggests that the malformation is due to the assumption, during development, by the propterygia, of a position which is more nearly related to the primitive position of the Elasmobranch pectoral fin-structures than the latter normally occupy in skates and rays. The fact that in specimen 6 A the posterior lobe of the ventral fin is also bifurcated adds interest to the question of the causation of such abnormalities in rays.

6 C and 6 D. By an odd coincidence two male rays of the same species (*R. microcellata* Mont.), taken in the same haul of the otter trawl,* showed sinuous twisting of the vertebral column.

6 C. This specimen measures 49 cm. across the disc, and the very abnormal condition of the tail is apparent from Text-Fig. 5 reproduced from a photograph. The appearance of the vertebral column (prepared by boiling and cleaning away the flesh) is shown in Text-Fig. 6. Attention is drawn especially to the pronounced "elbow" at (*l*), where in addition to the action of a wave of lateral displacement there is marked tortion in a clockwise direction through an angle of almost 90°. This twisting is, however, quite local to loop (*l*), the tail posteriorally retaining its normal dorso-ventral position although, of course, exhibiting the laterally-sinuous condition. The "elbow" at (*l*) was quite flexible, so that one imagines that the fish when alive could freely swing the tail posterior to it.

6 D. The second specimen, not figured here, was 48 cm. across the disc and more normal in appearance. The vertebral column was quite normal from the head backwards to the level of the distal ends of the ventral fins, but at this point there was one well-marked lateral looping, followed by a second in the region of the dorsal fins. There was nothing comparable to the tortion shown in specimen 6 B, nor, one thinks, was the fish unduly affected in its tail-action during life.

7. DOUBLE MONSTER OF THE SPUR-DOGFISH (*Acanthias vulgaris* Risso.)

This specimen was first noticed among the embryos in the offal from dogfish being prepared for market at Newlyn. It was forwarded to

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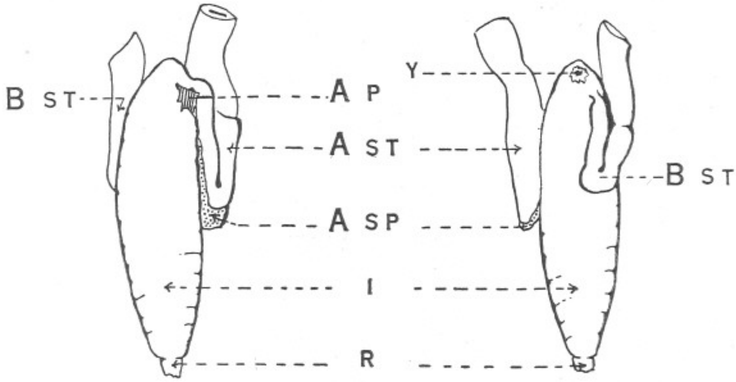
* My colleague, Mr. G. A. Steven, was aboard the *Salpa* on this occasion and brought back the specimens.

Plymouth in methylated spirit, curled up in a rather small bottle, and apart from the lack of the yolk-sac was entire.

External Features.

In size and development the monster may be likened to the union of two embryos between 13 and 15 cm. in length which had grown at the expense of not much more than one-half of the original supply of yolk. The two members lie with their ventral surfaces in apposition, and they are united from the level of the yolk-stalk backwards to the tail. The union is thus one of Gemmill's Class VI (**2**, p. 21). The larger member (A), in Plate V, appears normally developed with respect to the head, pectorals and two dorsal fins; the smaller member (B) also exhibits normal gills, pectorals and dorsals, while the head is typical save for malformed nostrils. The nostrils in (A) are quite normally separated laterally by an appreciable interval, whereas in (B) they are adjacent and lie in a shallow pear-shaped depression (Plate V (*n*)). The general pigmentation in both members is normal and most effectively indicates the identity of each. There is but one pair of pelvic fins (female in structure) situated on the left side as the monster is viewed with the larger member uppermost. On this same side a groove occupies the middle line from the anus backwards towards the tail. Still viewing the specimen with member (A) uppermost, it is seen that the body of the latter passes by a rather abrupt downward kink about 1 cm. behind the



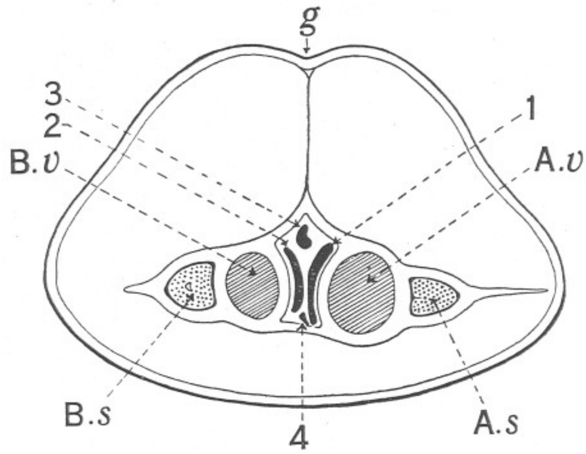
TEXT FIG. 7.—Gut of Double-monster of *Acanthias vulgaris* Risso.

A. ST.	Stomach of larger member A.
A. SP.	Spleen of larger member A.
A. P.	Pancreas of larger member A.
B. ST.	Stomach of smaller member B.
I.	Intestine.
R.	Rectum.
Y.	Opening of internal yolk-sac into intestine.

second dorsal fin into an almost normal heterocercal tail. Tracing the smaller member (B) backwards it would seem to possess no tail, the body stopping short somewhat suddenly to fuse with that of (A) at the level of the kink. At the root of the single well-formed tail, however, there is a small fleshy lobe, (c) in Plate V, left, which may represent the tail of (B).

Digestive System.

The digestive organs of the specimen presented an interesting condition which is, perhaps, most conveniently described by starting from the single short rectum (Text-Fig. 7, R) and working forward. The rectum, passes into a median intestine (I) with a spiral valve of the usual character. Near its front end the intestine receives on either side a two-limbed stomach. The larger of these two stomachs (A. ST.) can be traced to the œsophagus of the member A, and is supplied with a normal pancreas (A. P.) and spleen (A. SP.). The smaller stomach (B. ST.) leads to the œsophagus of the member B, but, unlike its fellow, is without either pancreas or spleen. At the front end of the intestine there is communication (Fig. 7, Y) with the internal yolk-sac. The latter is a bi-lobed organ, communicating on the one hand, as stated, by a median opening to the intestine at Y, and, on the other, to the external yolk-sac by a single channel in the yolk-stalk. Both members of the monster have



TEXT FIG. 8.—Hand-section of Double-monster across tail-end behind pelvics. Section cut in direction S—S indicated in Plate V.

A. v.	centrum of A.
B. v.	centrum of B.
g.	external groove.
A. s.	spinal cord of A.
B. s.	spinal cord of B.
1, 2, 3, and 4.	Blood-vessels in united hæmal arches.

a bi-lobed liver, but that of member B is much the smaller and very unequally lobed.

Hand Section across the Tail-region.

A hand section across the tail a short way behind the pelvic fins is shown diagrammatically in Text-Fig. 8. It is seen that members A and B retain their identity so far as the centrum and spinal cord are concerned, but that there is fusion of the hæmal arches, enclosing the blood-vessels of both. In the description of the external features of the specimen, reference was made to the small fleshy lobe (c) at the root of the single normal heterocercal tail, and the suggestion was made that (c) may represent the tail of B. Sections cut posterior to the one just described lend support to this view in that the identity of B can be traced backwards to (c).

The monster would thus appear to be the union of two embryos, of which one (A) is dominant. In a letter to *Nature* on May 25th, 1929, von Bonde and Marchand (**7**, p. 795) describe a somewhat similar union in *Squalus fernandinus*. Their specimen differs in having a more advanced duplication of the tail, while the nostrils of both members appear normal. The section across the tail region shown in their Figure 2 also differs from that represented in Text-Fig. 8 of this paper in several respects. In the section of *S. fernandinus* the blood-vessels are shown separated from the " lateral arch " facing the external groove by a thick line, presumably indicative of cartilage. But in *Acanthias vulgaris* a blood-vessel (Text-Fig. 8, 3) is seen to occupy this lateral arch, there being no cartilaginous cross-piece separating a hæmal arch from a " lateral arch." At the time of writing their letter von Bonde and Marchand had not dissected their specimen for an examination of the internal organs. It will be interesting to know, when they have done so, how far their specimen agrees with the present one in the characters of the alimentary canal.

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EXPLANATION OF PLATES.

PLATE I.

Sagittal Section of Head of Malformed Cod.

d. original left-half of lower jaw.
t. tongue lying in extension of mouth-cavity.
h. heart.

PLATE II.

Fan-tailed Pilchard.

Left: From X-ray photograph by Institute of Anatomy, University College, London.
Lower right: Tail of Fan-tailed Pilchard.
Upper right: Tail of normal Pilchard of approximately same length.

PLATE III.

Abnormal specimen of *Pleuronectes microcephalus* Donov. From X-ray photograph by Institute of Anatomy, University College, London.

PLATE IV.

6 A. Abnormal *Raia microcellata* Mont.
6 B. Abnormal *Raia clavata* L.

PLATE V.

Double-monster of *Acanthias vulgaris* Risso. (Photo, C. H. Gill.)

A. Larger member.
B. Smaller member.
c. Rudimentary tail of B.
n. Abnormal nostrils of B.
y. Severed end of yolk-stalk.

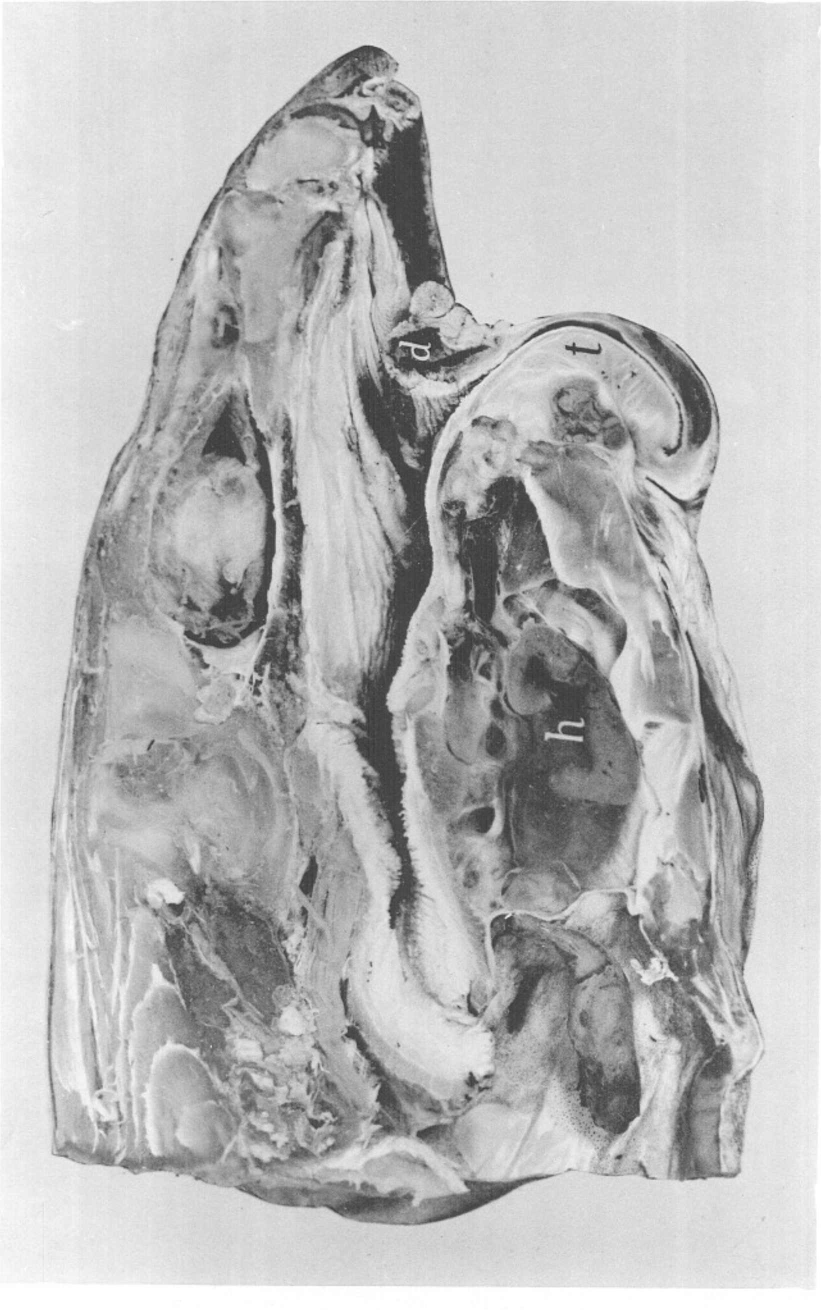
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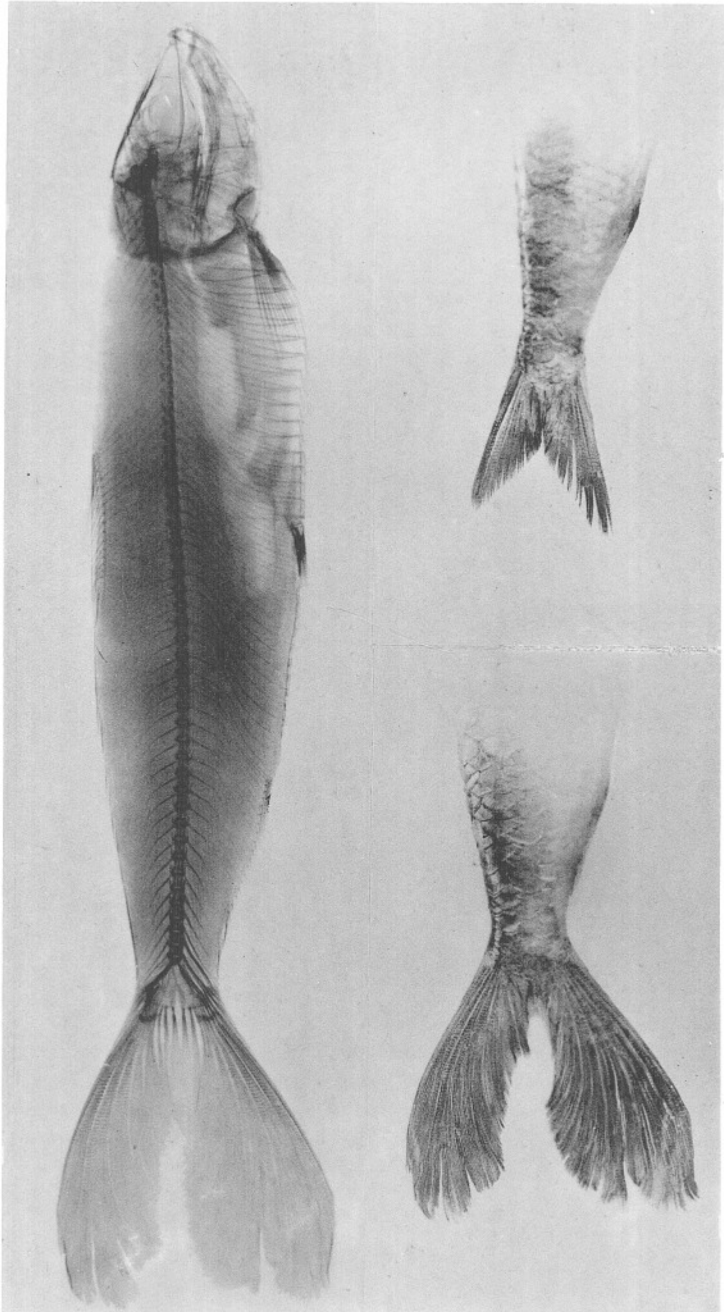
PLATE II.



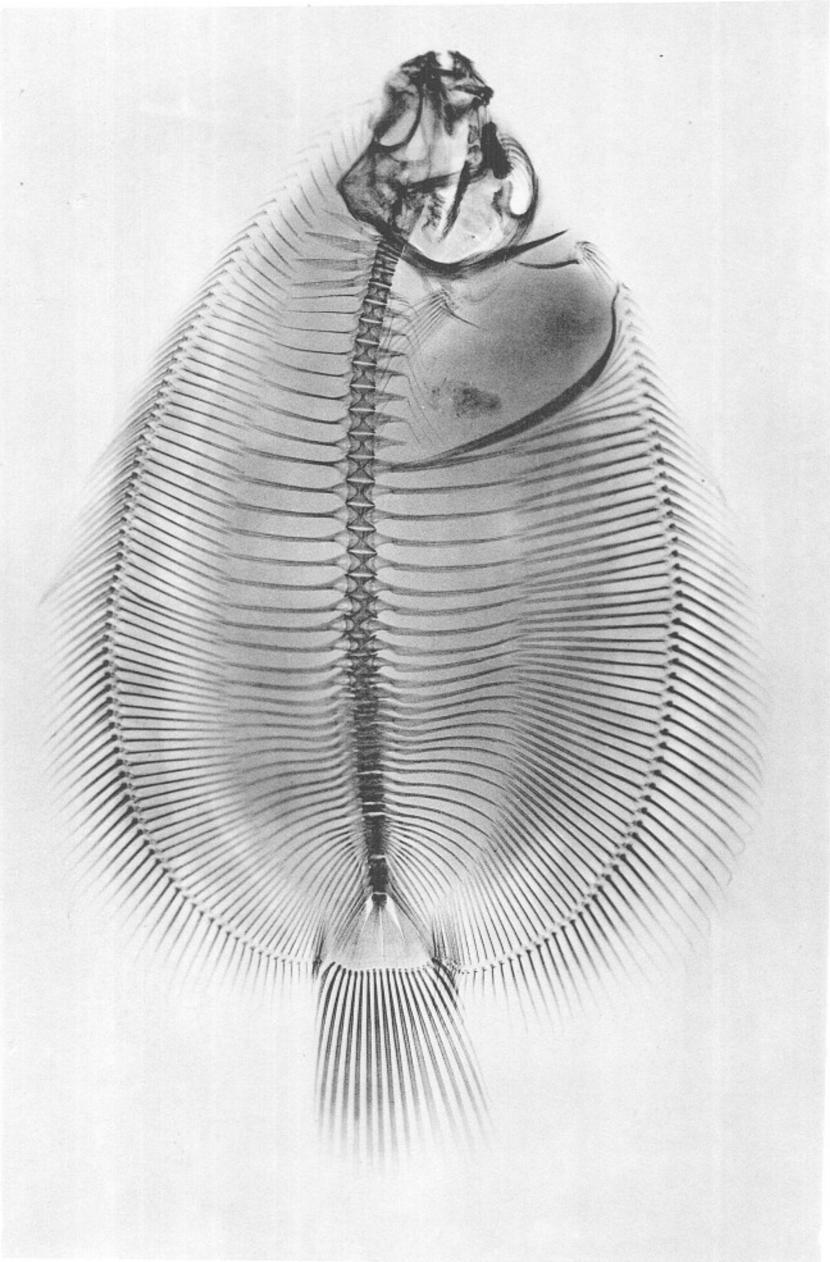
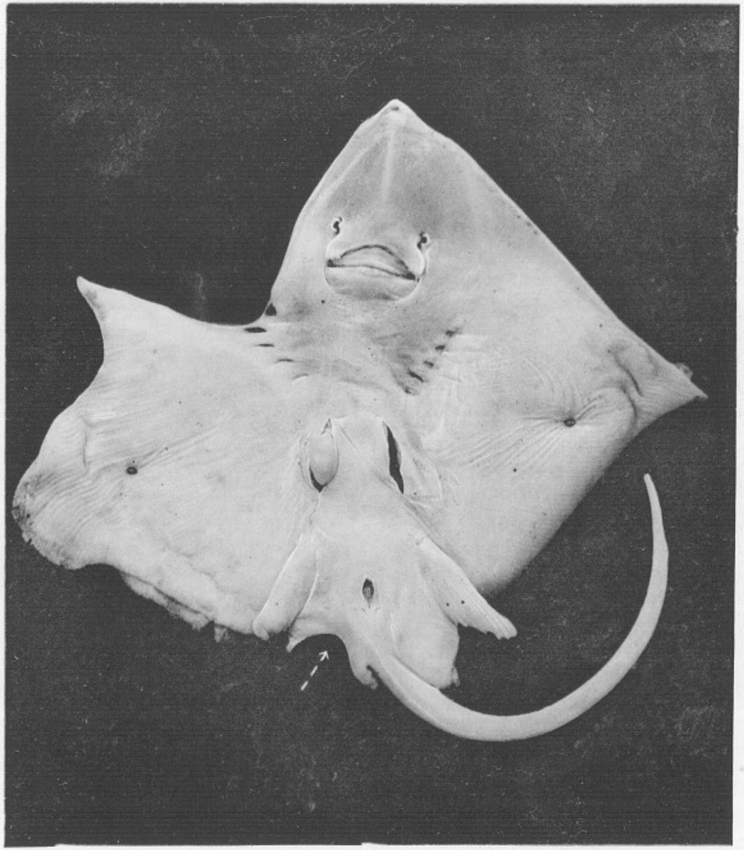
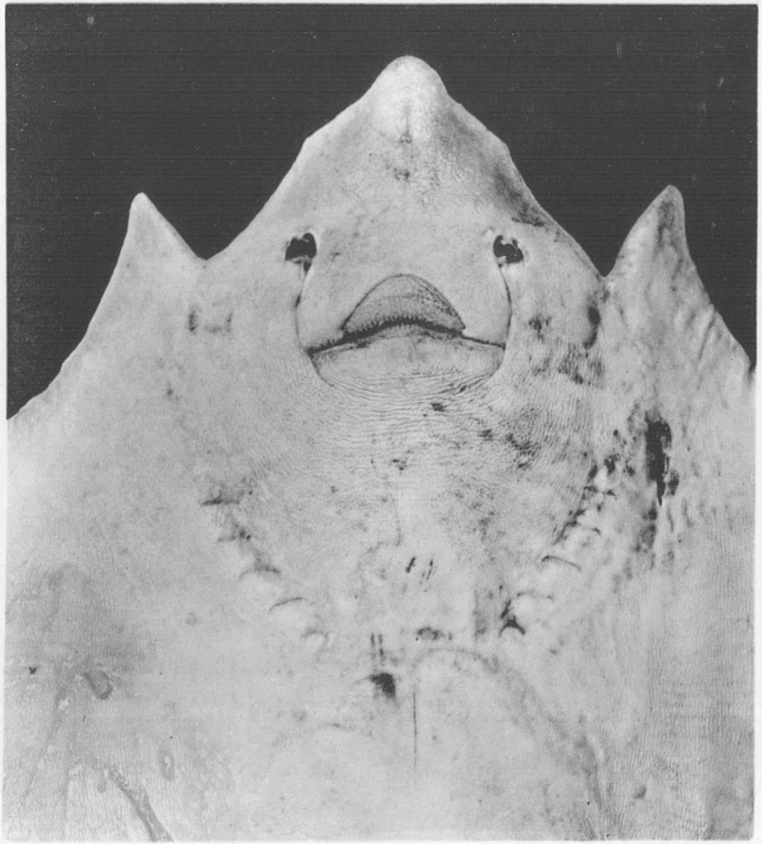


PLATE IV.

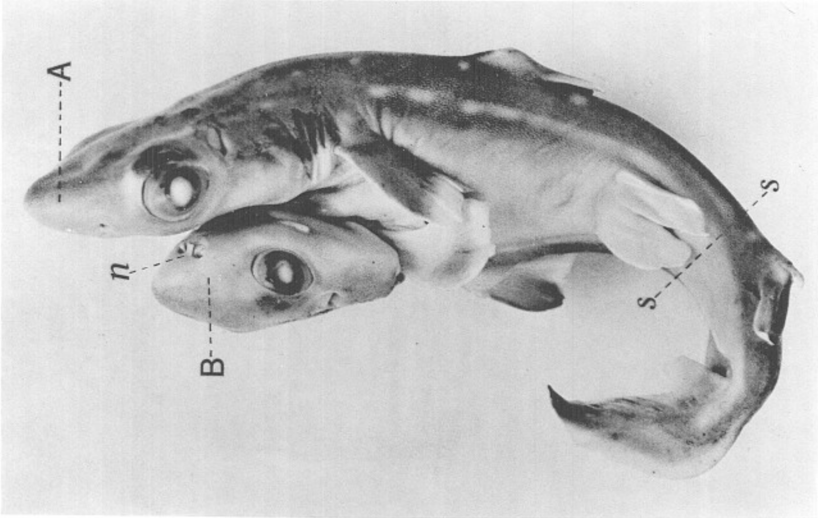


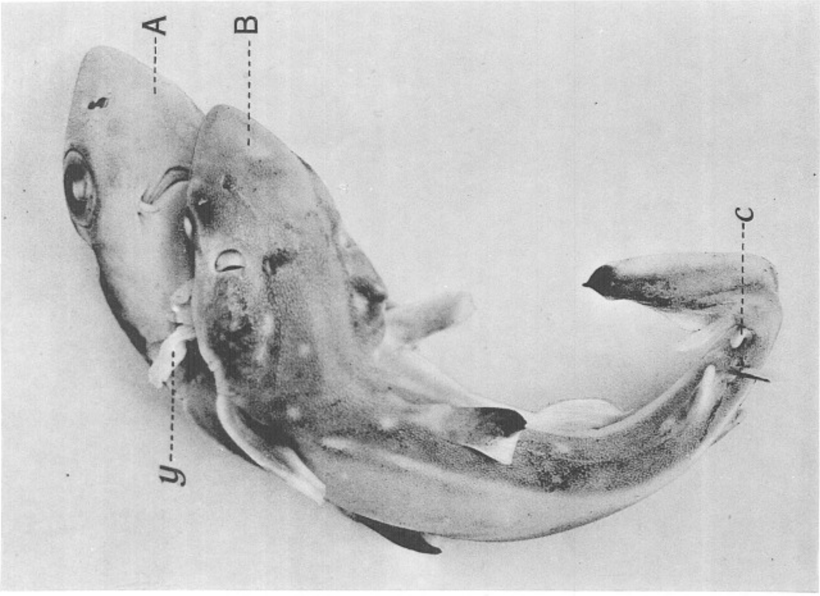
6A



6B

PLATE V.





On the Hypothesis of Mitogenetic Radiation.

By

Dr. Nine Choucroun.

With 3 Figures in the Text, and Plates VI and VII.

I. INTRODUCTION.

IN order to explain certain actions influencing at a distance the cellular development of living tissues, various authors have framed the hypothesis of a *mitogenetic radiation* emanating from cells in the act of division.

Gurwitsch (**1**) first of all pointed out the mitogenetic influence of cells of embryonic tissues, in the form of an emulsion or otherwise, on the root of the onion or on yeast cells. According to him, this action, which was exerted through sheets of quartz—but not of glass—is due to a radiation, or, to be more explicit, to an ultra-violet radiation of wave-length 2000 Ångström units, produced by the active material and capable of regular reflection.

Reiter and Gabor (**2**), who have since then carried out many more such experiments, also attribute the action to a mitogenetic radiation, the wave-length of which they have measured (according to them nearer to the visible) and can readily follow, so that, for example, they can separate the two rays reflected from the opposite faces of a sheet with parallel faces.

An analogous influence had been observed by M. Joseph Magrou and Mme. M. Magrou by exposing to *Bacterium tumefaciens*, through a sheet of quartz, a root or a stem of an onion, and later sea-urchin eggs. In the first case they verified the phenomena observed by Gurwitsch, without however affirming the existence of a radiation. In the second case they obtained aberrant larvæ, plutei opaque and with short arms or armless, instead of plutei transparent and elongated as are the normal larvæ. Histological examination seemed to indicate that these differences in appearance were related to differences in structure; in the irradiated larvæ the mesenchymatous cells were more numerous than in the controls. This case also might be explained on the theory of a mitogenetic action.

On the other hand, it did not seem that this action could have been due to a vapour carried by the air, for the controls, placed in the immediate neighbourhood of the lots exposed to radiation, gave a perfectly normal development. M. et Mme. Magrou were of the opinion that this action too, just as in the case of the onion root, could be attributed to a hypothetical radiation emanating from the bacteria.

But the action producing malformation was not always evident in the exposed lots, which indeed were not very numerous, and sometimes even the effect was not produced in a single one.

Unsuspected causes of lack of symmetry might conceivably have been at play either in themselves to provoke the observed phenomena or to prevent the action exercised by *B. tumefaciens* from becoming manifest.

It became a necessity, therefore, to establish with certainty the reality of an action causally connected with proximity to the culture. And for that an effort had to be made to realise, in the steps we took, the best possible conditions of symmetry and homogeneity for all the batches, controls and exposed.

II. Reality of the Phenomena.

To prove the reality of the phenomena was the task for us, M. Magrou, Mme. Magrou and myself, at the Marine Laboratory of the Institut Océanographique de Monaco (**3**).

This time we worked with a larger number of batches, about 24, namely, 12 controls and 12 exposed, selected at random. The controls were, for the greater part, placed on a table among the exposed.

Eggs of *Paracentrotus lividus,* from the very same animal and laid at the same time, were all fertilised in the same vessel by the same supply of sperm. Immediately after fertilisation the eggs were divided in a manner as similar as possible among the small quartz receptacles ; these were 3·5 cm. in diameter with optically-worked bottoms. Certain of these receptacles were placed on vessels of the same diameter containing a thick suspension of *B. tumefaciens* in nutritive broth, the suspension coming from a single supply of emulsion.

All the lots, control and exposed, were placed in identical conditions as regards illumination, air supply and temperature, in an incubator kept near 22° C., which temperature is favourable for the good development of the culture and is borne very well by the eggs used.

Under these conditions we verified the production of abnormalities observed in the earlier work, and the results obtained, based on a number of experiments, allow us *to conclude that there is a definite causal connection between the existence of an action and the presence of the culture.* But, as before, a certain proportion of the exposed lots (this time always about the same in the successive trials, thanks to the greater number of the receptacles) escaped all action.

It was natural to expect, on account of the degree of homogeneity realised, that in each lot a certain proportion of the eggs were more resistant than the others to the injurious action observed, giving rise therefore to larvæ normal in every respect. But it was difficult to admit that entire lots, made up of the same larvæ as the others, could completely escape the action if some cause of lack of symmetry were not in existence.

One might incriminate the culture and ask whether, once it had been subdivided, it retained the same activity throughout. As a fact, in certain vessels, the culture settled out, whereas in others it remained in an emulsion. Sometimes the absence of action coincided with this precipitation of the culture and sometimes it did not do so. In any case, this possible cause of lack of symmetry would disappear if one were to submit all the lots to the action of one single culture, and if in addition this culture were to revolve beneath the batches of sea-urchin larvæ kept at rest. This is what I proposed and carried out as follows :—

III. Realisation of a Homogeneous "Irradiation."

An annular vessel, A, of pyrex glass, about 30 cm. external and 25 cm. internal diameter, intended to contain the bacterial suspension, rotates around an axis O (Fig. 1) below another annular vessel, B, which covers it. Vessel B is pierced by circular holes in which are affixed, by joints of paraffin wax, the quartz receptacles, C, which contain the lots of sea-urchin larvæ.

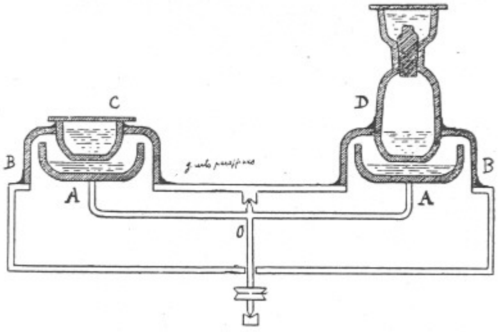


Fig. 1.

The vessel A is carried by an annular plate of metal which revolves around an axis, O, with a uniform and slow movement, about one turn in eight minutes. The upper vessel rests partly upon the edge of the apparatus, partly upon a central fixed plate, the mechanical disposition of the parts permitting of the complete separation, by means of paraffin wax joints, of the air in contact with the culture from that in contact with the sea-urchin eggs.

An exactly similar control apparatus functions at the same time, the only difference being that in it the vessel A contains no culture (Fig. 2).

Under these conditions of homogeneous "irradiation" one might expect to observe an absolute identity in the action. Now, in the experiments carried out at the Marine Laboratory of Banyuls, we indeed observed progress in this respect; but in certain experiments, irregularities existed (exposed lots remaining normal) which it became difficult to explain on the hypothesis of a radiation once homogeneity of irradiation had been realised.

On the other hand, the photographic plate substituted for the sea-urchin eggs never revealed the supposed radiation, in spite of very long exposures (48 hours). Stated more precisely, with the conditions under which the phenomena became manifest in the eggs, the plate, even when sensitised to the extreme ultra-violet, received absolutely no impression. I must say that for many physicists this negative result sufficed to render doubtful the existence, in this case, of a mitogenetic radiation.

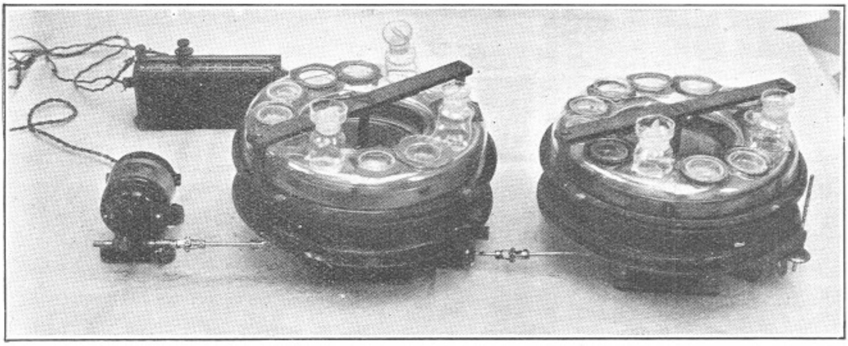


FIG. 2.

I then applied myself, in a new piece of work carried out this time at the Marine Laboratory at Plymouth, to test this hypothesis of radiation.

IV. IT IS NOT A RADIATION WHICH ACTS.

To investigate the above proposition, certain of the quartz capsules were replaced by quartz flasks, D, with ground stoppers, the base of which was intentionally constituted of capsules already used in the preceding experiments, and of which the stoppers were surrounded by a trough filled with frequent changes of sea-water (Fig. 1).

Each experiment consisted of twelve lots exposed (8 open capsules and

4 stoppered flasks) carried by the apparatus containing *B. tumefaciens* and 12 controls (10 open capsules and 2 stoppered flasks) carried by the other apparatus. According to the radiation hypothesis, the action should be shown in the same manner in the stoppered flasks and in the capsules. One should observe in these flasks an abnormal development simultaneously with a normal development in the control flasks of the blank apparatus.

Now, never did I observe any abnormality in the exposed stoppered flasks. The same culture of *B. tumefaciens* which exercised a strong action on the eggs in the capsules produced no effect on the eggs in the stoppered flasks ; the water-seal sufficed to stop all action. In three of the experiments, all the capsules exposed gave abnormal developments, whilst the four stoppered flasks gave normal developments as well as the twelve receptacles (capsules or flasks) of the blank apparatus.

In the photograph reproduced here by way of example, it may be seen that in the lots exposed in stoppered flasks the development is normal and comparable to what it is in the control vessels, whereas the anomalies are striking in the lots of the exposed capsules (Plate VI).

No longer, then, can one explain the observed action at a distance by a special radiation which exerts its effect through comparable media and would clearly reach equally well both the batches of eggs in the capsules and in the stoppered flasks.

More generally, and this is obvious, it is not possible to explain the observed phenomena by any action exerted *through* quartz vessels, for then it could not possibly suffice to close the flasks to stop all action.

V. Detailed Description of an Experiment.

Before speaking of the observations, that I have been able to carry out, in the light of a different interpretation, I should like to describe in detail one experiment, laying emphasis upon the precautions that I had to take to realise, in the steps we took, the greatest possible similarity between the exposed lots and the controls.

All the *receptacles* were washed for a long time with concentrated hydrochloric acid, then with water, then with alcohol, then with distilled water, after which they were sterilised. The same precautions were taken for the vessel, A, before containing the culture, for the perforated covers, B, also for the non-perforated covers, B_1, which were to protect the vessel A during filling or transfer to the mechanical apparatus (Fig. 3). The receptacles, capsules and flasks, were divided, *haphazard*, between the two perforated covers resting on sterilised paper. All the joints were sealed with paraffin wax (M.P. 50° C.), then with soft paraffin (M.P. 38° C.) to fill up possible cracks.

The sea-urchin *eggs*, of the species *Echinus miliaris*, coming from one oviposition were washed for a long while with fresh sea-water, then fertilised all at once by the same sperm suspension; they were then separated by decantation from the water in which they had been fertilised and finally suspended in a volume of sea-water sufficient for the eggs to develop well and withal small enough for their concentration in each receptacle to render observation easy. They were then divided uniformly, by the aid of a sterilised glass spoon, between the various receptacles, ladling out alternately the lots for the apparatus with *B. tumefaciens* and those for the control.

Once more must I insist upon the necessity for respecting the conditions of symmetry up to a point which may appear puerile.

The *Bacterium tumefaciens* was cultivated on agar (at a temperature of 38° C.) in large Roux flasks. It was then emulsified in ordinary broth Ph. 7·4 and the emulsion from each flask was poured with aseptic precautions into the vessel A furnished with its cover, B_1. With three Roux flasks a thickness of about 5 mm. emulsion was obtained. This vessel A and the empty control vessel, both furnished with their protective covers, B_1, were carried on the rotating plates of the apparatus. For these covers, B_1, were substituted the perforated covers B, carrying the vessels the bases of which were then within a few millimetres (about eight) of the free surface of the culture. The inner and outer edges of these covers were paraffined with a brush and the motors turning the plates bearing the vessels A were started. The experiment was allowed to proceed till the characteristic " pluteus " stage was reached, renewing, about every four hours, the sea-water contained in the troughs of the stoppered flasks so as to maintain a fresh water-seal, free from impurities.

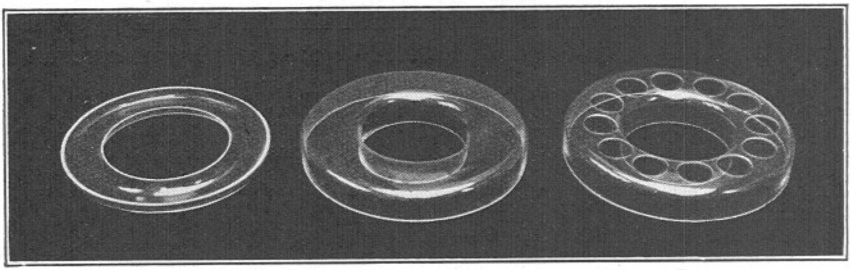

A. B_1. B.

FIG. 3.

The first experiment was carried out at a temperature of 17° C., the apparatus being enclosed in a water-oven regulated for this temperature. But the renewing of the water of the water-seal was difficult inside the oven. Accordingly in the following experiments the apparatus were simply placed upon the laboratory table. If necessary the general temperature was lowered so as not to exceed 20° C. Moreover, some additional control lots were placed right up against the apparatus containing *B. tumefaciens* as a test that, as was already known, the abnormalities were not produced by the very small temperature differences which might exist between the atmospheres of each apparatus.

As regards *observation*, each lot was examined in its position by the aid of a binocular glass which allowed one to have in the field, and in its depth, a sufficiently great number of larvæ for an estimate to be made of the relative proportion of the normal and abnormal larvæ in each lot.

All the lots having been examined and the observations recorded; *photographs* of the experiment were made, working in such a manner as to be entirely ignorant as to whether a control or an exposed lot was being taken. From each lot, after shaking, a small quantity of the emulsion was taken and placed in a numbered test-tube. To each test-tube were added a few drops of 1% chloral to stop the movement of the larvæ which then became aggregated at the bottom of the tube. Using a very finely drawn-out pipette a small quantity of liquid containing larvæ was removed from each tube and placed upon a microscope slide. The number of the corresponding lot was written on a label on the slide and *hidden*.

Then from among all the possible fields a choice was made of one which gave the best representation of the general aspect of the preparation.

It is only thanks to these precautions, of which some might seem puerile, that the photographs taken represent *objectively* the general aspect of the lots examined. This was indispensable to allow those who only saw the photographs to form an independent opinion.

VI. Attempt at Explanation.

Let us now return to the phenomenon itself.

If it seems no longer possible to explain the anomalies observed by a radiation, nor in a more general form by any action involving "passage through," it is equally impossible to doubt the existence of an action clearly established and confirmed by so many new experiments.

It seems difficult then to avoid thinking that something material, given off by the culture, reaches—in spite of the paraffin wax joints—the medium in which the eggs are developing, *travelling round* the wall of the receptacles.

It is fairly frequently observed that a bubble develops at the base of the exposed capsules. One may then raise the question as to whether a *film, monomolecular perhaps*, may not start from these, spread over the wall, insinuate itself between this wall and the paraffin joint, and introduce into the medium, in which the eggs are developing, very minute amounts of a substance which suffice however—and this is very remarkable—to exercise on the eggs an exceedingly injurious effect.

Concerning this I have made the following observations: in two experiments, certain quartz capsules contained only sea-water both on the apparatus with *B. tumefaciens* and on the blank apparatus. On each perforated lid there were five capsules with eggs, five with sea-water only and two stoppered flasks with eggs.

After having ascertained that the bacterial culture had acted on the lots of sea-urchins exposed in the capsules (never any action on those in the flasks) I withdrew the active culture; then I placed sea-urchin eggs (coming from a newly fertilised batch) in the sea-water which had been exposed, and in the unexposed sea-water of the blank apparatus.

Development was *very abnormal* in the receptacles which had been exposed to *B. tumefaciens* and normal in the controls. In one of the two experiments, stopped at the gastrula stage so as to be able to photograph certain peculiarities, the injurious action had been particularly intense. In one of the lots (Plate VII) the eggs had not even divided; in the others many eggs had not reached the blastula stage. In the majority of the lots advanced cytolysis could be observed even before the gastrula stage had been reached. This would seem to indicate that the active impurity is specially active during the first stages of development. According to our hypothesis of the transport of something material, however small it be, by a monomolecular film, it is understood that exposed sea-water must be, for the eggs introduced into it, a different medium from that in which the eggs are when themselves directly exposed to the culture. In this case, the active impurity, nothing at the start, goes on increasing during the experiment; whereas in the former case there has been, right from the beginning, a relatively great concentration.

Thus, exposed sea-water has been modified thanks to proximity to the culture, and this in spite of precautions which seemed adequate to guard against all material action.

The objection has been raised that the sea-water itself might very well have been modified by a hypothetical radiation. But then it would be impossible to understand why this modification had not been produced in the sea-water of the stoppered flasks containing eggs, necessitating an abnormal development for the eggs.

VII. SUMMARY.

1. The observed " action at a distance " undoubtedly exists.

2. This action cannot be ascribed to a radiation, nor more generally to an action " through the wall " of the receptacles.

3. This action must then be exercised " across the surface " of the wall of the receptacles by a mechanism which remains to be explained. This seems, however, to be of great interest in view of the apparently very small mass of the substance concerned in the action.

4. The action of something material is rendered probable from the fact that the eggs develop very abnormally in sea-water previously exposed to the active culture.

5. Although these experiments have only been carried out upon sea-urchin eggs, their conclusions may be valid in the case of the very numerous experiments concerning mitogenetic radiation.

In the first experiments it was thought that the sea-urchin eggs had been shielded from the action of any material emanating from the culture. An additional precaution (stoppered flasks) sufficed, however, to bring it about that the better isolated eggs remained insensible to the action at a distance which continued, however, to be exercised upon the other receptacles, which were less efficiently protected.

Experiment has shown that a water-seal sufficed to protect the eggs against all action producing deformity. If in this case abnormalities had again been found it would have been necessary to substitute sealed flasks for stoppered flasks. Only then, and if the abnormalities had again been found in sealed flasks exposed, but not in sealed control flasks, would it have been possible to conclude that the existence had been established of an action at a distance by means of a radiation, or more generally, an action exercised *through* quartz.

As far as the actions not studied here are concerned the conclusion must certainly be drawn that the existence of a radiation has not been proved.

It would at least be necessary, in order to carry conviction in this respect, that *rigorous* precautions should be taken to hinder *absolutely* all transport of material between the activating substance and that used as a test in the observations.

It has been possible to carry out these researches thanks to a grant from the Institut de Biologie physico-chimique, founded by M. Edmond de Rothschild.

On the other hand, I must specially thank Dr. E. J. Allen for the hospitality afforded to me in his laboratory. It has been very valuable to me, in the course of my work, to profit by the resources of the laboratory and above all from the friendly atmosphere created by Dr. Allen and the numerous research workers surrounding him. I should like to thank them all.

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EXPLANATION OF PLATES.

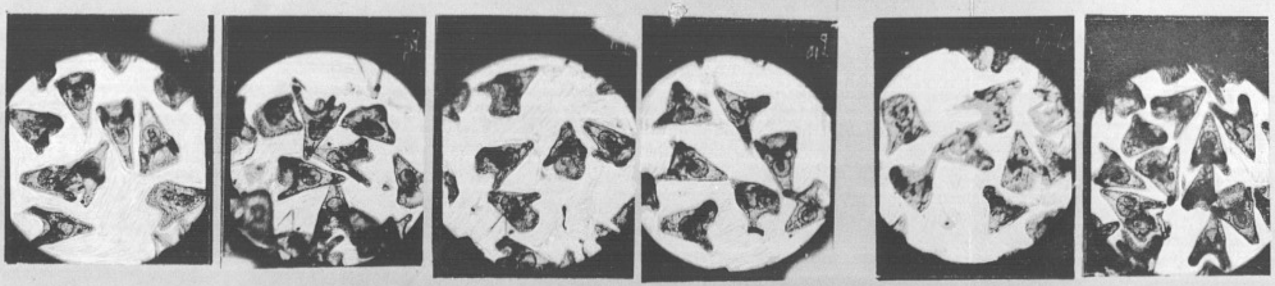
PLATE VI.

Experiment III. Shows normal development of sea-urchin larvæ in stoppered flasks and control vessels, and abnormal development in exposed quartz capsules.

PLATE VII.

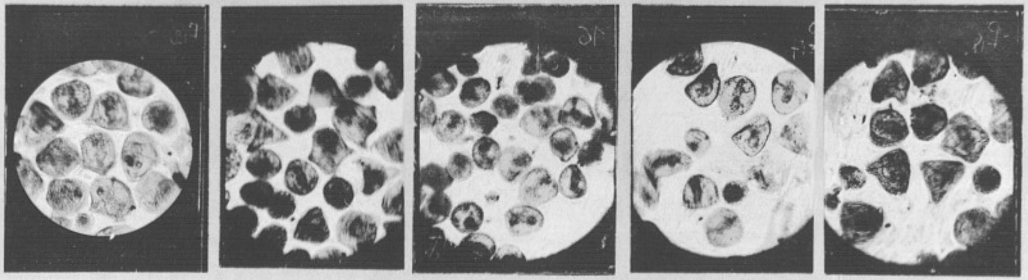
Experiment VIII. Shows abnormal development of sea-urchin eggs which had been placed in "exposed" sea-water, and normal development of controls.

PLATE VI.



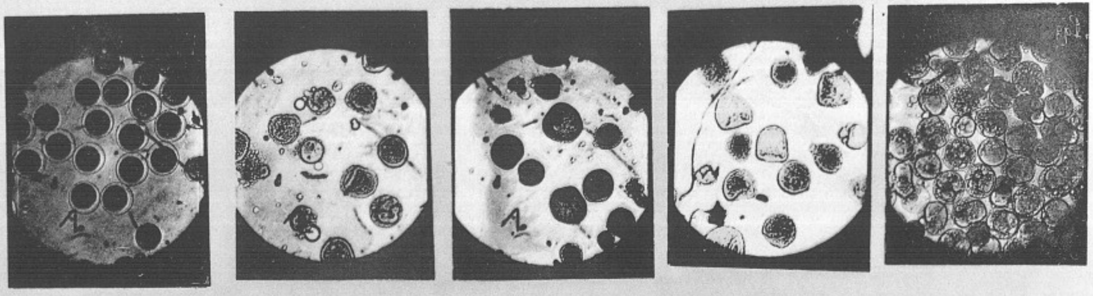
flacons bouchés émeri "traités"

Témoins



capsules quartz "traités"

PLATE VII.



œufs dans eau de mer "exposée"

œufs dans
eau de mer
témoin

The Absorption of Fats and Lipoids in the Plaice (*P. platessa* L.).

By

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Research Assistant at the Plymouth Laboratory.

With 11 Figures in the Text.

CONTENTS.

INTRODUCTION.

In a previous paper, an account was given of the histological structure of the alimentary tract of the plaice, which account was submitted as the basis of a series of studies on secretion and on the digestion and absorption of food substances in this fish. The aim of the work which is to be described presently is to show histologically how fats and lipoids are transported through the mucosa of the various regions of the alimentary tract and to indicate which regions are most concerned with the absorption of these substances. The possible function of lipoids as intermediary products in the resynthesis of true fat within the epithelial cells is considered and discussed briefly. The rôle of mitochondria and golgi elements in fat absorption has not been determined, presenting as it does a distinct and separate problem, but useful fat pictures have been obtained, as have also data on the question of absorption in fishes.

HISTORICAL.

It appears that Weber (1847) was one of the first workers to demonstrate histologically the absorption of fat. He observed that during fat digestion and absorption the cells of the duodenal villi become swollen and opaque, or filled with transparent, oily fluid. Kölliker (1857) demonstrated the absorption of fat by the stomach of the mouse, cat and dog, and observed that fat is always present in the gastric mucosa in variable quantities from the second day after birth onwards. Krehl (1890) showed that fat is taken up in solution and not in globular form and that it is re-formed into droplets within the cells of intestinal ephithelia. His observations and conclusions received support from Pflüger (1900). Schilling (1901) observed fat in the gastric epithelium of the calf after a milk meal and noted the occurrence of fat droplets in the connective tissue beneath this epithelium and also in the lymphatic glands. In 1908, van Herwerden published comprehensive studies on gastric digestion in fishes, chiefly sharks but also teleosts. He fed fish artificially with oil or egg-yolk emulsions and observed that a number of hours later, fat drops were to be found in great numbers in the epithelia and sub-mucosæ, which tissues he noted as being free from fat during starvation. His work appears to be the first of its kind carried out upon fishes. Greene (1912) demonstrated histologically the absorption of fats by the stomach of the salmon, later (1913) extending his observations to include all regions of the alimentary tract, finding that the primary function of the pyloric cæca is that of fat absorption.

A host of workers attacked the problem from the chemical point of view, and it is interesting if not entirely relevant to consider briefly the general trend of this work. Marcet (1858) and Cash (1880) were concerned with the lipolytic properties of mucosa extracts, noting increased fatty-acid content of the stomach during the digestion of a fat meal. Interest centred chiefly on the questions of the reversibility of lipolytic activity and the resynthesis of fats, and the researches of Brucke, Rochford, Monk, Moore and Rockwood, Ewald, Hamburger, Cunningham and others led to the classical investigations of Kastle and Lœvenhart (1900). From these investigations it is held that fats are first split up into fatty-acids and glycerol, which products pass through the borders of alimentary epithelia to be resynthesised to form fat again within the epithelium cells as a result of the reversible nature of lipolytic activity. Moore (1903) and Frank and Ritter (1906) could find no evidence of the occurrence of resynthesis " in vitro " and the theory does not receive universal support. Bradley (1913) attempted to discover some correlation between the quantities of storage fat and the concentration of lipase in certain tissues of a variety of marine animals. Instead of correlation, he found that some of the tissues richest in fat are poorest in lipase and vice versa, and concludes that a comparison of fat and lipase in animal tissues gives no positive evidence in support of the theory of enzyme synthesis.

It is generally accepted, however, that the cleavage products of fats are passed through the clear margins of epithelia to be resynthesised in some way to form fats again within the cells. Mayer, Rathery and Schæffer (1914) suggested that mitochondria possibly supply phospholipid which serves as an intermediate stage in resynthesis, while Cramer and Ludford (1925) show that the golgi apparatus may be the cell structure mainly concerned, and that mitochondria do not appear to take an active part in the process of fat absorption. Sinclair (1929), adopting a chemical point of view, finds that during the absorption of fat there is a pronounced change in the composition but no change in the amount of phospholipid fatty-acids of the intestinal mucosa and of the liver. He suggests that absorbed fatty-acids are transformed into phospholipids in the cells of the intestinal mucosa, as an essential step in the resynthesis of fat.

BRIEF STATEMENT ON THE TECHNIQUE OF FAT STAINING.

Albrecht applied the term "liposome" to small refractive droplets observed in freshly mounted sections of liver and other tissues. These droplets appear more numerous and more sharply defined if the sections are cleared in potassium hydroxide solution before mounting. But they are not proven to be entirely lipoid in character, and Bell (1910) uses the term in a more restricted sense to denote such of these drops as may also be stained with Herxheimer's Scarlet Red (2·0 gm. NaOH added to 100 c.c. of 70 per cent alcohol with subsequent addition of Scarlet Red to saturation). Osmic acid and simple alcoholic solutions of Scarlet Red and Sudan will stain many of the liposomes but do not invariably give positive results. Altmann (1894) demonstrated the reduction of osmic acid by oleic acid and triolein and showed that no reduction takes place with tripalmitin, tristearin or their acids. Starke (1895) and others, maintain that osmic acid will blacken all fat if sections are kept for some time in alcohol after the osmic treatment. He concluded that palmitin and stearin do reduce osmic acid, and Handwerck (1898) agreed with him, but maintained that at least a trace of olein was essential if reduction was to occur. Heidenhain (1907) rejected the osmic-alcohol treatment, which blackens bodies that are not true fat and does not affect others which undoubtedly are fat. Mann showed that osmic acid may be reduced and hydrated by alcohol into $OS(OH_4)$ and rejected the osmic-alcohol treatment. Bell (1910) found that "on the whole osmic acid is a useful reagent for the study of liposomes. It often gives a brown colour to droplets not stained at all by the simple alcoholic solutions of Scarlet Red and Sudan." Gatenby (1919) holds that the blackening effect of osmic acid can take place in the presence of a chrome compound, e.g. chromic acid, and that fresh palmitin and stearin are blackened by osmic acid after treatment with formalin. In the *Microtomists' Vade-Mecum* (1928) we are told that "the true fats and the lipoids are all blackened by osmic acid," and that the various groups differ in the readiness with which they are blackened as well as in the depth of blackening produced. True fats blacken most readily and deeply, while substances such as cholesterol are not readily blackened. Treatment with bichromate solutions accentuates these properties and prevents substances showing only weak reducing powers from reducing osmic acid, so that after such treatment only true fats and fatty-acid, cholesterin mixtures are blackened. In order to examine lipoids, Ciaccio fixed tissues in a formalin-bichromate acetic mixture which he believed fixes lecithin so that it is not removed by the ordinary fat solvents. Bell maintained that it is not proven that the droplets so preserved consist of lecithin. Ciaccio (1921) preserved fatty acids of the saturated series by fixing small pieces of tissue in a saturated solution of zinc acetate, staining sections with Sudan or Scarlet Red.

MATERIAL AND METHODS.

The fish used in the following experiments were trawled in Cawsand Bay or in the nearby vicinity by s.s. *Salpa* of the Marine Biological Association. As soon as possible after trawling they were placed under circulation and later transferred to fish-boxes in the pond at Pier Cellars, boxes such as are at present being used in connection with work on Growth and Maintenance in the Plaice, and were allowed to become settled. Individuals showing signs of any ill-effect due to trawling were removed at once and the remainder were fed regularly on a diet of *Mytilus edulis* fragments. All the fish used took food avidly and were apparently perfectly sound, and the physical conditions under which they were kept approximated closely to the natural ones, the fish living in boxes in the sea.

Primarily, a number of fish were fasted for several days, after which they were killed by a blow on the head which pithed the brain and the tissues of various regions of the alimentary tract were appropriately fixed to serve as controls. Other fishes were fasted for two or three days, fed in various ways and killed the requisite number of hours afterwards in order to preserve tissues in various stages of absorption. Several lines of treatment were adopted. In some cases, a single meal of Mytilus or Nereis was supplied, the time at which food was taken being noted. In other cases, a second meal of similar food was given at various times after the first, but usually about twenty-four hours later. Because of the great avidity shown by the fish for food, the stomach was invariably filled during a few minutes following the presentation of food, while the fish were still under observation. Thus the times could be recorded with great accuracy. Several fishes were given olive oil or olive oil emulsion meals by injection through the mouth both during the "empty" condition of the gut and also following upon a meal. And, finally, a number of fishes were fed for several consecutive days upon Mytilus fragments liberally mixed with olive oil. Freshly trawled fish were used in several instances.

Several methods of fixation were employed. Initially frozen sections were prepared of material fixed in 10% formalin, which sections were stained with Sudan or osmic acid. But this method was discontinued in favour of more applicable ones. Some material was fixed in equal parts of Müller's fluid and 1% osmic acid, but only in a few instances could this method be regarded as successful. Comparison was afforded with tissues fixed by Kolatschev's slightly modified Champy fluid, and this latter fixative was largely used subsequently with great success. Tissues were kept for 24 hours in fluid consisting of 4 parts of 1% chromic acid, 4 parts of 3% potassium dichromate, and 2 parts of 2% osmic acid. They were washed for several hours in running water and treated for 3 days with 1% osmic acid. Sections were mounted in xylol balsam, Apathy's gum syrup and glycerine, those in balsam lasting well.

Materials corresponding to those fixed in Champy fluid were also fixed by Ciaccio's method (Schmorl, 1925) in a mixture consisting of 80 c.c. of 5% potassium bichromate, 20 c.c. of formaldehyde, and 5 c.c. of glacial acetic acid. This was followed by treatment for 5–8 days in a 3% solution of potassium dichromate, after which the tissues were washed for 24 hours in running water and passed through alcohols and xylol to wax in the usual manner. This technique is claimed to preserve lipoids, although true fats are removed in the alcohols and xylol. A potent solution of Sudan was obtained by dissolving the dye in boiling 85% alcohol, as Fischer suggested for fats. To 95 c.c. of this solution, 5 c.c. of acetone were added and the stain applied to the sections for an hour or more at a temperature of about 30° C. The sections were then differentiated and counterstained faintly with iron hæmatoxylin. This technique also gave good results. The mounting medium employed was Apathy's gum syrup.

NOTES ON THE MORPHOLOGY AND HISTOLOGY OF THE ALIMENTARY TRACT.

The alimentary tract of the plaice is differentiated into regions, of which the important ones from the point of view of absorption are stomach, duodenum, intestine and rectum. The stomach comprises about $\frac{1}{6}$th of the entire length of the tract and is separated from more posterior regions by the pyloric valve. The post-pyloric intestine, which takes up approximately half the whole length of the tract, is for convenience regarded as consisting of two equally long regions, the duodenum and intestine. Four very small pyloric cæca open into the duodenum immediately posterior to the pylorus. The terminal portion of the tract or rectum is separated from the intestine by a second valve, the intestino-rectal valve.

Histologically, the tract consists of a serosa, outer longitudinal and inner circular muscle bands, an areolar tissue layer and a mucous membrane. The mucous membrane of the stomach is very thick, being formed into numerous simple, or slightly branched, tubular glands consisting of three types of cell, (1) columnar cells forming a superficial epithelium, which is continued into the crypts marking the openings of the glands, (2) cubical, mucus-producing cells, which form the neck of each gland and (3) granular cells which build up the basal portions of the gland tubules. Processes of the areolar tissue layer pass between adjacent gland tubules. In the duodenum, with its pyloric cæca, intestine and rectum, the mucous membrane consists of a simple epithelium of extremely tall and slender columnar cells interspersed with goblet cells. It is gently corrugated into a large number of folds which simulate, but are not, villi. The areolar tissue layer follows the mucosal folds, passing into the tips of even the most slender of these. The degree of mucosal folding is much greater in the pyloric cæca than in other parts of the post-pyloric intestine.

PROTOCOLS.

(1) *Plaice, 20·0 cm. in length, killed 30 hours after taking a single meal of Mytilus fragments. Tissues fixed by modified Champy and Ciaccio methods.*

Stomach.—The superficial epithelium shows a moderately heavy loading with fat, in osmicated material, although some folds are relatively fat free. Fat globules are relatively scarce in the cells of the crypts and altogether absent from the mucus-producing cells forming the necks of the glands (Fig. 1). The cells of the basal portions of the gland tubules each contain several fat globules ranging in numbers from one or two to about ten (Fig. 1). The areolar tissue layer is devoid of fat. In the cells of the superficial epithelium the fat globules are distributed on each side of the nucleus, but are larger and more numerous on the outer aspect of it. The outer $\frac{1}{5}$th part of each cell is devoid of fat (the clear cell margin takes up rather less than half of this). The next deeper $\frac{1}{5}$th part is densely crowded with moderately large globules, below which comes the region of the nucleus, where there are no globules. Smaller globules occur below the nucleus, extending to within $\frac{1}{5}$th part of the depth of the cell from the base (Fig. 2).

In chromed material, fine, Sudan-stained lipoid granules are distributed somewhat similarly to osmicated fat. The outer halves of the cells are crowded but the outer $\frac{1}{8}$th is clear. In some parts of the epithelium, granules occur in groups below the nucleus, but these are not as common as are the fat globules.

Duodenum.—Fine Sudan-stained lipoid granules are crowded in the outer halves of the cells at the tips of the mucosal folds. In osmicated material, corresponding cells show crowds of minute, brown-stained, and in some cases blackened, particles. The cells of the mucosal troughs are blank.

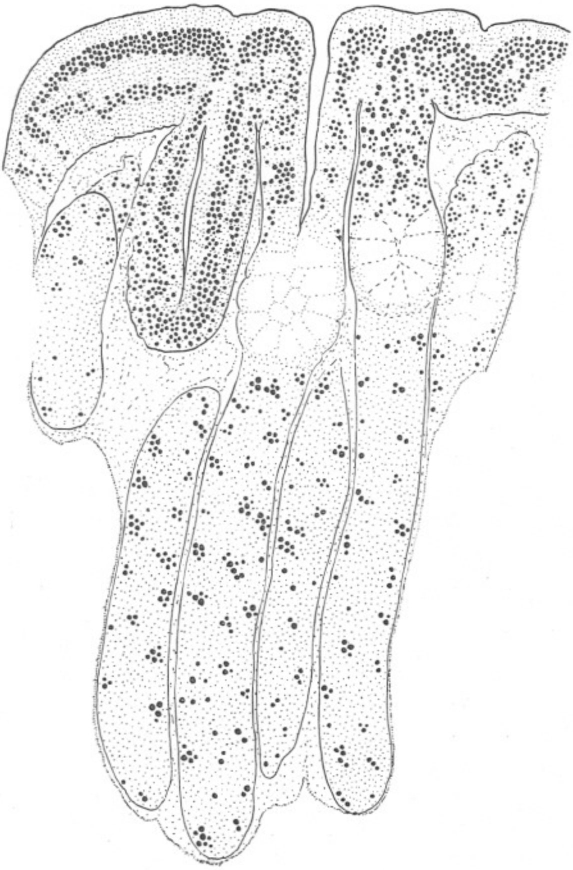

FIG. 1.—Vertical section of the gastric epithelium of the plaice referred to in Protocol (1). Unstained preparation of Nassanow—Champy-Kull material. Showing the loading of the superficial epithelium and the basal cells of the gland tubules with fat, and also the absence of fat from the mucus-producing cells forming the necks of the gland tubules. ×460.

In all other regions of the alimentary tract fat globules are absent.

(2) *Plaice, 17·8 cm. in length, killed 50 hours after taking a single meal of Mytilus fragments. Fixation as before.*

Stomach.—The loading of the superficial epithelium with osmicable fat globules is greater than that after 30 hours' digestion (Protocol 1).

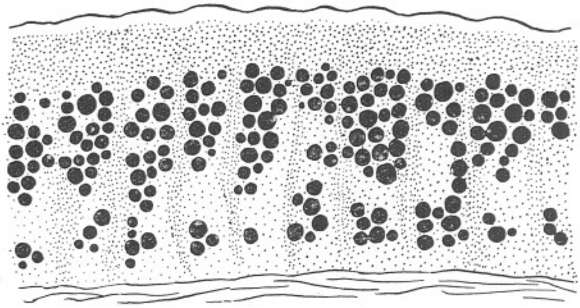

FIG. 2.—Vertical section of the superficial epithelium of the stomach of the fish referred to in Protocol (1). Unstained preparation. Tissue fixed by modified Champy-Kull. The sizes and distribution of the fat globules have been rendered as accurately as possible. ×1300.

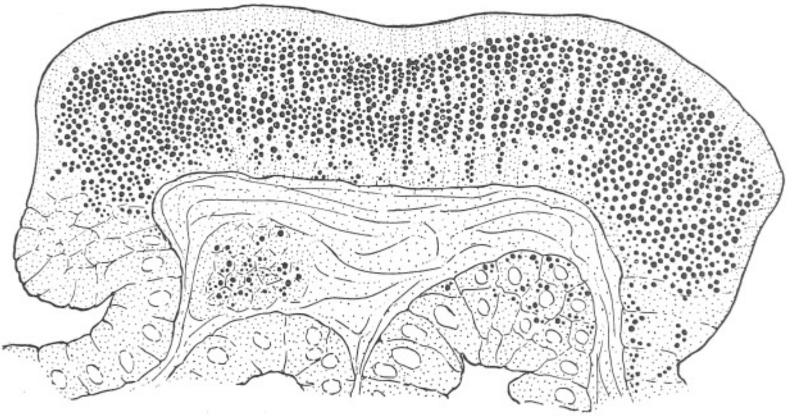

FIG. 3.—Vertical section of the gastric mucosa of the plaice referred to in Protocol (2). Unstained preparation. C.–K. fixation. Showing a heavy loading of the superficial epithelium with fat except in the parts lining the crypts, where fat is relatively sparsely distributed. ×780.

The outer $\frac{1}{6}$th of each cell is clear, while in the body of each cell large droplets are arranged in two or three longitudinal rows lying so close as almost to touch each other (Fig. 3). In some folds, however, there is but little fat, as before. Fat is also relatively scarce in the cells lining the crypts (Fig. 3), whilst in the mucus-producing cells of the neck and the basal cells of the tubules fat is absent. Nor does fat occur in the areolar tissue layer. In the gastric epithelium adjacent to the pyloric sphincter, where gastric glands do not occur, there is a considerable loading with fat droplets, which is not as heavy as in the glandular part of the stomach.

In chromed material, minute Sudan-stained lipoid granules are to be found crowded in the cells of the superficial epithelium. They occur in all parts of the cells but appear to be more numerous and more densely aggregated in the basal parts. They are much smaller than the droplets observed in osmicated material. The mucus-producing cells and basal cells of the tubules do not show such granules, although the latter cells show dense aggregations of greyish stained granules in the half of the cells bordering the gland duct.

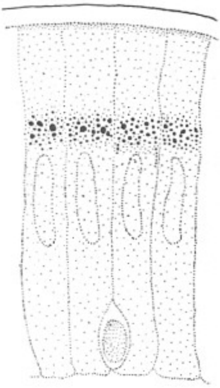

FIG. 4.—Vertical section of the intestinal epithelium of the plaice referred to in Protocol (2). Unstained preparation. C.-K. fixation. Showing the first stage apparent during fat absorption. Small droplets appear about ⅓rd of the depth of the epithelium from the outer boundary. ×1100.

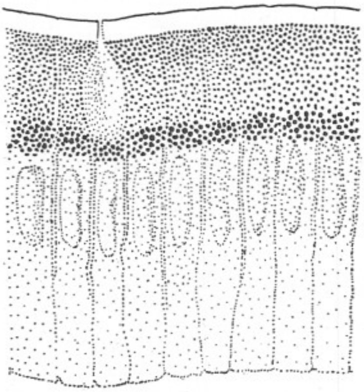

FIG. 5.—Vertical section of the intestinal epithelium of the plaice referred to in Protocol (2). The stage of fat absorption shown is slightly later than that shown in Figure 4. The droplets noted in Figure 4 are here enlarged and brown-stained and smaller droplets occur between these and the clear, cell margin. Unstained preparation. Fixation by C.-K. ×1100.

Pyloric cæca and Duodenum.—In osmicated material, cells near the tips of the mucosal folds show moderately dense clusters of extremely minute granules few of which are completely blackened. By far the greater part of the mucosa is devoid of fat, but clusters of cells are found to be partly filled with fairly large globules. These clusters occur in both duodenum and cæca but rarely.

Intestine.—Fat droplets are far more numerous than in the duodenal epithelium. They appear in the tips and limbs of almost every fold. In most folds they occur as extremely minute blackened bodies occupying a fixed position within the cells about ⅓rd of the depth of the cells from the clear margin (Fig. 4), so that under low powers of the microscope a thin, dark line follows the folds of the epithelium. But in some folds or portions of folds, larger droplets occupy this fixed position, the cytoplasm between these and the clear cell margin being densely crowded with smaller droplets (Fig. 5). In a few cells, small globules have been formed.

Minute, Sudan-stained granules are abundant in Ciaccio fixed material. These completely fill the outer halves of the epithelial cells, extending close up to the clear cell borders (Fig. 6). Undoubtedly, many of these granules appear brownish in colour in Champy fixed material. But there is no size differentiation in any parts of the epithelial folds and the granules are more numerous than the osmicated droplets.

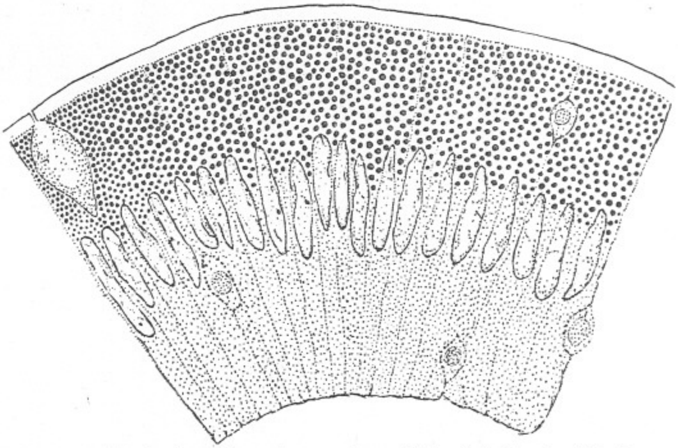

Fig. 6.—Vertical section of a portion of the intestinal epithelium of the plaice referred to in Protocol (2). From the limb of a mucosal fold. Fixation of tissue by modified Ciaccio. Stained with Sudan and iron hæmatoxylin. Showing the outer halves of the cells crowded with lipoid granules. × 1100.

(3) *Plaice, 24·4 cm. in length ; given a mussel meal, interval of 26¾ hours, given a second mussel meal and killed 19 hours later. Fixation as before.*

Stomach.—There is little or no osmicated fat in the superficial epithelium, except in the region of the pyloric sphincter, where the cells contain numerous small globules chiefly occupying a basal position.

In Ciaccio fixed material there are no Sudan-stained lipoid granules.

Duodenum and Pyloric cœca.—The epithelial cells are very heavily loaded with osmicated fat, especially in the tips and limbs of the mucosal folds, where the outer halves of the cells are rendered almost opaque with fairly large globules (Fig. 7). The inner halves of the cells contain fewer and smaller globules although much fat is present. In the heavily loaded cells only the thin, clear cell margins are without globules. Stretches of epithelium, forming the limbs or troughs of the mucosal folds, do not contain fat, so that a single fold may carry much fat and yet possess cells without it. (Fig. 7 shows how the fat content of adjacent cells varies.) In the areolar tissue layer very small clusters of extremely minute droplets occur here and there, but generally, the layer does not contain osmicated fat.

In Ciaccio fixed material, minute, Sudan-stained lipoid granules occur in all parts of the mucosa, i.e. in the tips, limbs and troughs of the folds. The granules are very numerous, crowding the outer halves of the cells. In some cases the outer $\frac{1}{5}$th part of the cell is relatively clear of granules, but generally the granules extend close up to the clear cell border. In the troughs of the mucosal folds granules occur in a basal position within the cells also, where they are slightly larger. Large masses of granules also occur in the areolar tissue layer (c.p. with absence of osmicated fat).

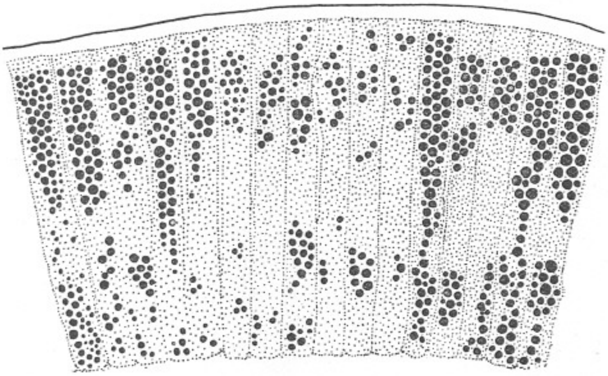

FIG. 7.—Vertical section of a portion of the duodenal epithelium of the plaice to which reference is made in Protocol (3). From the limb of a mucosal fold. Unstained preparation. Fixation by C.-K. Showing how the fat loading varies in different cells lying close together. The maximum load shown here is not the heaviest seen in this epithelium. × 1000.

Intestine.—The loading of the epithelium with osmicated fat is similar to but not as heavy as that in the duodenum. Smaller globules occur in the outer halves of the cells while the inner halves are clearer. The areolar tissue layer is devoid of osmicated fat.

Sudan-stained lipoid granules are just as abundant as in the duodenum, especially in the tips of the folds. But few granules occur in the areolar tissue layer.

Rectum.—Small fat droplets and globules occur in osmicated material but rarely. There is little absorption. Similarly in Ciaccio fixed material, a few Sudan-stained granules occur in some cells, but the vast majority of cells are devoid of them.

Liver.—Much osmicated fat is present in the liver cells, the globules being of all sizes from very large to minute. But there are no lipoid granules present.

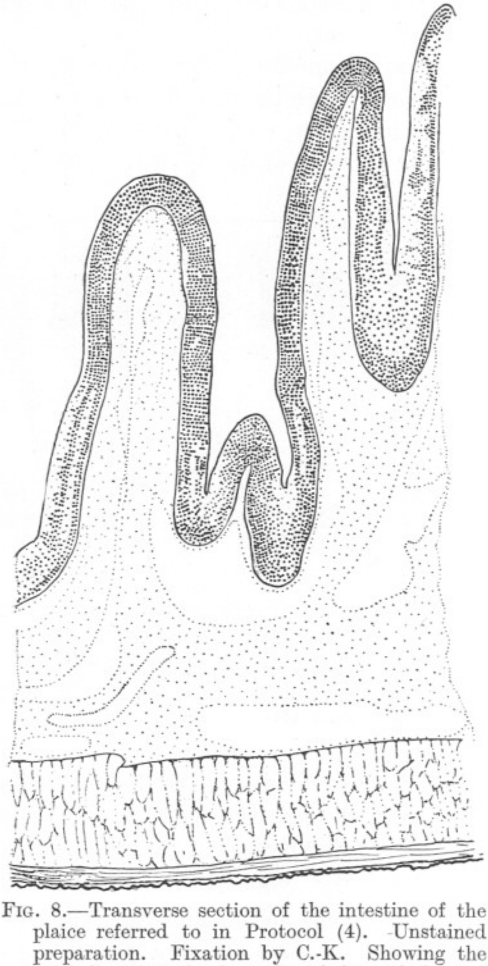

FIG. 8.—Transverse section of the intestine of the plaice referred to in Protocol (4). Unstained preparation. Fixation by C.-K. Showing the epithelium heavily charged with fat and also the fat-free areolar tissue layer. × 90.

(4) *Plaice, 23·3 cm. in length ; given a mussel meal, interval of 48 hours, given an injection of olive oil emulsion (pH=8·3) through the mouth and killed $50\frac{1}{4}$ hours later. Fixation as before.*

Stomach.—Practically no absorption of fat or lipoids has taken place. Small osmicated globules and Sudan-stained granules occur but very rarely.

Duodenum and Pyloric cæca.—In osmicated material, the cells of the tips of the mucosal folds show a fairly heavy loading with fat globules. In the cells forming the limbs of the folds fat is not as abundant, the globules being confined chiefly to the central zones of the cells. Some folds are relatively free from fat. Fat is absent from the areolar tissue layer.

In Ciaccio-fixed material, there are no Sudan-stained, lipoid granules. These are absent from the epithelial and areolar tissue layers.

Intestine.—The epithelium is very heavily loaded with osmicated fat in all parts of the mucosa, i.e. in the tips, limbs and troughs of the folds (Fig. 8). The tips of the folds contain most fat, large globules completely filling the cells from the clear, outer hems to the basal parts. Near the bases of the cells the globules become smaller (Fig. 9). There is not a trace of osmicated fat in the areolar tissue layer (Fig. 8).

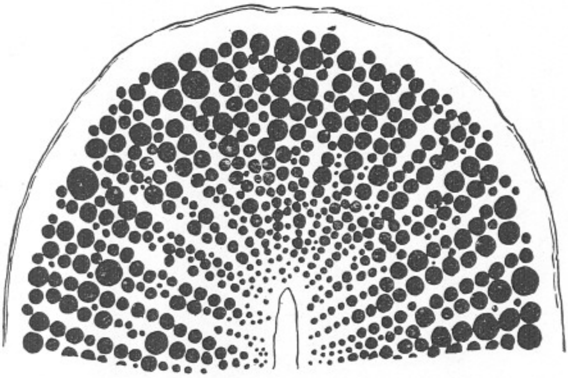

FIG. 9.—Vertical section of the epithelium forming the tip of a mucosal fold from the intestine of the plaice referred to in Protocol (4). Unstained preparation. Fixation by C.-K. Showing the maximal loading of the epithelium with fat. The size and distribution of the globules shown has been carefully treated. × 800.

Ciaccio-fixed tissue shows the absence of Sudan-stained lipoid granules from all layers of the tract. In the epithelial cells, the vacuoles left after the removal of true fats by alcohols and xylol following the chroming treatment, are most conspicuous (Fig. 10). There is no trace of granules in the areolar tissue layer.

Rectum.—Neither osmicated fat globules nor Sudan-stained lipoid granules occur in any part of the epithelial or areolar tissue layers.

(5) *Plaice, 29·0 cm. in length; killed after fasting for 6 days. Fixation by Kolatschev's modified Champy method.*

Stomach.—Osmicated fat globules occur in all parts of the superficial epithelium. In the parts lining the crypts of the gastric glands, the globules are few in number and localised in the basal portions of the cells (Fig. 11), while in the parts between adjacent crypts they occur also to some extent in the outer halves of the cells. The globules are generally much smaller than those occurring during fat absorption.

Occasionally a few minute globules occur in the mucus-producing cells forming the necks of the gland. But a small cluster of moderately large globules occurs in the basal cells of each tubule, these presenting a constant feature. The numbers vary, some cells possessing only one or two, others six or seven, but every cell appears to contain fat (Fig. 11). There is no trace of fat in the areolar tissue layer.

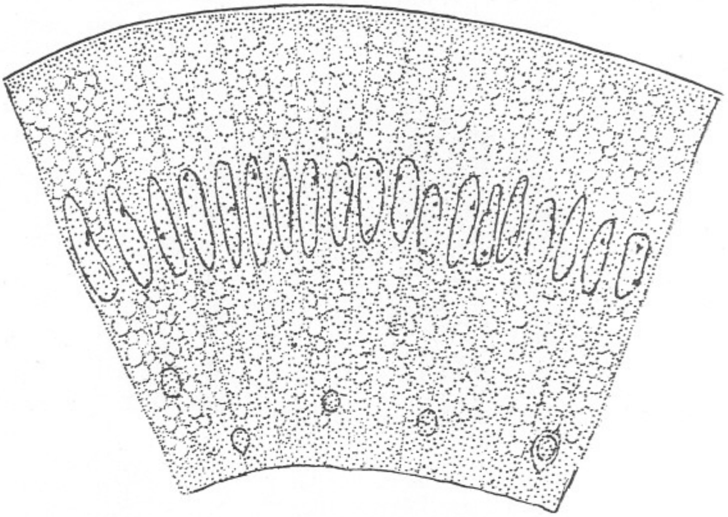

FIG. 10.—Vertical section of the intestinal epithelium of the plaice referred to in Protocol (4). Fixation by modified Ciaccio. Staining with Sudan and iron hæmatoxylin. Showing the absence of lipoid granules and the vacuoles left in the cytoplasm of the cells after removal of fats by the solvents employed in this technique. × 1300.

All the fat described above is capable of extraction if sections are left overnight in turpentine.

The epithelial and areolar tissue layers of more posterior parts of the alimentary tract, i.e. of the duodenum and pyloric cæca, intestine and rectum, are free from fat and provide perfect blanks.

(6) *Plaice, 28·5 cm. in length ; killed after fasting for 6 days. Fixation as before.*

Stomach.—Fat is present in the superficial epithelium, its distribution closely following that of the fat observed in the corresponding cells in the

29·0 cm. plaice described in Protocol (5). The neck-cells are similarly without fat, which is also absent from most of the deeper glandular cells. There is no fat in the areolar tissue layer.

Perfect blanks are obtained from all post-pyloric regions of the tract in every layer.

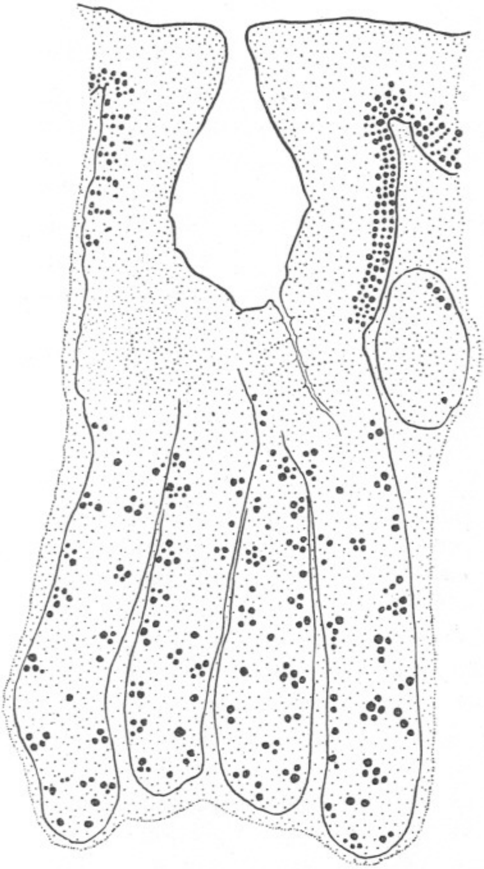

FIG. 11.—Vertical section of the gastric epithelium of the plaice referred to in Protocol (5). Unstained preparation. Fixation by C.-K. Showing the distribution of fat globules in the superficial epithelium, and the basal cells of the gland tubules and the absence of fat from the mucus-producing cells forming the necks of the tubules. × 500.

(7) *Plaice, 28·4 cm. in length ; killed after fasting for 7 days. Fixation as before.*

Stomach.—There is no osmicated fat in the cells of the superficial epithelium. The mucus-producing cells of the neck of the glands similarly are without fat. But the basal cells of the gland tubules show fat globules as seen in the 28·5 cm. plaice of Protocol (6). The areolar tissue layer is without fat.

Note.—In a fish (32·5 cm.) killed after fasting for 6 days, Sudan-stained lipoid granules were absent from all regions of the alimentary tract.

Absorption of Fats and Lipoids in the Stomach.

The stomach of a plaice which has been fasted for six or seven days is usually collapsed and contains a small quantity of clear fluid apparently rich in mucin. Fat is to be found in the epithelial layer of all parts of the organ after such a fast. It occurs in the form of small globules localised chiefly in a basal position within the cells (in the epithelium lining the crypts) (Fig. 11), but also in the outer halves of certain cells (in the epithelium between adjacent crypts). The mucus-producing cells may contain each a few minute fat droplets but may be altogether without fat (Fig. 11). The basal cells of the tubules contain fat in variable quantities at the end of such a fasting period. In some cases every cell appears to contain a number of large globules, in others many cells may be without even droplets (Fig. 11). Fat does not occur in the areolar tissue layer.

In fish killed 30 hours after taking a single meal of Mytilus fragments, following on a period of fasting, the superficial epithelium shows an increased loading with fat globules. Only the outer $\frac{1}{5}$th part of each cell is consistently free from fat (Fig. 1). Below this zone fairly large globules are densely aggregated outside the nuclear zone, and rather smaller globules inside the nuclear zone extend to within $\frac{1}{5}$th of the depth of the cell from the base. The superficial epithelium lining the crypts of the glands shows a relatively lighter loading with fat, although more is present than after a period of fasting (c.p. Figs. 1 and 11). Fat is completely absent from the mucus-producing cells forming the necks of the tubules (Fig. 1), but globules occur in the basal cells of the tubules. After 50 hours of gastric digestion and absorption of Mytilus fragments, the loading of the superficial epithelium with fat is further increased (c.p. Figs. 3 and 1). The clear, outer zone is narrower and fat globules are so densely crowded into the outer halves of the cells as in many cases to render these parts solidly black in appearance under low powers of the microscope. Two or three longitudinal rows of globules are contained within a single cell, these rows extending closer to the basal margin of the epithelium than hitherto (c.p. Figs. 1 and 3). But there has been no passage of fat into the mucus-producing cells of the glands nor is there any sign of fat in the basal cells of the tubules. It is not possible to trace the fate of the fat observed in these latter cells after a fast and during the earlier stages of digestion. It does not reappear while active digestion is taking place, so that it may be a metabolite during the process of digestion. The areolar tissue layer is devoid of fat droplets, so that if fatty elements are passed through this layer into the blood-stream, either there is no resynthesis of the elements or the resynthesised fat globules are so small as to be incapable of resolution under the highest powers of the microscope. After a single mussel meal then, the stomach is capable of fat absorption, the superficial epithelium being the most important element of the mucosa thus concerned.

In both cases of digestion and absorption of Mytilus fragments noted above, lipoid granules show a distribution similar to that of true fat globules. The granules are smaller in size, and although present in larger numbers they do not form the same bulk as the fat globules.

After the digestion of two mussel meals there is hardly a trace of fat in the superficial epithelium of the stomach, although considerable absorption has taken place in post-pyloric regions of the alimentary tract as shown by tissues subjected to precisely the same details of technique. In a fish 18·7 cm. long (not included in the protocols), which was supplied with six consecutive meals of Mytilus fragments liberally mixed with olive oil at 24-hour intervals and was killed 48 hours after the last meal, there was a loading of the superficial epithelium with fat globules yet not as heavy a loading as was obtained in the other fish killed about 50 hours after a single mussel meal. The probable significance of these findings is discussed briefly in the next part of this paper.

ABSORPTION IN THE DUODENUM, PYLORIC CÆCA, INTESTINE AND RECTUM.

During a period of fasting, various changes occur in the condition of the alimentary tract of the plaice. Usually, as has been mentioned, the stomach is collapsed and empty or almost empty of fluid, but it may be filled to distention with clear fluid. The condition of the post-pyloric part of the alimentary tract also changes during such a period. The duodenum, which is the anterior half of that portion of the tract included between the pyloric and intestino-rectal valves, is usually moderately distended with clear, watery fluid but may be greatly distended or, on the other hand, contracted and empty. This also holds for the intestine and rectum. There appears to be some correlation between the conditions of the tract in the various regions, for when the duodenum is collapsed, the intestine is usually greatly distended, when the intestine is collapsed and empty, the rectum is full to distention. The changes from region to region at different times are similar to those occurring during the active digestion of food, the same peristaltic activity of the walls of the tract being in evidence. The rectum assumes insignificant proportions when collapsed, but its walls are capable of greater distention than obtains in any part of the intestine anterior to the rectum. It holds a considerable volume of fluid at certain times, but whether the bulk of this fluid is removed by absorption or by way of the anus has not been determined, although it is shown that the rectal epithelium can absorb fats to some slight extent.

In fish supplied with a single meal following upon a period of fasting, changes similar to those mentioned above are observed. For a number of hours after the meal is taken, the stomach is greatly distended with food, while the more posterior regions are either distended with clear, colourless fluid or are collapsed and almost empty of fluid. In a number of experiments on the rate of digestion, the results of which are as yet unpublished, it was found that, at summer temperatures such as obtained when the observations on fat absorption were made, and when *Mytilus edulis* is the food supplied, the fluid in the duodenum is clear in fish killed 15 hours (16·7 cm.) and 16 hours (14·7 cm.) after taking a single meal. But in fish killed 18¼ hours (20·1 cm.) and 18⅓ hours (15·8 cm.) after taking a single meal, the fluid in this part of the tract is yellowish in colour and contains shreds of finely divided solid food, which are seen to be in the act of passing through the pylorus. Thus the first slight relaxation of the sphincter takes place at from 16 to 18¼ hours after taking a single meal. Such times as have been noted are likely to vary with variations in temperature, but with this we have no concern at present. It is interesting to note, however, that when Nereis is supplied as food but other conditions identical, the times were different. After 22½ hours (19·0 cm.) the stomach is greatly distended and the duodenal fluid clear, but after 24 hours (21·5 cm.) the duodenum contains brownish fluid but no solid, the stomach being greatly distended. With Nereid worm as food, therefore, the sphincter is not relaxed until almost 24 hours have elapsed since the taking of food. The results given above are taken from a much larger mass of data.

Then it was found that the stomach of the plaice retains food for a period of from 40 to 48 hours after the time of taking food. At the first relaxation of the sphincter and for a number of hours afterwards, only fluid and finely-divided solid particles, forming some at least of the products of the gastric digestion of Mytilus or Nereis fragments, are allowed to pass through into the duodenum, the relaxation being incomplete. Total relaxation of the sphincter occurs at summer temperatures at 40–48 hours after the taking of food, when large and relatively undigested fragments of food are passed into the duodenum.

The time taken for food to pass along the duodenum into the intestine is probably short, but no doubt considerable variations occur ; 18½ hours after taking a mussel meal a plaice shows duodenal contents of a straw colour containing shreds of finely divided solid matter, while clear, colourless fluid fills the intestine (20·1 cm.) ; 19¼ hours after a meal is taken, the intestinal contents are coloured like those of the duodenum (19·4 cm.). In fishes killed 21, 21½, and 27 hours after taking a mussel meal, the intestine was full of brown fluid containing shreds of solid, while in fishes killed 27¾ and 30 hours respectively after taking food, the anterior part of the intestine was considerably distended with brown fluid, the posterior part being contracted and empty. Only fish originally filling the stomach with food were considered in any of the cases mentioned above. In view of these results, it appears that absorption in the intestine commences within an hour or two, or at most a few hours, of duodenal absorption, and long before the stomach is completely emptied of the solid food remaining from the single meal.

Food appears to stay in the duodenum and intestine for a variable period. In all fish killed 30 or fewer hours after taking a meal only clear fluid was contained in the rectum. In a fish (14·4 cm.) killed 38½ hours after taking a meal intestine and rectum alike contained brown fluid and finely divided solid. In almost every fish killed after a longer period of digestion the rectum contained fluid coloured with mussel food. In a 16·9 cm. fish killed 39¾ hours after taking a meal, the intestine was contracted and empty, its walls appearing yellow and opaque, while the rectum was distended with brown fluid and finely divided solid. It is seen then that partly digested food remains in the duodenum and intestine for more than 20 hours and that a part of the food of the single meal is passed into the rectum as fluid or finely divided solid before complete relaxation of the pyloric sphincter occurs, i.e. whilst solid food remains in the stomach. The time taken for complete removal of a single meal is not easy to determine. Only finely divided mussel fragments were observed in the posterior part of the tract towards the end of the meal. After 54 hours food particles and brown fluid still remain, but after 60 hours only clear fluid remains in every part of the tract.

Summarising these results for a single mussel meal and taking times from the moment the stomach is filled with food, the following approximations are obtained :—

1. Partial relaxation of pyloric sphincter after from 16–18 hours.
2. Finely divided solid and fluid food reaches intestine after 19 hours.
3. Food particles first reach rectum after 38 hours.
4. Complete relaxation of pyloric sphincter after from 40–48 hours.
5. Alimentary tract finally cleared of food after from 54–60 hours.

TABLE I.

Passage of Food through Alimentary Tract of Plaice: 2 Meals of Mytilus Fragments.

Length of fish (cm.).	Time after 1st meal (hours).	Time after 2nd meal (hours).	Food in Stomach (gm.).		Food in Duodenum and Intestine.		
			From 1st meal.	From 2nd meal (carmined).	Nature of food.	Weight of solid (gm.).	Nature of rectal contents.
27·0	28	1¼	3	7	Br.F. & F.D.S.	–	Br.F. & F.D.S.
23·1	29¾	3	3	4·5	Br.F., F.D.S. & S.	2	Br.F.
23·4	31½	5¼	7	2·5	Br.F. & F.D.S.	–	C.F.
24·4	45¾	19	Nil	5	Br.F., F.D.S. & S.	4	C.F. (1·5 gm. S. passing in)
22·3	49¼	22½	Nil	3	Br.F., F.D.S. & S.	3	C.F. & F.D.S. passing in.

Br.F. = Brown fluid. F.D.S. = Finely divided solid. S. = Solid. C.F. = Clear fluid.

A few experiments were carried out to show what changes, if any, occur in the rate of passage of food through the alimentary tract when 2 meals are supplied on consecutive days, following a period of fasting. The series is incomplete, but the results are sufficiently conclusive to merit their being presented in the accompanying table. The food was supplied in the form of pieces of mussel weighing about 0·2 gm., the pieces forming the second meal being covered with carmine particles. Although a cloud of carmine particles pass out through the gills when the fish swallows the food, yet in every case it was possible to distinguish the second meal from the first in the gastric contents. In all these instances presented, the pylorus had been partially relaxed presumably before the second meal was presented, so that the finely divided solid and brown fluid found in the duodenum and intestine in each case is to be expected. Also, since with a single meal the pyloric sphincter is completely relaxed after 40–48 hours, it is partly anticipated that none of the particles forming the first meal in the last two instances will remain in the stomach. But differences are seen in the rate of progress of the first meal along the tract. It is seen that after 29¾ hours much of the first meal has passed into the duodenum as large particles of solid. And in two instances food has passed into the rectum after 28 hours, while in another, solid food is passing into the rectum after 45¾ hours. These results although incomplete suggest that food from a meal passes along the tract more rapidly if a second meal is taken. If completely established the point would be of great significance, since it would be implied that the more frequently the fish takes food, the less efficient it becomes, or more precisely, a fish feeding once per day is less efficient than one taking food on alternate days or less frequently, assuming that digestion of large food particles is also a measure of absorption.

It is evident from the above results that if a fish is killed 30 hours after taking a meal of Mytilus fragments, following upon a period of fasting, partly digested food materials have been present in the duodenum, in fluid and finely divided solid condition, for approximately 12 hours, and in the intestine for an hour or two, or at most several hours less than 12. These conditions hold then for the fish to which reference is made in Protocol (1). In this fish it was seen that only the epithelial cells forming the tips of the mucosal folds have undertaken the absorption of fats and lipoids. These cells show lipoid granules and minute brown-stained osmicated particles crowded into their outer halves. There are no granules or fat particles in the cells of the limbs and troughs of the mucosal folds, so that absorption apparently commences in the parts of the mucosa which are likely to project furthest into the lumen of the distended gut.

In a fish killed 50 hours after taking a mussel meal, the duodenum and intestine must have contained food materials, which may or may not have been partly digested in the stomach, in the form of fluid and finely divided solid particles for about 30 hours. In addition, food remaining in bulk after complete gastric digestion has taken place was passed into the duodenum a number of hours (less than 10) previously. These conditions hold then for the fish to which reference is made in Protocol (2). In the duodenum of this fish, fairly dense aggregations of minute fat droplets occur in the cells of the tips of the mucosal folds and groups of cells contain clusters of fairly large globules. In the intestine, what is probably the earliest histologically demonstrable stage in true fat absorption is seen. Extremely minute osmicated droplets occur in a constant position within the cells at about $\frac{1}{3}$rd of the depth from the clear, outer boundary (Fig. 4). But in corresponding material the whole of the outer halves of the cells from the clear margin to the nuclear zone is crowded with minute lipoid granules (Fig. 6), which are thus more numerous than true fat droplets and also have a wider distribution.

In the case of the fish referred to in Protocol (3), the stomach was distended with carmined Mytilus fragments of the second meal (about 5 gm.). The duodenum was distended with brown fluid and fine solid, but also contained about 4 gm. of coarser solid. The posterior part was contracted but the intestine was distended, as if food was in the act of passing backwards, which view was supported by the fact that solid particles were passing through the intestino-rectal valve into the clear rectal fluid. The walls of the anterior half of the intestine and the whole duodenum appeared yellow and opaque. Food could not have been in contact with the epithelium of the duodenum and intestine for as long a period as with that of corresponding regions of the fish referred to in Protocol (2), since the times from the taking of the initial meal were

$45\frac{3}{4}$ hours and 50 hours respectively. But more material had been available for duodenal and intestinal absorption, since a portion of the second meal had been passed over. Accordingly an increased degree of absorption might reasonably be anticipated, but not more than twice the amount seen after a single meal. It is to be noted that the mussel samples used in these meals were kept as constant as possible, and that several pieces of tissue from different parts of the same organ were fixed at one and the same time. Comparisons of the data presented briefly in Protocols (2) and (3) show conclusively that the increase in absorption in the post-pyloric part of the tract is very great when two meals are supplied, much more than twice as great.

After two meals, the cells of the tips and limbs of the mucosal folds of the duodenum and intestine, and especially the former, are very heavily loaded with fat globules, so that the outer halves of the cells forming these parts of the folds are rendered solidly black. Only the clear cell margins are devoid of globules. So heavy is the loading that it is not possible to show the detail in a text-figure. The tissue shown in Figure 7 was from a part of the epithelium showing relatively little fat, and was selected to show how cells vary in their fat content. In the case of lipoid granules, there is no considerable increase in numbers within the epithelial layer, but masses of granules occur in the areolar tissue layer, showing that increased absorption of lipoids has ensued.

When it is remembered that after two mussel meals there was little fat and lipoid material in the gastric epithelium, an explanation is afforded for the increased absorption of these materials in the duodenum and intestine. The marked decrease in gastric absorption and equally well-marked increase in intestinal absorption strongly suggest that the absorptive function is largely transferred from the stomach to the duodenum and intestine when two meals are taken in quick succession, and that the stomach plays a greater part as an organ of absorption when rations are restricted, the post-pyloric intestine assuming the rôle of principal agent of absorption when food is abundant.

The quantity of fat in Mytilus flesh is not very great. According to the most recent analyses (Daniel and Doran (1926)), the fat in the wet flesh of *Mytilus edulis* ranges from 2·0 per cent before spawning to 0·5 per cent immediately after spawning. The wet flesh also contains cholesterol and probably highly unsaturated fatty acids.

According to Bolles-Lee, not only fats but also cholesterin-fatty acid mixtures are affected by osmic acid following upon treatment with bichromate. Cholesterin alone is unaffected. It appears, therefore, that the droplets browned and blackened by osmic acid during Champy fixation of tissues taken from fish which have digested mussel fragments, are either true fat or cholesterin-fatty acid mixtures. In materials fixed by the Ciaccio method used, some of the Sudan-stained granules are undoubtedly those affecting osmic acid also. It may be that these common elements are cholesterin-fatty acid mixtures. It is assumed, out of a consideration of the chemical composition of the food, that Sudan-stained granules not evident in osmicated preparations are granules of cholesterol.

As has already been mentioned, various true fat meals were supplied to certain fish. The fish to which reference is made in Protocol (4) was given an injection of olive oil emulsion prepared by adding phenol phthalein to olive oil and titrating with standard soda to a faint pink ($pH=8{\cdot}3$). The alimentary tract had not contained food for two days previously and two days elapsed further before the fish was killed. Thus the absorption of pure oleic fat is being considered. The intestinal epithelium is very heavily loaded with fat in all parts, i.e. in the tips, limbs and troughs of the mucosal folds (Fig. 8). The loading is more consistently heavy than is that in any part of the post-pyloric intestine after two mussel meals. The cells are crowded with osmicated globules of all sizes, those of the mucosal tips being especially densely crowded (Fig. 9). It appears from the evidences afforded, that although there is no histological differentiation in any parts of the post-pyloric epithelia, yet the tips of the mucosal folds play a greater part in fat absorption than do other parts, since absorption commences here and is also more intense.

Lipoid granules are completely absent from all parts of the tract in any region (Fig. 10). It was inferred above that the technique employed favours cholesterin and cholesterin-fatty acid mixtures in Mytilus-fed fish. But it probably affects other lipoids also. The absence of lipoid granules has a special significance. Recently (1929), Sinclair investigated the rôle of phospholipids in fat absorption in mammals, from the chemical point of view. Upon evidence he collected he put forward the hypothesis that, "within the epithelial cells of the intestinal mucosa there is a 'specific' phospholipid which occupies an intermediary position between fatty acids and neutral fat, as represented by the equation :

$$\text{Fatty acids} \underset{\dashleftarrow}{\longrightarrow} \text{Phospholipid} \underset{\dashleftarrow}{\longrightarrow} \text{Neutral fat.}$$

It is an invariable characteristic of this process that the *amount* of phospholipid remains constant. As soon as fatty acids are absorbed into the epithelial cells molecules of the 'specific' phospholipid react with the free fatty acids (or soaps) to form neutral fat ; immediately, however, the phosphoric acid-base complex unites with absorbed fatty acids and glycerol to form phospholipid, thereby maintaining the amount constant." The synthesised molecules of neutral fat coalesce to form droplets.

It follows from the above that phospholipid material should be present in cells fixed during active absorption of fats at any time, if only in a form not capable of resolution under the microscope, and especially in cells which have not taken up and resynthesised the cleavage products of fats. In the latter cells it is not unreasonable to anticipate the presence of phospholipid bodies of resolvable size. But in the cells of the intestinal and duodenal epithelium (and also the gastric epithelium) granules such as are preserved with the lipoid technique used are completely absent. It may be that the technique does not favour the "specific" phospholipid, or that the groups of molecules are too small to be visible under the highest powers of the microscope; but in any case, it is not possible to present evidence which supports this hypothesis.

In the duodenum of the emulsion-fed fish, the epithelial cells show relatively less fat than those of the intestine. Fat droplets and globules present in the tips and limbs of the folds are localised in the nuclear zone of the cells, the outer and basal halves of the cells being clear. This is taken as indicating the final stage in fat absorption, when the cells are becoming relieved of the fat they have taken up and when the cleavage products of fats are no longer being presented to the cells from the materials remaining in the lumen of the alimentary tract. Briefly recapitulating the stages observed in fat absorption in the post-pyloric part of the alimentary tract, we have :—

1. The formation of minute fat droplets in a constant cytoplasmic zone about $\frac{1}{3}$rd of the depth of the cell from the clear cell border (Fig. 4).
2. The formation of minute droplets between the above-mentioned zone and the clear cell border, with contemporary enlargement of the droplets noted in (1) (Fig. 5).
3. The coalescence of minute droplets into globules with which the cells become crowded in all parts, larger globules occurring in the outer halves of the cells (Figs. 7 and 9).
4. The removal of fat in all parts of the cells except the region of the nucleus and the final clearing of the cells.

Only in one or two instances was fat noted in the areolar tissue layer and in these only very few small clusters of extremely minute droplets. From the results thus obtained it is concluded that the cleavage products which pass out of the epithelial layer into the areolar tissue layer are not resynthesised into fats in this layer, unless the process of resynthesis ends with the production of fat droplets so small as to be incapable of resolution under the highest powers of the microscope. Even most minute droplets appear to be absent. It is beyond the scope of this work to suggest that the cleavage products are passed on to the liver as such, but this appears possible. Lipoid granules are commonly seen in the areolar tissue layer after a mussel meal or meals. And in several fishes not mentioned in the Protocols of this paper the liver contains much fat after a meal, but lipoid granules are completely absent. The blood from the digestive organs is conveyed to the liver by the hepatic portal veins directly, so that either there is no storage of these lipoids in the liver or some chemical transformation takes place in this organ.

The rectum is capable of some slight degree of fat and lipoid absorption, but is not a typical organ of absorption. Small clusters of fat globules and lipoid granules are to be found in some of the rectal epithelial cells during digestion and absorption of a meal. But the quantity of these substances present is negligible from the point of view of practical ends attained.

There is no storage of fat in any part of the post-pyloric division of the alimentary tract.

SUMMARY AND CONCLUSIONS.

1. Fat occurs in all three types of cell composing the gastric epithelium at the end of a period of fasting extending over 6 or 7 days, but is completely absent from the mucosa of all post-pyloric regions of the alimentary tract at such a time.

2. There is a marked increase in the fat content of the superficial epithelium of the stomach after 30 hours and 50 hours of gastric digestion, the stomach being thus shown to be an effective organ of fat absorption.

3. Considerable quantities of fat are present in the duodenal and intestinal epithelia after fat-containing meals have been digested. The rectum is capable of some slight absorption, although its capacity in this respect is very much smaller than that of the duodenum or intestine.

4. It is suggested that there is a transference of the function of fat absorption from the stomach to the post-pyloric intestine when the frequency with which meals are taken is increased.

5. Globules of true fat are not typically observed in the areolar tissue layer of the alimentary tract, although lipoid granules may occur in abundance. It is suggested that resynthesis of the cleavage products of fats does not occur in this layer.

6. Data are presented bearing upon the rate of digestion of *Mytilus edulis* and Nereid worm.

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Growth and Maintenance in the Plaice (*Pleuronectes platessa L.*). Part I.

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With 19 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE experiments to be described below were proposed by the Ministry of Agriculture and Fisheries and were carried out under the auspices of the Marine Biological Association, being subject to the direction of Dr. E. J. Allen, F.R.S., and Dr. E. S. Russell. Mr. Harvey, hydrographer to the Association, directed the construction of the sea-water pond and the fish boxes during the early stages of the preliminary work and assisted in organising supplies whenever alterations were made to the apparatus.

The aim of the experiments is to determine the food requirements of the plaice with respect to the maintenance of life apart from growth, and to ascertain what quantity of food is available for purposes of growth after basal requirements are satisfied, in the case of an actively feeding fish during its third season of growth. The work thus affords an indication of the growth-rate of a 2-year old plaice and also the relation existing between the quantity of food taken and growth.

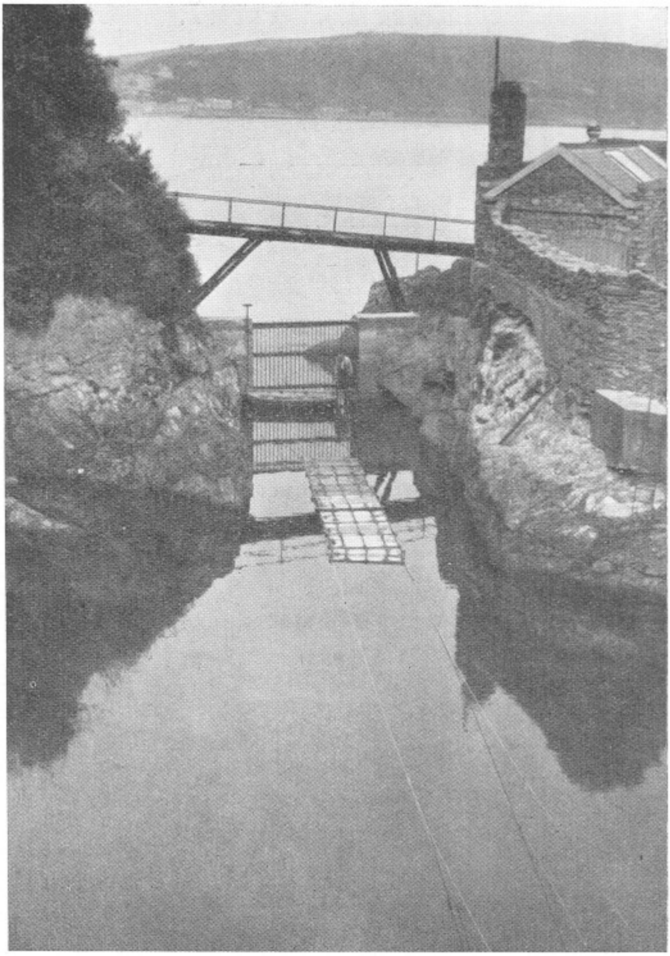

Fig. 1.—View looking out over the sea-water pond at Pier Cellars into Cawsand Bay, showing the constructed sea-wall with its grating. The hawser system is shown and the boxes are seen in situ in the neck of the pond. Only a portion of the pond is shown, but the low-water limits are, roughly, those seen in the picture.

The investigations were carried out at Pier Cellars, which lies on the west shore of Cawsand Bay and thus immediately outside Plymouth

Sound. Here, a rectangular cove some 120 feet by 70 feet opened on its northerly aspect, by a narrow neck roughly 20 feet wide, into Cawsand Bay. During the spring of 1928, when Mr. H. O. Bull was in charge of the work, this narrow neck was closed by a reinforced concrete sea-wall provided with a strong grating of vertical bars, horizontal girders, and stout $\frac{1}{2}''$ mesh galvanised iron wire-netting. The grating measures 12 feet by 9 feet, and the total depth of the sea-wall is 15 feet, so that, as the grating is fitted into the upper part of the wall, with its long axis horizontal, a depth of 6 feet of water is accommodated in the cove at low water, to provide a permanent sea-water pond (Fig. 1). The pond possesses a shingle beach at its south end so that between mid-tide and low water the depth of sea-water in it shallows from about 6 feet in the neck to nil on the beach. The depth of the portion of the wall below the grating was so arranged that the sea enters the pond about 3 hours before high tide and finally leaves it about 3 hours after high tide. Thus each day is divided into 4 parts of approximately six hours duration each. During the first period, say, the pond is in open communication with the sea outside, for the tide is either running into it or ebbing out of it. During the second period, the water in the pond is quiescent at its lower level, the tide being off the wall outside. The third and fourth periods each day are repetitions of the first and second periods of course. By this means, the pond is provided with an adequate circulation of water, for, with a spring tide rising to 16 feet above the Plymouth datum line, roughly 7 feet 6 inches of water flows over the wall through the grating, bringing the depth of water in the deepest part of the pond to about 13 feet 6 inches.

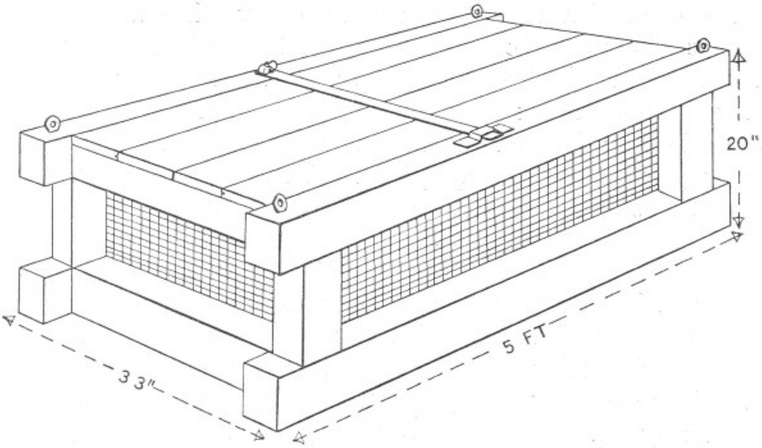

FIG. 2.—Diagram of a fish box as used in the Cawsand preliminary experiments of 1928.

Two steel wire hawsers were stretched out from end to end of the pond and over its surface, passing along the narrow neck. These were fixed at one end to the bars of the grating, at the other end to stout pins fixed vertically in the beach. The boxes into which the fish were placed subsequently, were slung on this hawser system, so that they floated at the surface of the water, as shown in Fig. 1.

Each box, with inside dimensions of 4 ft. 6 in. × 2 ft. 3 in. × 1 ft. 6 in., consisted of a strong deal framework and was provided with a solid bottom and a solid but halved, hinged lid, secured by means of hand bolts and a wrought-iron cross-bar fitted with a staple and a bolt and wing nut. The vertical faces of the box consisted during the early stages of the experiments of $\frac{1}{2}$-inch mesh galvanised iron wire-netting to ensure an adequate circulation of water through the box. Fig. 2 shows one of the boxes. Towards the end of the year 1928, when there appeared some likelihood of the boxes being damaged during gales, the framework of each box was further strengthened with wrought-iron plates and cross bolts, and an additional hawser system was introduced. But auxillary floats were employed in order to keep the boxes at the surface of the sea.

METHODS.

Upon completion of the preliminary arrangements, a number of 2-year old plaice were trawled in Cawsand Bay or in the nearby vicinity, kept under circulation on board s.s. *Salpa* and placed into storage boxes in the pond at Pier Cellars as promptly and carefully as possible. These fish were fed daily and were observed frequently for a number of days following their capture by Mr. H. O. Bull, who removed any individuals showing signs of ill-effect due to trawling or any other cause. From the remaining fish, 36 individuals were selected, this number being equally divided between the sexes. From the 18 fish of each sex three groups each containing 6 individuals were formed, each group being housed in a separate box. Thus 3 boxes each contained a group of 6 male fishes, and 3 boxes each a group of 6 females.

Subsequently, at the commencement of the preliminary experiments, one group of fish of each sex was provided with minimum rations, an attempt being made to satisfy basal requirements without allowing growth, i.e. to keep the length and weight of the fish constant. Trial and error methods together with periodic adjustments gave a reasonable measure of success. Further, one group of fish of each sex was supplied with maximum rations, arranged to satisfy the appetite of the fish and to allow full growth. The third groups of fish of each sex were given rations intermediate between the minimum and maximum ones.

The food supplied to the fish consisted of the best specimens of *Mytilus* *edulis* obtainable, opened, allowed to drain for 30 minutes, and then cut up into pieces of suitable size. Small particles of food were studiously avoided so as to prevent undue loss. In the description which follows, mention of food implies food of the nature mentioned above. Food rations were presented to each group of fish daily as consistently as possible and at a time when the water in the pond was in a quiescent state, so that the chances of food being washed away by a rising tide were minimal ones. The times of feeding were noted and daily records were

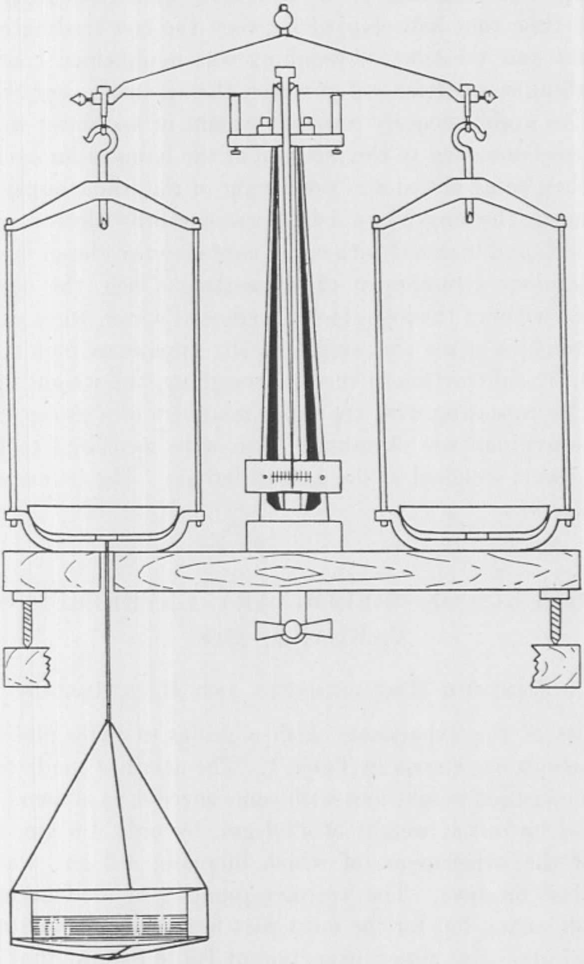

FIG. 3.—Diagram showing the weighing apparatus. The two large clock glasses and the shallow glass dish containing sea-water are slung from the left side of the balance by means of a wire basket.

kept of the temperature of the water in the vicinity of the boxes. A look-out was maintained for parts of rations uneaten and the behaviour of fish upon presentation of food was noted.

Measurings and weighings of the fish were carried out fortnightly, and always, the time that had elapsed between the last feeding operation of the fortnight and the time of weighing was maintained constant. The actual weighing was carried out in water, the apparatus used being shown in Fig. 3. An approximately constant weight of sea-water was placed in the glass vessel attached to the left arm of the balance for each weighing, the vessel then being closed and the weight of the whole apparatus taken. After measuring the length of a fish, it was carefully blotted with a clean, dry glass-cloth and inserted with equal care into the closed vessel. After a few preliminary attempts at thus inserting a fish, the operation can be performed without the loss of even a trace of water, when care is taken. A second weighing gives the weight of the apparatus plus a single fish, from which, by subtraction of the first weighing, the weight of the fish is obtained. By repeating with the other members of a group, the weights of all the individuals are obtained. Fish were measured to the nearest 0·1 cm., and were weighed to the nearest 0·5 gm. The balance used is by Oertling (Fig. 3).

I. RESULTS OF PRELIMINARY EXPERIMENTS AT CAWSAND, 1928.

1. Minimum Requirements and Maintenance.

The results of the experiment with a group of male plaice fed with minimum rations are shown in Table 1. The attempt made to maintain the fish at a constant weight met with some success, as is seen. The mean fish increased its initial weight of 42·0 gm. by only 4·8 gm. during the 176 days of the experiment, of which increase, 4·2 gm. was obtained during the last 39 days. The average quantity of food taken daily by the mean fish varies, but for the most part between such narrow limits as 0·6 gm. to 0·7 gm. But closer inspection of Table 1 shows that the results of the experiment are modified by a remarkable event. It is seen that the fish designated A1 steadily declined during the course of the experiment, and gradually lost weight until late November, when it died.

It was observed during feeding operations that these male fish generally displayed avidity for food, rising towards the surface of the water as soon as it was presented, and even snapping at each other at feeding time before food actually was offered to them. As soon as the lid of the box was opened, the fish were seen to be in great readiness to take food. But the fish A1, and during the early stages of the experiment A5 also, was invariably too slow to obtain food. After a short time it made no attempt to compete with its fellows, but steadily sulked in a corner of the box, watching the feeding attempts of the others. It was completely subjugated and, as the rations were taken by the other fish immediately they were placed in the water, it is doubtful if it succeeded at all in obtaining an appreciable quantity of food. Because of this factor, it seems reasonable to suggest that the fish A1 be excluded from consideration in the preparation of weight-length averages and mean maintenance ration estimates. It must be observed here that although individual values are arranged in order in Table 1, yet it was not possible to recognise each individual with certainty during the course of the experiment, and the order presented is not the only possible one. But certain fish are definitely recognisable, e.g. A1, which was originally the longest fish in the group and which came to be distinguished by its slight weight, and A5, the smallest fish of the group.

The values shown on the right-hand side of Table 1 are obtained when the fish A1 is excluded from consideration. There appears to be reason for maintaining that they are more accurate than values which take this fish into consideration. During the course of the experiment, the mean fish increased its initial weight of 41·6 gm. by 5·2 gm., while the daily food allowance varied, for a greater part of the time between 0·7 gm. and 0·8 gm. Thus, if the suggestion made above is accepted, the value for the daily maintenance ration obtained from data concerning the whole group must be increased by 0·1 gm. Between August 14th and November 30th the corrected daily ration varies between 0·017 and 0·019 of the average body-weight for each period, and may be taken as approximately constant at 0·018 for a 42·0 gm. mean fish. During December and the early part of January the fraction of the average body-weight which must be supplied in food per day, which fraction will subsequently be referred to as the maintenance ratio, falls appreciably. As is shown in Table 1, during the last 39 days of the experiment, the corrected mean fish increased its weight by 4·2 gm. as against 1·0 gm. for the previous 137 days on a reduced ration per day corresponding to 0·014–0·015 of the average body-weight.

The results of the experiment with a group of female fish fed with minimum rations are presented in Table 2. The problem of the decline of certain individuals, due to lack of success in the competition for food within the minimum groups, is obvious, if not as well marked as in the cases of the males. But the declining females B1 and B5 undoubtedly were able to obtain food, since for periods up to 32 days their body-weights were maintained constant. These fish showed the same disregard for food as did A1 amongst the males, but it is impossible to correct the mean values obtained for the whole group, since for periods they undoubtedly must have obtained food. In great probability, the mean values shown are higher as regards food quantities than the true values desired.

The females were supplied with rations similar to those given to the males, and because of the difference in size were thus allowed more than sufficient for purposes of maintenance. Thus, during 147 days from August 14th, a daily allowance of rather more than 0·6 gm. on the average resulted in an increase in body-weight of the mean fish of 15·7 gm. It is seen from Table 2 that during the period ending July 30th, a daily allowance of 0·5 gm. of food resulted in an increase in body-weight of 0·9 gm., while in the following period 0·4 gm. of food per day enabled the body-weight to be kept approximately constant. It appears likely that for female plaice of 25·0 gm. body-weight, a daily food allowance of 0·4–0·5 gm. would prove adequate. The maintenance ratio would lie between 0·016 and 0·020, and would compare fairly closely with that obtained for males.

2. Maximum Requirements and Growth.

Data concerning fully growing male fish are presented in Table 3. After 176 days of growth the mean fish had increased its initial size of 16·0 cm. and 38·8 gm. by 6·6 cm. and 86·0 gm. The initial length is thus increased by rather less than half its value while the initial weight is rather more than tripled. The total quantity of food taken is about 1129 gm., or approximately 14 times the average body-weight for the whole period, and an average of about 6·4 gm. per day. Of the whole quantity of food consumed, an uncertain quantity had been used for purposes of maintenance. It is not possible to know the exact amount of food necessary to maintain this mean fish, since the values determined experimentally for the single set of males kept on minimum rations do not correspond to those of fully growing fish, as the maintenance requirements must vary with size. But an approximation will be obtained if it is assumed, in the absence of experimental data in these preliminary experiments, that the ratio, spoken of as the maintenance ratio (M), is constant for fish of any size within the range of these experiments. In Table 3 are given estimations of the maintenance requirements of the mean, fully growing male fish, the maintenance ratio being taken from the corresponding periods shown in Table 1. These estimates are probably high, expecially during the latter stages of the experiment, because it is likely that the value of the ratio will fall with increase in size of a fish. But this rough estimate indicates that approximately ⅕th part of the total food consumed is used up in satisfying the maintenance requirements of the mean fish, only ⅘ths of the total being available for purposes of growth. About 900 gm. of food used for growth purposes produced 86 gm. of mean fish, so that for the whole period the fish requires 10 to 11 gm. of food over and above the maintenance ration to increase its weight by 1·0 gm.

It is seen from Table 3 that the increments of growth in weight are much more irregular than the corresponding food increments. Thus, for the three periods included between August 14th and September 26th, the average quantity of food consumed per day falls slightly in successive periods, while the increase in weight falls for the second period to rise again in the third. There is also a striking acceleration of growth in weight during early December which appears disproportionate to the quantity of food taken. This may be due in part to a fall in the quantity of food necessary for pure maintenance allowing of more food being available for purposes of growth. But it is probably also dependent upon other factors, as a glance at the results for the period ending January 8th will serve to show.

The results of the experiment with fully growing female fish are more complete than those concerning corresponding males. There was no accident such as interfered with the results in the latter case, when a box was forced open and three fishes gained their freedom. From Table 4, it is seen that the mean female fish was initially 16·1 cm. in length and 43·3 gm. in weight, and was finally 23·3 cm. long and weighed 151·2 gm., showing an increase in length of 7·2 cm., in weight of 107·9 gm. Considerable variation in growth occurs, for while the initial weight of D4 is less than tripled, that of D5 is quadrupled. It is interesting to note that during a whole growth-season a small initial difference in weight between two fishes may become considerably amplified. Thus in an environment holding an abundance of food, an initial difference of 13 gm. in the body-weights of the fishes D5 and D6 (Table 4) results in a difference of 90 gm. in these weights at the end of the growth-season. The same fact is shown by comparison of the initial and final body-weights of D2 with those of D5.

During the entire period, the mean fish takes 1129 gm. of food—rather less than 12 times the average body-weight for the period, and an average of 6·4 gm. per day. It appears likely that the females make better use of food for purposes of growth than do the males, since 1129 gm. of food produce 107·9 gm. of mean female fish as against 86·0 gm. of mean male fish, when the initial sizes were comparable.

No attempt has been made to estimate the maintenance requirements of the fully growing female fish. It was noted above that considerable growth took place in the mean female fish supplied with maintenance rations. Moreover, the selection of fish at the commencement of the preliminary experiments was such that, despite considerable growth, the females given minimum rations were smaller at the end of the experiment than were the females given maximum rations at the commencement.

But, assuming that the maintenance ratio is approximately constant at from 0·018 to 0·020, the maintenance requirements of the fully growing female fish will range from 200 gm. to 245 gm. of food for the whole period. This rough estimate is suggested tentatively.

3. Growth and Intermediate Food Supplies.

As was mentioned above, groups of male and female fish, each containing six individuals, were supplied with quantities of food intermediate in value between the minimum and maximum rations. This intermediate ration was about $\frac{1}{3}$rd of the maximum one. The results of the experiment with males are shown in Table 5, where it is seen that the mean fish increased its initial size of 16·0 cm. and 42·5 gm. by 3·8 cm. and 51·1 gm. during the 176 days of the experiment. During this period it took 393 gm. of food, an average of 2·2 gm. per day. Table 7 shows initial lengths and weights, final lengths and weights and the total quantities of food consumed by each of the three groups of each sex. It is seen that in maximum-fed males, 13·3 gm. of food are required to produce 1·0 gm. of fish on an average for the whole period of 176 days. In the case of intermediate-fed males, only 7·7 gm. of food is required to produce the same quantity of mean fish. Thus there appears to be some difference in efficiency of the two groups. This question will be returned to later.

Returning to Table 5, it will be seen that the initially larger fish fared much better than did the smaller ones, c.p. E1, E3, and E4 with E2 and E6. Ultimately, the group comes to consist of a mixture of " maximum " and " minimum " fish. A problem comparable with that of the decline of individuals in the minimum groups thus arises, due to the competition for food existing between the members of the group. It was observed during feeding operations that certain individuals took liberal helpings of food while others made no attempts to obtain it while under observation. It was made a rule after a short time to close up the box immediately following the presentation of food in order to eliminate the possibility of fish refusing to take food in the presence of the observer. But in spite of such a precaution, certain individuals soon come to dominate the group, others apparently being subjugated. Undoubtedly, such fish as come to dominate a group will take maximum rations as far as possible, while subjugated fish may or may not succeed in obtaining food.

The feature mentioned immediately above is also shown amongst females of the intermediate groups. In Table 6 it is shown that the initially smallest fish, F6, does not succeed in doubling its initial weight during the course of the experiment, while other fish easily achieve this result (F1, F2, F3 and F4). But the results of the competition for food within the intermediate-fed groups are not as well marked among females as among males.

A comparison of Tables 5 and 6 will serve to show that the growth of intermediate-fed females closely follows that of the corresponding males. Table 7 shows that these females make rather more use of food for purposes of growth than did the corresponding males, 7·2 gm. and 7·7 gm. of food being required to produce 1·0 gm. of fish on the average, for females and males respectively. The difference is not as well marked, however, as in the cases of maximum-fed fish, where the corresponding food quantities are 10·5 gm. and 13·3 gm. But in both male and female groups there appears to be a marked increase in efficiency in the intermediate groups. This is difficult to explain, particularly in the case of the males, where a virtual mixture of maximum and minimum fish obtains. In order merely to balance the food bill of the intermediate group for the whole period, such a mixture of fish would need to consist of not more than two maximum fish to four minimum ones. Yet three or four of the fishes in the intermediate male group could be regarded as maximum fish as far as size is concerned, if rather poor ones. There thus appears some reason to believe that fish make more use of food for purposes of growth when it is present in medium quantity, than when it is particularly abundant. In work on digestion in the plaice, the results of which are unpublished as yet, it was found that food stays longer in the stomach if no second meal is given than it does if a second meal is taken. There may be relatively more complete absorption of food substances, therefore, when food is relatively more scarce. But it is not intended to stress unduly these differences of efficiency. It appears possible that although food from a previous meal was never observed in a box containing maximum-fed fish, yet particles of food left over from a meal might conceivably have been swept out of the box by a rising tide. Thus the question is left open to doubt on the results of the 1928 experiments alone. But it appears that much interesting information would be obtained by following up such suggestions as are here afforded by more conclusive experiments.

4. Conclusions Drawn from the Experiments of 1928.

(1) A male fish 16·0 cm. in length and 42 gm. in weight requires approximately 0·7–0·8 gm. of food per day in order to maintain its weight constant. For the major part of a growth-season of 176 days the maintenance ratio, i.e. the ratio of the quantity of food required daily to the body-weight, varied from 0·017 to 0·019, and may be taken as approximately constant at 0·018. During the months of December and January the ratio falls to 0·014.

(2) A female fish initially 13·4 cm. in length and 24·3 gm. in weight is able to increase its weight by 16·7 gm. when supplied with an average daily food ration of 0·6 gm. for 176 days. It is suggested that the true maintenance ration for such a fish lies between 0·4 gm. and 0·5 gm. per day. The maintenance ratio would then lie between 0·016 and 0·020.

(3) A fully feeding " mean " male fish initially 16·0 cm. in length and 38·8 gm. in weight increased its length by about 6·6 cm. and its weight by about 86 gm. during a period of 176 days from July 16th, 1928. It consumed 1129 gm. of food, an average of about 6·4 gm. per day for the period. It is estimated that roughly ⅕th of the total quantity of food consumed was required for purposes of maintenance.

(4) A fully feeding " mean " female fish, initially 16·1 cm. in length and 43·3 gm. in weight, increased its length by 7·2 cm. and its weight by 107·9 gm. during a period of 176 days following July 16th, 1928. It appears probable that, since the total food taken was the same in quantity as that taken by the corresponding male fish, females make slightly better use of food for purposes of growth than do males.

(5) Considerable variation is shown in the growth taking place in different individuals in an environment holding an abundance of food. A difference of weight of 12–13 gm. between two fish at the commencement of the third season of growth may become amplified into a difference of 80–90 gm. by the end of this season.

(6) Fish supplied with daily rations of food intermediate in value between maximum and maintenance rations and about ⅓rd the value of the former, appear to make better use of food for purposes of growth than do fish supplied with maximum rations. A comparison of efficiencies is given in Table 7 and probable explanations are afforded.

(7) In fully feeding fish, there appears to be no simple relation between the quantity of food consumed in a given period and the increase in weight.

II. OBJECTIONS TO THE FORM OF THE PRELIMINARY EXPERIMENTS.

Among the objections raised to the form of the preliminary experiments, there are several which are capable of being remedied or removed altogether. It was seen that, if a group of fish is supplied with food sufficient merely to satisfy maintenance requirements, the ration is not

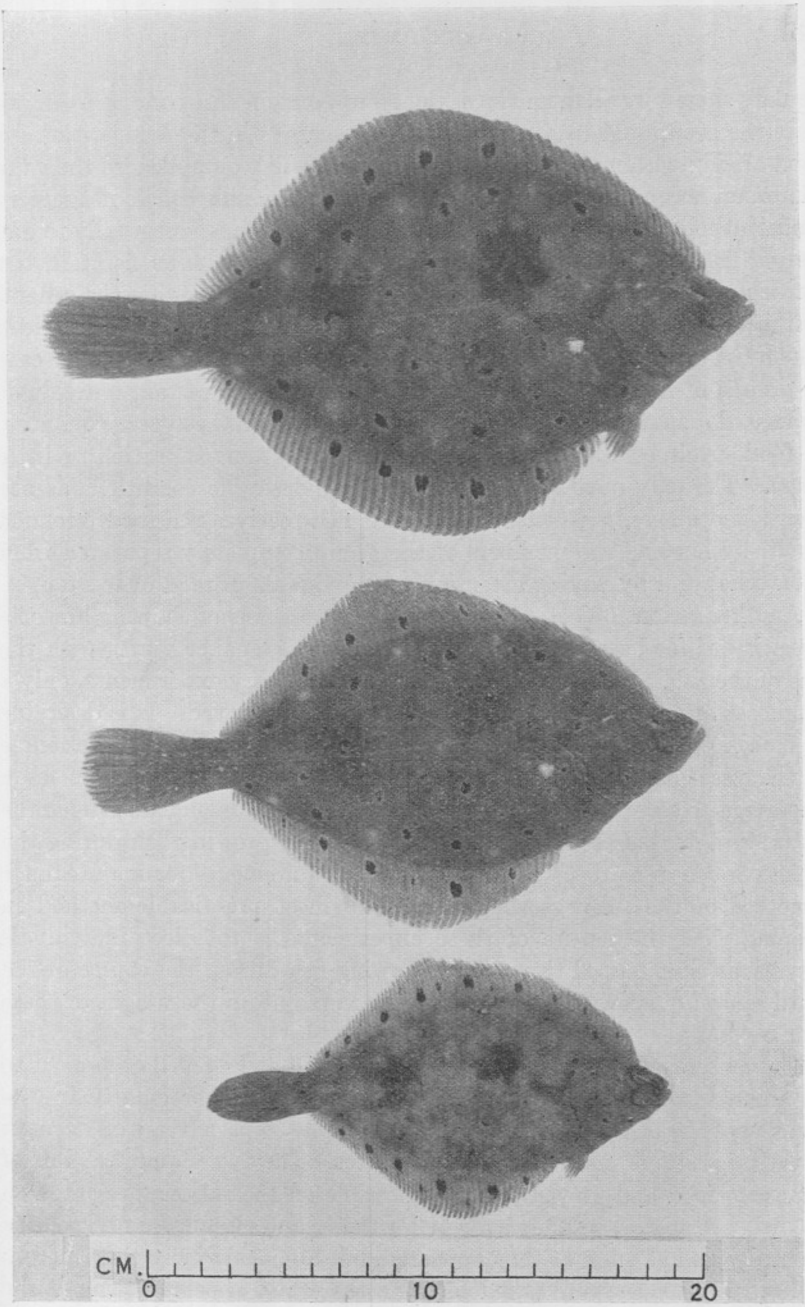

FIG. 4.—Female plaice photographed at the end of the preliminary experiments of 1928 [Cawsand]. The lengths are 16·8 cm. [bottom], 22·6 cm. [middle], and 25·7 cm. [top]. At the commencement of the experiments, the fish were of approximately equal size. The fish shown at the top of the figure was supplied with maximum rations and growth was unrestricted; that shown at the bottom was supplied with minimum rations sufficient to satisfy maintenance requirements without allowing of growth, while the middle fish consumed rations intermediate in quantity between the maximum and minimum ones, so that growth was slightly restricted.

Photograph by Mr. D. P. Wilson.

equally shared by all members of the group, certain fish coming to dominate the group and to overpower other members in the competition for food arising within the group. The dominant fish obtain more than the minimum ration intended for them, while the remaining fish do not receive sufficient food for purposes of maintenance, and decline, eventually to die. Larger fish may succeed in this competition where smaller fish fail, but size is not the sole factor determining success. It may be that the general condition of the fish is a factor. In any case it is not possible to ascertain which fish of such a group would fail to obtain food. Similarly in the case of groups of fish supplied with intermediate rations, certain individuals come to dominate the situation and obtain more than the average quantity of food, while certain others obtain a bare maintenance ration or little more. The only means of removing such undesirable conditions as are mentioned above, is to ensure that each fish receives the food intended for it, by keeping the members of the group completely separated from each other and by paying attention to individuals instead of to groups.

Another serious objection is the lack of any means of showing how the quantity of food necessary for purposes of maintenance varies with the size of the fish. During the course of the preliminary experiments, only a single set of minimum-fed fish of each sex was employed. It is desirable to show how the maintenance requirements of a fish vary during the course of the year, e.g. with differences of water temperature, but it is more important to ascertain how they vary for fish of sizes included between the initial and final sizes of the maximum-fed, fully growing fish during the same period, so as to be able to infer the requirements for maintenance purposes of the fully growing fish. The most practicable method in keeping with the nature of these experiments is to select individuals of various sizes passed through by growing fish during the course of the third season of growth and to endeavour to maintain the weight of these fish constant.

The presence of prawns in the sea-water pond at Pier Cellars proved to be a great source of annoyance. They were found regularly in the vicinity of the boxes, into which they were able to pass freely on account of the large size of mesh of the vertical faces. They were quite capable of removing food and preyed as far as possible on the rations presented to the fish. A special watch was kept for them, and they were removed as promptly and as often as they appeared, but obviously more than merely palliative measures were called for. As there also appeared some doubt as to whether or not food was ever swept out of the boxes, it seemed advisable to substitute a finer meshwork into the vertical faces of the boxes, a meshwork large enough to allow of an adequate circulation of water through the boxes and at the same time small enough to prevent the ingress of prawns and the egress of food particles.

III. MODIFICATION OF APPARATUS AND METHODS (1929).

Before commencing the experiments of 1929, alterations were made to the apparatus in order to eliminate the undesirable factors mentioned above. The $\frac{1}{2}$-in. mesh wire-netting windows of the boxes were removed and, in place of these, windows of perforated ebonite were substituted. Every box was provided with 4 windows each 12 in. × 12 in., and 4 more each 12 in. × 6 in., the perforations being $\frac{3}{16}$ in. in diameter and being set $\frac{5}{16}$ in. apart. The cavity of each box was divided into 4 equal compartments, by means of $\frac{1}{2}$-in. mesh, wire-netting partitions, provided with a 6-in. sill at the base to prevent the passage of food from one compartment of a box into another. Six boxes were thus transformed, so that accommodation was afforded for 24 fishes, and it was decided to continue the experiment with maximum-fed and minimum-fed fish only.*

During the course of the revised experiments, each fish was kept quite separated from its fellows, and received an independent food ration daily, or as nearly daily as was found practicable. In all cases, whether of minimum-fed or maximum-fed fish, food was placed in the box one day and the portion uneaten was weighed back before food was presented on the following day. It is important to observe carefully what portion of food is left over, particularly as a measure of the appetite of a fish on one day is by no means a certain measure for the following day, and since it is found that if food is left over it remains untouched subsequently until decomposition is complete.

Six separate fish of each sex formed minimum-fed groups and six of each sex maximum-fed groups, and the sizes of fish in each maximum-fed group were arranged to be as similar as was practicable. At the outset, minimum fish of as nearly as possible the same size as the maximum ones were employed. After a time the original minimum fish were in certain cases changed for larger fish, which were then kept on minimum rations. An attempt was thus made to ascertain the maintenance requirements of the freely growing fish, but difficulties were met with. A hasty substitution of fish meets with failure. For a variable period after capture, fish taken freshly from the sea refuse to feed, and lose weight to a considerable extent. It is better in practice to store such fish as are intended for later inclusion in the experiment as singly kept fish, in storage boxes in company with others of their kind. Newly captured fish which refuse to take food when kept alone, usually feed if kept with others of their kind.

It is very difficult to " match " freely growing fish with minimum fish. To do this a large number of " stored " fish of various sizes are required. There is considerable variation in the rate of growth of different individuals,

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* This was the ruling of the officers of the Ministry of Agriculture and Fisheries.

and one cannot predict the increase in length of any fish a fortnight in advance, and a fortnight or more is needed to allow freshly-trawled fish to become settled. It was not practicable to store large numbers of fish alive at Pier Cellars, and hence little success was obtained in attempts to "match" such fish as were already included in the experiment. But some success was met with in the general aim of determining the maintenance requirements of fish of different sizes.

Weighings were made fortnightly as in the case of the preliminary experiments. But each individual fish was separately treated, the weighing apparatus and its water contents being reweighed for every single fish.

The experiments proper commenced on May 22nd, 1929, but for a period of days previously a large number of fishes were fed and observed regularly, all apparently unsound individuals being removed. From the remaining fish a selection based upon size requirement was made. The experiments were continued until December 12th, 1929, although severely interfered with during the gales which occurred early in the month. In most cases the data obtained during the last fortnight of the experiments were rejected, and in other cases damage to the apparatus resulted in the loss of fish so that data were not forthcoming.

It must be mentioned that great care was taken throughout the course of the experiment to keep the boxes free of epifauna and epiflora. The small size of the perforations in the ebonite windows made it imperative to keep the boxes clear of sedentary forms of life of all kinds, in order to maintain a circulation of water through the boxes.

IV. RESULTS OF THE CAWSAND EXPERIMENTS OF 1929.

1. Minimum Requirements and Maintenance.

Table 8 presents data obtained in experiments with a group of six male fish and a second group of six female fish, all kept separately and supplied with minimum rations from May 22nd to July 5th, a period of 44 consecutive days. During the period, four measurings and weighings were made, although in the table cited only the initial and final lengths and weights are given.

It is seen that, in males and females alike, the quantity of food necessary for purposes of maintenance varied in individuals of approximately the same size. Among the males, C4 lost 3·0 gm. in weight during the period when supplied with 0·43 gm., or 0·025 of the body-weight, of food per day. The fish C5, of smaller initial size, gained 3·0 gm. in weight when supplied with an almost identical average daily ration, while C3 maintained its weight constant (but increased its length) on 0·42 gm. of food per day. The mean fish increased its initial weight of 16·7 gm. by 1·7 gm. during 44 days, when supplied with 0·42 gm., or 0·024 of the body-weight, of food per day. Among the females, A2, A5, and A6 show some variation, while the mean fish increased its initial weight by 0·5 gm., when supplied with an average daily ration for the period of 0·42 gm., or 0·019 of the body-weight of food. The increase in weight of the mean fish for the period is greater in the male group, so that the maintenance ratio is correspondingly smaller than the table indicates, approximating more closely to that of the female mean fish.

Data obtained from the experiments with the minimum-fed male fish C5a, C4a, and C6a from July 5th to November 28th, 1929, are shown in Tables 9, 10, and 11. The fish C5a lost weight during the early part of the experiment and never completely regained it, coming to within 1·0 gm. of its initial weight after 146 days. C4a and C6a also lost weight slightly during the early stages, but regained it and finally increased in weight slightly. The early loss of weight is due in all three cases to the fish's refusal to take food.

Inspection of Tables 9, 10 and 11 will serve to show that the average daily ration can hardly be fixed so that the weight of the fish remains constant. For example, C5a, for the periods ending August 30th, September 16th, and October 1st, when sea temperatures were fairly uniform, gained 2·0 gm. in 14 days, 1·5 gm. in 17 days, and 1·0 gm. in 15 days when taking 0·64 gm., 0·66 gm., and 0·80 gm. of food per day for respective periods (Table 9). Similar examples of the apparent variation in maintenance requirements are shown in Tables 10 and 11. It appears impossible to supply a fixed daily ration for purposes of maintenance so that the body-weight of the fish will be maintained constant.

In Table 12 is shown how the ratio of food taken per day/average body-weight varied for the fishes C5a, C4a, and C6a during the course of the experiment. The values of the ratio are calculated for each period and also cumulatively. Side by side with the data thus obtained are arranged the periodic increases in body-weight of the fish. The initial and final weights of a fish are shown on each side of the index of that fish. It is seen that for any fish, the slight increases in weight are disproportionate to the maintenance ratio, so that for the same fish a constant fraction of the body-weight of food per day will not serve to maintain the weight of the fish constant. Thus for C6a during the periods ending August 16th, August 30th, September 16th, and October 1st, when the maintenance ratio is 0·023, 0·023, 0·022, and 0·020, the increases in body-weight are 2·0, − 0·5, 1·0, and 0·5 gm. respectively. There is an appreciable fall in the value of the maintenance ratio during November, when the temperature of the sea-water of the pond falls. And it is seen also that the value of the maintenance ratio falls with increase in weight of the fish. Thus, the mean value of the ratio for the whole range of the experiments is 0·019 for C5a and 0·016 for C6a. This difference is rendered more conclusive when it is observed that the larger fish was able to increase its initial weight on the food supplied.

The results of the experiments with the minimum-fed female fish A4a, A6a, and A3a respectively, are shown in Tables 13, 14, and 15. As was found to be the case in males, the relationship between the quantity of food supplied to any fish per period and the slight increase in weight of the fish for the corresponding period, varies from time to time [compare the daily ration per period and the weight increase per period for periods ending August 16th, August 30th, September 16th, and October 1st, A4a (Table 13), A6a (Table 14), and A3a (Table 15)]. The same fact is emphasised when the daily maintenance ration is expressed as a fraction of the body-weight, as in Table 16. The variations in the ratio of food supplied per day to the average body-weight of the fish are not considerable, except during the early stages of the experiments when food was refused and for A3a during the period ending October 15th, but the differences in the increases in body-weight are well marked, e.g. during the periods between August 2nd and October 1st for the fish A6a.

The results shown in Table 16 do not show conclusively any appreciable fall in the value of the maintenance ratio with increased size of fish, but the fall in value of this ratio during November is admirably shown. Table 17 is compiled from Tables 9–16, to show as nearly as is possible, and for the whole range of the experiments, how the maintenance requirements of fish of various sizes and of both sexes varied. It is seen that for fish of approximately the same size there is no appreciable differences of these requirements for the two sexes. Table 18 shows how the maintenance requirements of fish of various sizes varied for a relatively shorter period towards the end of the experiments and particularly how the value of the maintenance ratio diminishes as the sea temperature falls during November. It must not be overlooked that the increases in weight shown on the right are for a period of 14 days; those on the left for a period of 43 days.

A striking feature concerning growth in length is observed in the results of these experiments. Table 9 shows that for the whole range of the experiment with C5a, there was a loss of weight of 1·0 gm., although an increase in length of 0·4 cm. For C6a from July 12th to October 1st, the weight decreased by 0·5 gm., while the length increased by 0·5 cm. (Table 11). For the females A4a and A6a, during the course of the experiments to October 1st and September 16th respectively, the weights decreased by 1·0 gm., while the lengths increased by 0·5 cm., in each case (Tables 13 and 14). It appears, therefore, that when loss of weight occurs, it is not usually accompanied by decrease in length, and that when weight is regained there occurs contemporarily an increase in length. The effect of this phenomenon is to lower the general condition of the fish as indicated by the weight/length^3 ratio.[*] Thus, taking the female fish A4a, which lost 7·0 gm. in weight during the period of 14 days ending July 19th (Table 13), the initial value of this ratio was 0·010. By July 19th the value had fallen to 0·008 and the initial value was never regained during the course of the experiment, the values for October 15th and November 27th being 0·009. Similarly, the female fish A6a incurred a loss of weight of 3·5 gm. during the first fortnight of the experiment, and did not recover the initial value of the weight/length^3 ratio (0·010) until November 27th, although consistently gaining in weight after the first loss. The male fish C5a did not show a value for the ratio as high as the initial one of 0·010 during the whole range of the experiment.

2. Maximum Requirements and Growth.

The results of the experiments with maximum-fed fish are varied. There was shown considerable variation in the rate of growth of different individuals, and in several cases failure was met with, where what appear to be abnormal fish made no appreciable growth whatsoever. The final results obtained with the six fishes of each sex are shown in Table 19. The total increases in size are indicated side by side with the total quantities of food consumed and the average daily rations for the whole period are shown. It is important to realise that references to food quantities are also references to appetite shown by the fish, since throughout the experiment, food left over from a meal was consistently "weighed back" before the following meal was presented.

It will be agreed that certain fish can be excluded from consideration (Table 19). A 2-year old fish which increases its weight by 5·0 gm. during 117 days, or 7·0 gm. during 175 days, is not progressing satisfactorily. The fish B3 showed signs of inability to co-ordinate movements, swimming inverted and settling down on the vertical faces of the box as if on the floor of it. Accordingly, such fish as D6, B3, and B5 will be disregarded. In the D group, D3 made most progress, and will receive special consideration as showing the maximum growth for the experiments. The fishes D2 and D4 will be compared with D3. In the B group, B1 and B4 show the maximum growth for the experiment, and B2, B5a, and B6 will be compared with them.

It is seen from Table 19 that the average quantity of food consumed per day for the whole range of the experiments is about 3·3 gm. for the fish showing maximum growth, males and females alike. The weight of

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[*] The constant K, which is a measure of the general condition of a fish, is usually defined as $\frac{W \times 100.}{L^3}$. Here it is taken as $\frac{W.}{L^3}$.

food necessary to produce 1·0 gm. of fish, estimated for the whole range of the experiment works out as follows :

D3 (♂)—6·6 gm.
B1 (♀)—7·6 gm.
B4 (♀)—7·2 gm.

In these instances, therefore, the efficiency of the male appears to be greater than that of the female, contrary to the findings during the preliminary experiments. For all fish, good, bad and indifferent, and for the whole range of the experiment, 11·6 gm. of food produces 1·0 gm. of mean male fish and 13·9 gm. of food produces 1·0 gm. of mean female fish, so that here again the male appears to possess greater efficiency.

The data concerning the male fish D3 are shown in Table 20. It is seen that increases in body-weight for any specified period reach a maximum during September. This is also shown in the acceleration curve (i.e. a curve showing the increase or decrease in value of periodic increments from time to time, or in other words, showing the rate of change of growth) of body-weight in Fig. 5. The quantity of food consumed per day is a maximum during early October, but is near its maximum value during September, as is also shown in Fig. 5. The general condition of the fish as indicated by the value of the weight/length^3 ratio, is at its best when the appetite of the fish is greatest and when maximum growth is taking place, as would perhaps be anticipated.

Periodic increases in body-weight are shown in Fig. 5 in the form of an acceleration curve, while the growth curve of weight is shown above. The latter is seen to be a smooth, slightly asymmetrical, sigmoid curve of typical form. The steepest part occurs during mid-September, and the point of inflection for the season is not reached at the close of the experiment. No attempt has been made to find the equation to this single-fish curve.

It is also seen from Table 20 that the efficiency of the fish, as expressed by the quantity of food necessary to produce 1·0 gm. of fish, varies from period to period during the course of the experiment. The efficiency is greatest during September, when the weight increments of growth are greatest, when 4·8 gm. to 4·9 gm. of food are required. Thus it is indicated that factors other than merely the quantity of food consumed operate. There is a period of increased efficiency during early July, and it is worthy of remark that two peaks occur on the temperature graph for the season which closely correspond with these periods. The efficiency of the fish estimated to any date varies between 5·6 gm. and 8·8 gm. of food per gm. of fish over the initial weight.

Growth in length of the male fish D3 appears to be a linear function of time, at least for the major part of the experiment, as is shown by inspection of the figures given for length in Table 20. Plotting length against time, we obtain the curve shown in Fig. 9. Until the middle of October, the points plotted arrange themselves evenly and fairly closely about a perfectly straight line.

The results of the experiment with the male fish D2, which are shown in Table 21, are distinctly interesting. As in the case of D3, the quantity of food consumed per day reaches a maximum during late September, when the condition of the fish, as indicated by the weight/length³ ratio, was at its best. But growth in weight is not at all regular, and the efficiency of the fish varies in a striking manner (see Column 8, Table 21). During July

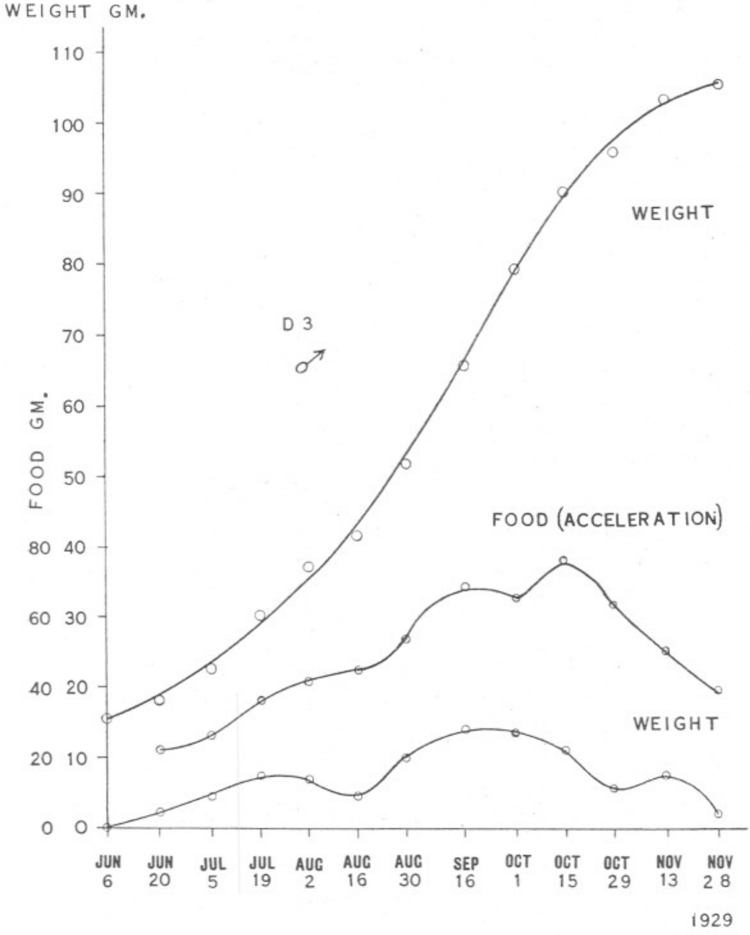

Fig. 5.—Growth curve of weight of the male plaice D3 together with acceleration curves of periodic body-weight and food-weight increments. (Cawsand, 1929.)

there is an acceleration of growth in weight (Table 21 and also Fig. 6), then during August a retardation, followed by a great acceleration during the early part of September. There is here a strong suggestion that growth in weight is connected with temperature, the two accelerations in growth coinciding with peaks on the temperature graph (Fig. 11), the retardation with a fall in temperature during August. The curve of growth in weight (Fig. 6) suggests that this fall in temperature interfered in some way with the metabolic processes of the fish and that growth was slowed down until the great acceleration during September, which proved too late to produce a typical result such as was shown by the fish D3. The efficiency of the fish D2 during early September, when 3·6 gm. of food produced 1·0 gm. of fish, is truly remarkable. It greatly transcends that of D3 for any period during the year, although the appetite for food after the first fortnight was never as great as in the latter fish.

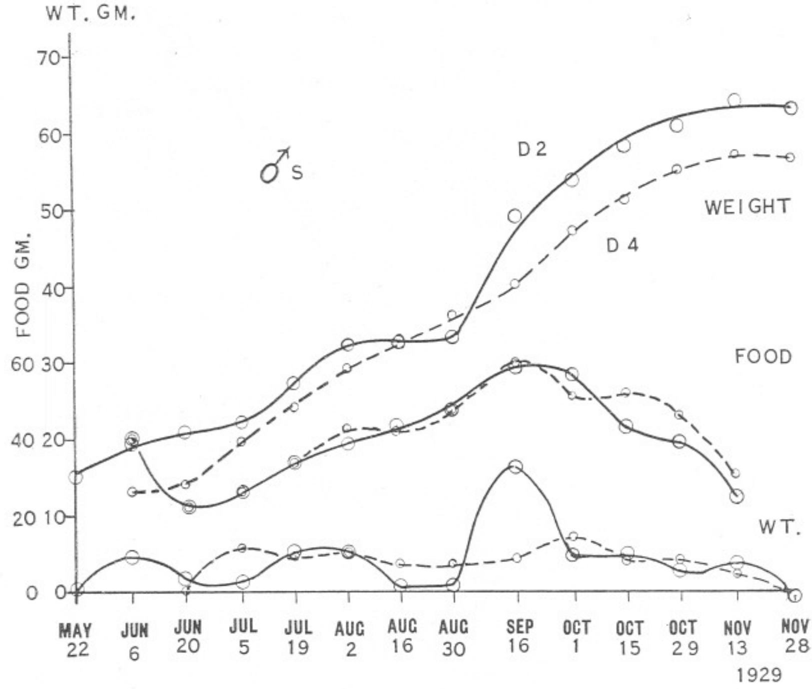

Fig. 6.—Curves of weight and acceleration curves of body-weight and food increments for the male fishes D2 and D4. (Cawsand, 1929.)

The growth in weight of D4 follows that of D2 fairly closely. The total increase in weight for the whole period (Table 22) is comparable with that shown by D2, as is also the total quantity of food taken, and therefore the average efficiency of the fish. But in the case of D4, there is no phenomenal acceleration of growth in weight. Instead, growth is more regular, but attains a maximum during late September. There is shown a slight retardation of growth during August, which is comparable with the more marked one shown by D2 (Fig. 6).

A consideration of the growth of the male plaice D3, D2 and D4 shows

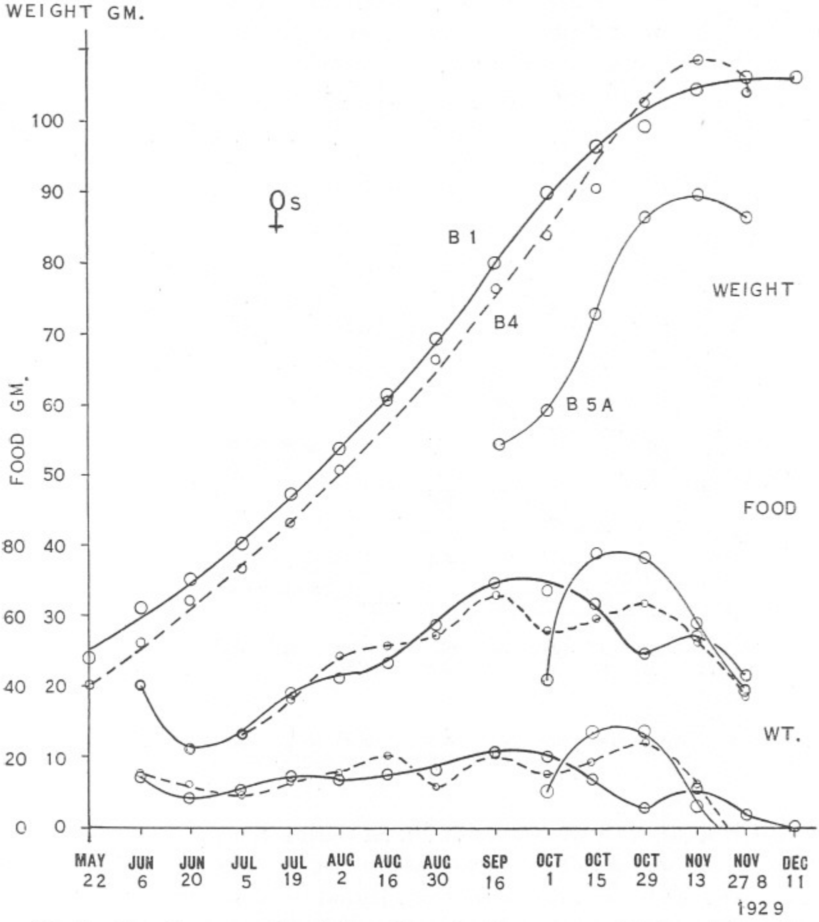

FIG. 7.—Growth curves of weight and acceleration curves of body-weight and food-weight for the female fishes B1, B4 and B5a. (Cawsand, 1929.)

then that September is the month of greatest appetite and maximum growth. It is also apparent that temperature influences growth and that, given a suitably high temperature, fish which have suffered a retardation of growth are able to become increasedly efficient in an attempt to compensate for the growth inhibition.

It has been observed above that the growth taking place in female fish closely follows that in the male fish, for individuals showing the maximum growth for the experiments. The females B1 and B4 show a very close agreement and can be considered side by side. Table 23 presents the data concerning B1, Table 24 that concerning B4. In the case of B1, the maximum growth in weight occurs during September, when over 20 gm. are added to the body-weight. In the case of B4, growth is accelerated during September, but attains a maximum during October, when over 18·5 gm. are added to the body-weight. In each case maximum growth is accompanied by maximum appetite. In the case of B1, the weight/length³ ratio is also a maximum during the period of maximum growth. As was found to be the case in the male fish D3, the efficiency of the females B1 and B4 varies from period to period during the growth season, but there is no marked increase in efficiency when growth and appetite attain maximal values.

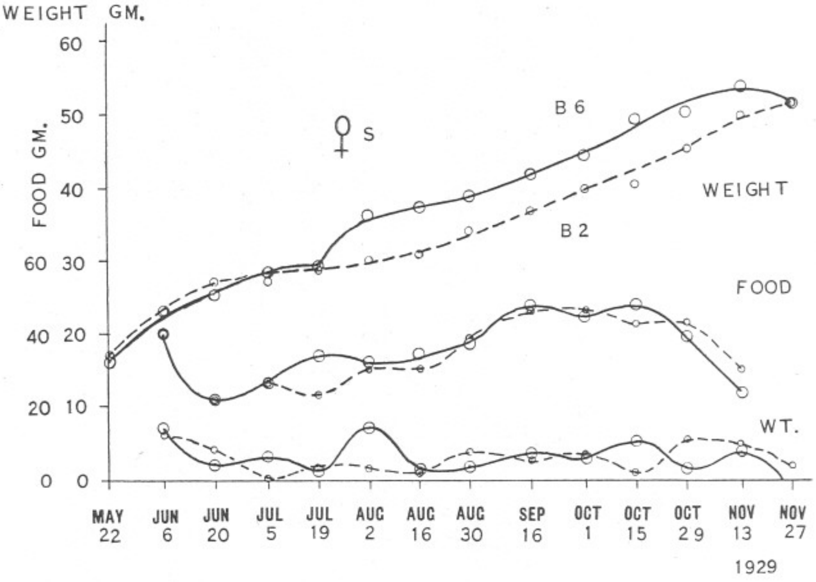

FIG. 8.—Growth and acceleration curves of body-weight and food-weight for the females B6 and B2. (Cawsand, 1929.)

The curves of growth in weight of the females B1 and B4, like that of the male D3, are sigmoidal in form (Fig. 7). During the first half of the experiment the curves follow each other closely, but differences are shown towards the end of the period. The point of inflexion of the curve for B4 is reached in mid-November, while that of the curve for B1 may be considered as reached during early December. The acceleration curves of food and body-weight increments for the fish B1 and B4, shown in Fig. 7, suggest that there is some connexion relating them, despite the periodic variations in efficiency indicated from period to period.

The curves of growth in length of the fishes B1 and B4 are shown in Fig. 9, side by side with the corresponding curve for the male D3. It is seen that, as in the case of the male, this curve is a straight line one for the early part of the experiment in each case, and that the curves for the female are very similar. The slopes of the B1, B4 curves are less steep than that for the D3 one. Even during the latter parts of the experiments, the relationship between length and time appears to be a linear one, a straight line with a lesser slope being obtained.

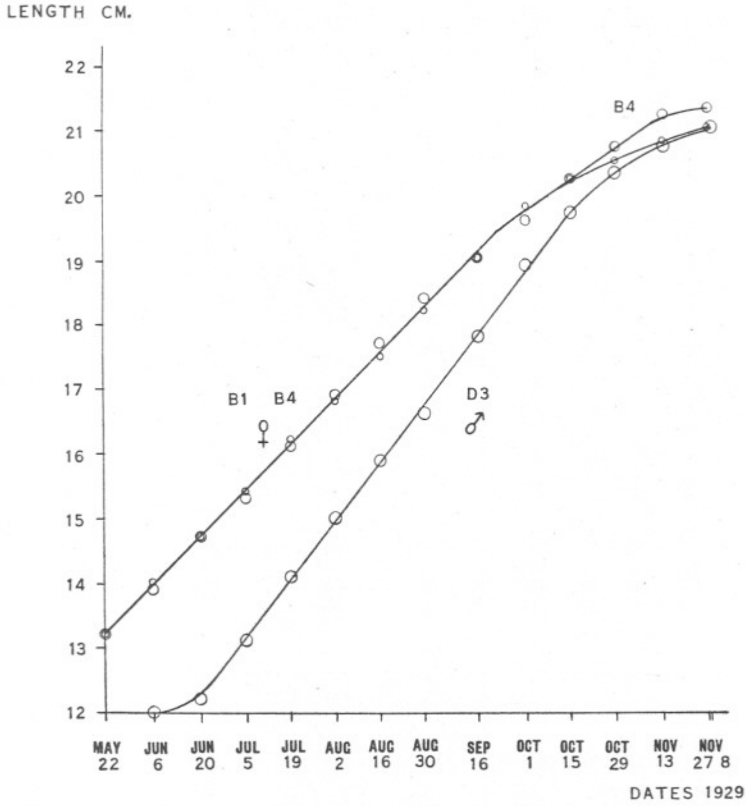

Fig. 9.—Growth curves of length for the male D3 and the females B1 and B4. (Cawsand, 1929.)

On September 17th the female fish B5a was substituted for an unsatisfactory fish B5, and the data concerning the substituted fish are shown in Table 25. The curve of growth of this fish, together with acceleration curves for body-weight increase, and food increments is shown in Fig. 7.

This fish is especially interesting in that it shows a remarkable acceleration of growth in weight during October, together with a greatly increased appetite for food and a rapid improvement of the general condition as indicated by the weight/length³ ratio. The body-weight of this fish was increased during October by more than 27 gm., and during this month it consumed at least 1·0 gm. of food per day more than the fishes B1 and B4, at the same time showing an increased efficiency over these fish. The point of inflexion of its growth curve was reached very shortly after the period of maximum growth and towards the end of the experiment it was losing weight.

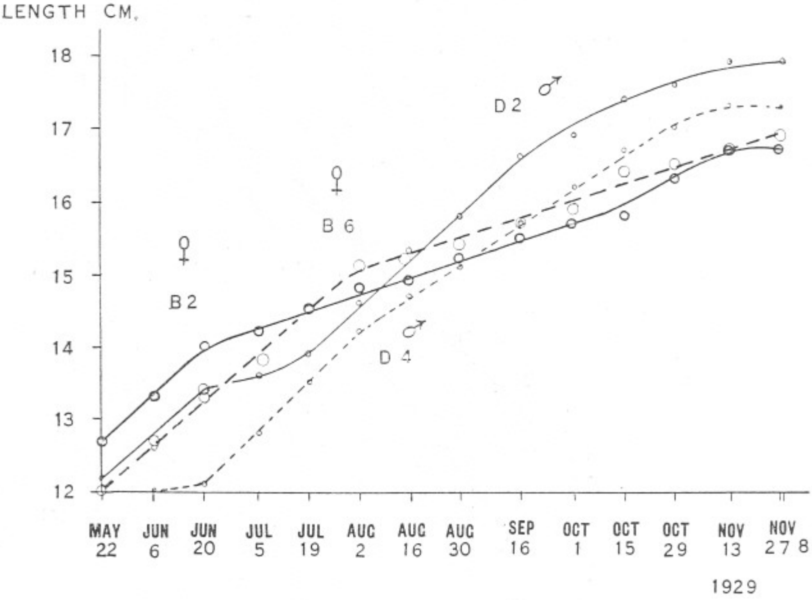

FIG. 10.—Growth curves of length for the males D2 and D4 and the females B2 and B6. (Cawsand, 1929.)

Growth occurring in the fishes B2 and B6 during the earliest periods of the experiments compares closely with that occurring in the fishes B1 and B4. They gained substantially in both length and weight (Tables 26 and 27), and improved in general condition. But both received setbacks which inhibited growth and from these never completely recovered, although B2 made attempts during late August and September, B6 during late July and early October. B6 maintained a good general condition, as measured by the weight/length³ ratio, throughout. The growth curves and acceleration curves of body-weight and food increments are shown in Fig, 8.

The growth curves of length for the females B2 and B6 are shown in

Fig. 10 along with those for the males D2 and D4. Taking B2 first, it is seen that inhibition of growth in length took place during late June, after a short period of what appears to have been typical growth. This inhibition of growth in length is paralleled by a corresponding inhibition shown by the male D2. A difference is seen to follow the inhibition. Whereas in B2 the inhibition is permanent, the relationship between growth in length and time continuing to be a linear one yet a different one as shown by the change in the slope of the curve (Fig. 10), that in

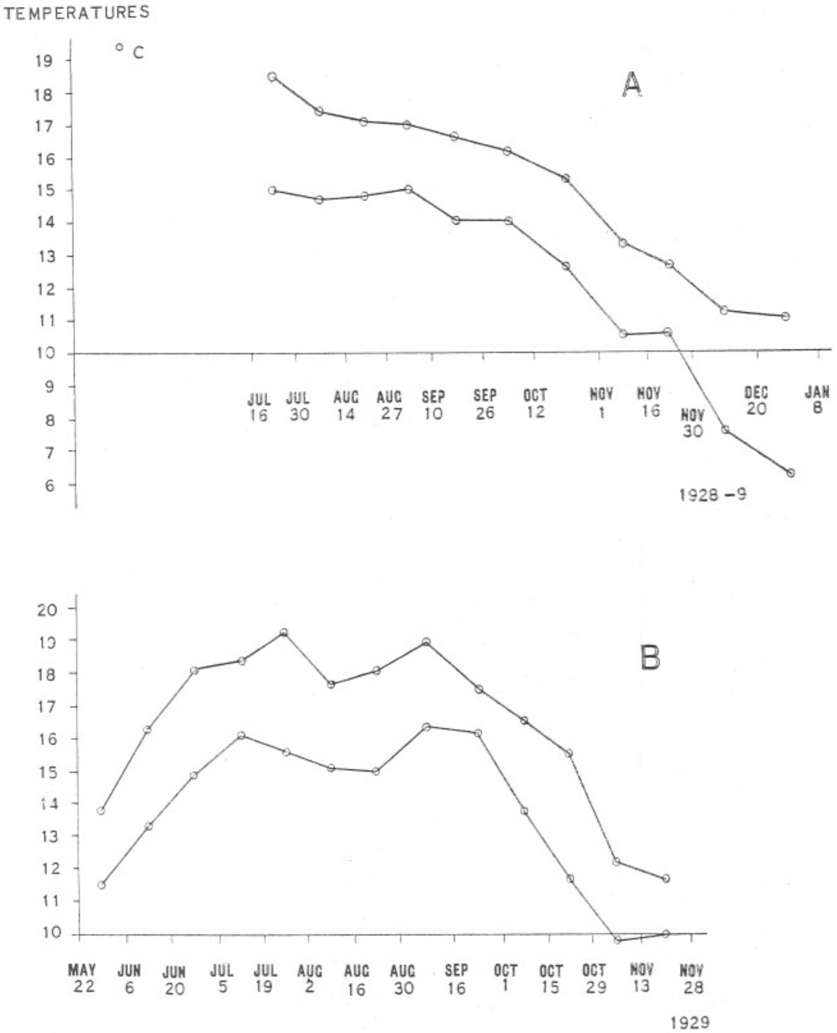

FIG. 11.—Graph of maximum and minimum temperature at Cawsand. [A] 1928–29; [B] 1929.

D2 is temporary, the old linear relationship being continued at least until mid-September. These characteristics are also shown by the curves of growth in weight, D2—Fig. 6, and B2—Fig. 8. The inhibition of growth in weight shown by the male fish D2 during the month of August and attributable to a fall in temperature is not accompanied by inhibition of growth in length, the same linear relationship between growth in length and time obtaining throughout, from mid-July to mid-September. The case of the female B6 is different, however. Growth in both length and weight is typical until August, after which growth inhibition occurs in both respects (Figs. 10 and 8). This inhibition may be attributed to fall in temperature of the sea-water in the pond. It thus appears that growth in both length and weight is influenced by temperature.

A temperature graph for the 1929 experiments is shown in Fig. 11 (B). A similar graph for the preliminary experiments of 1928 is also shown (A).

3. CONCLUSIONS DRAWN FROM THE EXPERIMENTS OF 1929 (CAWSAND).

(1) A mean male fish 12·7 cm. in length and 16·7 gm. in weight was able to maintain itself and also to increase its weight by 1·7 gm. during 44 days from May 22nd, 1929, on an average daily ration of 0·43 gm. of Mytilus flesh. The maintenance ratio, i.e. the ratio of food consumed per day/average body-weight, approximates to 0·025, but it is suggested that this value is high as is shown by the slight increase in weight. A more accurate value would approximate more closely to the value obtained for the mean female fish (*vide infra*).

(2) A mean female fish 13·6 cm. in length and 22·1 gm. in weight gained 0·5 gm. in weight during the period stated above, when it consumed an average daily ration of 0·42 gm. of food, or 0·019 its average body-weight.

(3) The average daily ration of food required to maintain the weight of any male or female fish constant appears to vary from period to period during the course of the experiments.

(4) The ratio of food required per day for purposes of maintenance/average body-weight of a fish appears to vary in different fish. In general it tends to fall in value with increase in size of the fish.

(5) The maintenance requirements of any fish appear to diminish appreciably during late October and November, and the fall is synchronous with fall in temperature of the sea-water.

(6) Loss of weight shown by any fish is not generally accompanied by decrease in length, and the regaining of weight is accompanied by

increase in length. The results of such loss of weight may be shown in the lowered general condition of the fish, as indicated by the weight/length^3 ratio, for months following the loss, even though a slight food allowance is available for purposes of growth.

(7) The growth curve of weight of fully-fed male and female fish is sigmoidal and asymmetrical. The maximum acceleration of growth in weight appears to occur during late September, when appetite for food is also a maximum. The efficiency of a fish, as measured by the quantity of food required to produce 1·0 gm. of fish, varies from time to time. In the male fish the greatest efficiency obtains when growth and appetite attain maximal values.

(8) Growth in length of male and female fish alike is an arithmetical function of time. The relationship holds good for the period of most rapid growth during the season.

(9) Growth inhibition may be followed by a strikingly increased acceleration of growth, when the fish displays a greatly enhanced efficiency. Appetite may be increased tremendously at the same time.

(10) Temperature appears to influence growth directly. Thus a fall in temperature may induce an inhibition of growth in both length and weight. If an increase in temperature follows the inhibition is overcome, other things being equal, and growth acceleration occurs. But such inhibition may also be rendered permanent for the growth season considered.

V. RESULTS OF THE LYMPSTONE EXPERIMENTS OF 1929.

1. Introduction.

A series of experiments similar to the revised experiments of Cawsand was carried out at the Ministry of Agriculture and Fisheries Mussel Tanks at Lympstone in the estuary of the River Exe, commencing on June 24th, 1929, under the care of Mr. H. Lees, Tank Superintendent. The boxes used were made at Cawsand and were identical with those used in the revised Cawsand experiments. They were suspended in the large tank A. The methods employed were precisely the same as those employed in the Cawsand experiments, and the same precautions were taken in weighing back food left over from any meal. Mr. Lees also kept temperature records of the water daily. The data obtained from the experiments were handed over to me by Dr. E. S. Russell in order that a comparison could be afforded of the two series of parallel investigations.

2. Minimum Requirements and Maintenance.

The results of the experiments on minimum requirements and maintenance with the male fishes, L1, L4, L3 and L2 are shown in Tables 28, 29, 30 and 31. It is seen that in all cases, excepting that of L4b, there is a slight loss of weight during the early stages of the experiments, but that in all cases the lost weight was regained and slight increases of weight occur.

The average quantity of food taken per day by the male fish L1 during periods included between September 16th and November 25th is seen to have been fairly constant (Table 28), but the weight of the fish varies during successive periods. For the periods ending September 30th, October 14th and November 11th approximately 0·95 gm. of food allows of an increase in weight. For the periods ending October 28th and November 25th, 0·90 gm. of food per day results in a slight loss of weight. Thus, between 0·90 gm. and 0·95 gm. per day appears to be a measure of the maintenance requirements of this fish. For the whole range of the experiment to November 25th (and it is not until slightly later than this that both maximum and minimum temperatures fall below 10° C.), 0·90 gm. of food per day allows of an increase over the initial weight of 3·8 gm. during 95 days. The average weight of the fish has been 52·2 gm.

L4a, a fish of 84·7 gm. weight, loses weight on 0·85 gm. of food per day, which, judging according to the requirements of L1, seems an inadequate daily ration. However, for a period of 14 days, 0·88 gm. of food per day allows of a slight increase in weight (Table 29). The slightly smaller fish, L4b, to November 25th, loses weight if the daily ration falls below 1·0 gm. (and in one case when it is as high as 1·30 gm.). For the whole range of the experiment to November 25th, an average daily ration of 1·11 gm. of food allows of a slight increase in weight (1·8 gm.).

L3, with an initial weight of 105·3 gm., loses weight if less than 1·30 gm. of food is taken daily per any fortnightly period, and gains weight if more than 1·38 gm. is taken (Table 30). For the whole period to November 25th, a daily ration of 1·32 gm. of food allows of an increase in weight of 4·1 gm. During this period, 78 days, the fish has taken approximately its own weight of Mytilus flesh.

L2 suffers loss in weight when the daily ration for any fortnightly period to November 25th is less than 1·30 gm., and gains in weight if this ration is over 1·66 gm. Taking the whole range to November 25th, 1·44 gm. of food per day results in a loss of 0·5 gm. from the initial weight of 129·9 gm. (Table 31).

In Table 32 are shown the results of two shorter range experiments, which do not appear to conform to those of the longer range experiments mentioned above. The maintenance requirements of L1a appear especially to be relatively low ones, those of L2a high ones taking the loss of weight into account (cp. with L1, Table 28).

In Table 33, the daily rations supplied to the male fishes L1, L4b, L3 and L2 are shown as fractions of the average body-weight. The order presented is one of increasing body-weight from left to right, initial and final weights being shown on each side of the fish index. The maintenance ratio is shown for each fortnightly period and also cumulatively from the commencement of the experiment. For L1 the value of the ratio for periods from August 19th to November 25th varies between 0·015 and 0·019. For L4b the corresponding variation is from 0·010 to 0·018, for L3 from 0·010 to 0·015 and for L2 from 0·009 to 0·014. Thus the range tends to become lowered with increase in size of the fish. If the whole period to November 25th be taken, the values of the ratio for these fish, taken in the order presented above, are 0·017, 0·015, 0·012 and 0·011. The accuracy of the last figure is open to some doubt being slightly beyond the accuracy of the weighings, but the argument is not thereby robbed of its force, especially as the values given are all subject to the same errors. Thus there appears reasonable proof of the fall in value of the maintenance ratio with increase in size of the fish. The same conclusion is reached if the values for the daily rations, estimated to November 25th, are plotted against the body-weight of corresponding fish.

For female fish the results are similar to those of males. Neglecting for the moment results obtained after November 25th, L5 shows a loss in weight if the average daily ration falls below 0·81 gm. (except in one instance), and an increase in weight if it is 0·81 gm. or over (Table 34). To November 25th 0·88gm. of food per day results in an increase over the initial weight (62·8 gm.) of 4·1 gm. L6 (initial weight, 71·2 gm.) loses weight when the daily ration falls as low as 1·1 gm. and gains weight if it is over 1·2 gm., except during late November. To November 25th an average daily ration of 1·19 gm. results in a slight loss of weight (1·1 gm.) (Table 35). L7 (initial weight, 104·8 gm.) suffers loss of weight if an average quantity of food less than 1·4 gm. per day is taken, except during November, and to November 25th loses 4·2 gm. in weight after having consumed an average daily food ration of 1·32 gm. (Table 36). L8a (initial weight, 102·0 gm.) requires approximately 1·3 gm. of food per day, while L8b (initial weight, 114·0 gm.) loses 0·4 gm. in weight on an average of 1·51 gm. of food per day (Table 37).

The average daily rations of the female fishes mentioned above are shown as fractions of the average body-weight in Table 38. Estimates are shown for each fortnightly period, and also cumulatively from the commencement of the experiments. The fall in value of the maintenance ratio with increasing size of fish is not as well marked as in the case of males, but is shown all the same. To November 25th the values, taken for increasing sizes (left to right, Table 38) are 0·014, 0·017, 0·013 and 0·013. The fishes L5 and L6 are of approximately the same size and these results show the likelihood of considerable individual variations in maintenance requirements.

The results of shorter range experiments are presented in Table 39. The smallest female, like the smallest male, requires a relatively high average daily food ration. This is also shown in Table 40, where it is also seen that despite considerable variations, there is a decrease in value of the maintenance ratio in larger fish.

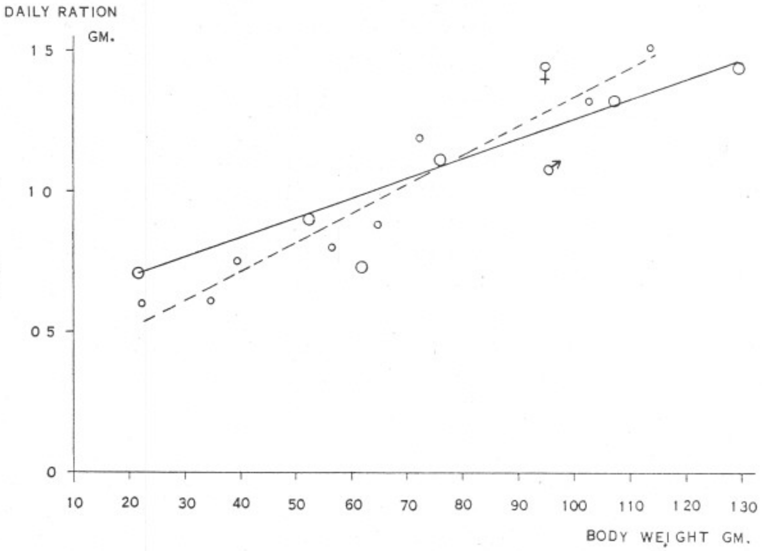

FIG. 12.—Graph showing the variation in maintenance requirements with size of fish. The abscissæ represent body-weights, the ordinates values of daily rations for purposes of maintenance. (Lympstone.)

Fig. 12 attempts to show graphically the relationship between the size of various fish and their maintenance requirements. These values are taken from preceding tables, and represent averages to November 25th except in the lower part of the graph where values from Tables 32 and 39 are employed. The points plotted are :

[♀] (gm.)	L6a	L5a	L8a	L7a	L5	L6	L7	L8a	L8b
Average Body-Wt.	22·3	34·6	39·4	56·5	64·8	71·7	102·7	103·2	113·8
Average Daily Ration	0·60	0·61	0·75	0·80	0·88	1·19	1·32	1·32	1·51

[♂] (gm.)	L2a	L1a	L1	L4b	L3	L2
Average Body-Wt.	21·6	62·0	52·2	76·0	107·3	129·6
Average Daily Ration	0·71	0·73	0·90	1·11	1·32	1·44

It is seen that the value of the ratio probably falls off with increasing size of fish, more rapidly in males than in females.

3. MAXIMUM REQUIREMENTS AND GROWTH.

The final results of the experiments on maximum requirements and growth at Lympstone are summarised in Table 41. As in the Cawsand experiments, considerable variation is shown in the growth of different individuals. One male (L11) made great progress, while two females made very satisfactory efforts to rival this male. The average quantities of food taken per day vary considerably, and for the fish displaying the most rapid growth-rate the quantity is slightly more than 6 gm. per day. It is surprising to note that this average daily ration is almost twice as great as that consumed by the most actively growing fishes at Cawsand (3·3 gm. per day). Growth was correspondingly greater at Lympstone, but the efficiency of the Cawsand fish was slightly greater, in male and female alike. At Lympstone the male again appeared to be rather more efficient than the female.

Data concerning the experiment with the male fish L11 are shown in Table 42. Maximum growth takes place during August although the increments added to the weight of the fish during September and October are almost as great as those for August.* This is also shown in the acceleration curve for body-weight increase increments (Fig. 13). The general condition of the fish, as shown by the weight/length^3 ratio, is best during October and November, and better than was found in any instance at Cawsand. The appetite of the fish is greatest during late September and early October, when the efficiency of the fish is near its maximum value, and the maximum daily ration on the average for the experiment is 7·5 gm. It is noteworthy that this fish took from 7·0 gm. to 7·5 gm. of food per day consistently from July 22nd to October 14th, i.e. there are no peaks on an acceleration curve of food increments such as are found on the corresponding curve for increments of increase in body-weight. The efficiency of the fish varies considerably from time to time, which suggests that there is no continuous direct relationship between the quantity of food consumed and growth in weight. Growth in length appears to follow a linear relationship with time (Fig. 14), and it appears strange that the curve for growth in weight is representable as a straight line curve to November 11th, when inhibition takes place (Fig. 13).

The male fish L10 barely doubled its initial weight during 98 days (Table 43), consuming 9 times the average body-weight for the whole period of food. Maximum growth occurred during July, but the best general condition obtained during late August, when the appetite was greatest and the efficiency low. The curve of growth in weight is shown in Fig. 13. And L9 did not succeed in doubling its initial weight although it consumed 8½ times its average body-weight for the whole range of the

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* The increase in weight for July 8th is neglected.

experiment (Table 44). Maximum growth obtained in this fish during late July and early August and here, when appetite was a maximum, efficiency was very low. The growth curve of weight is shown in Fig. 13. The male fish L12 displayed a greater average growth-rate (Table 45).

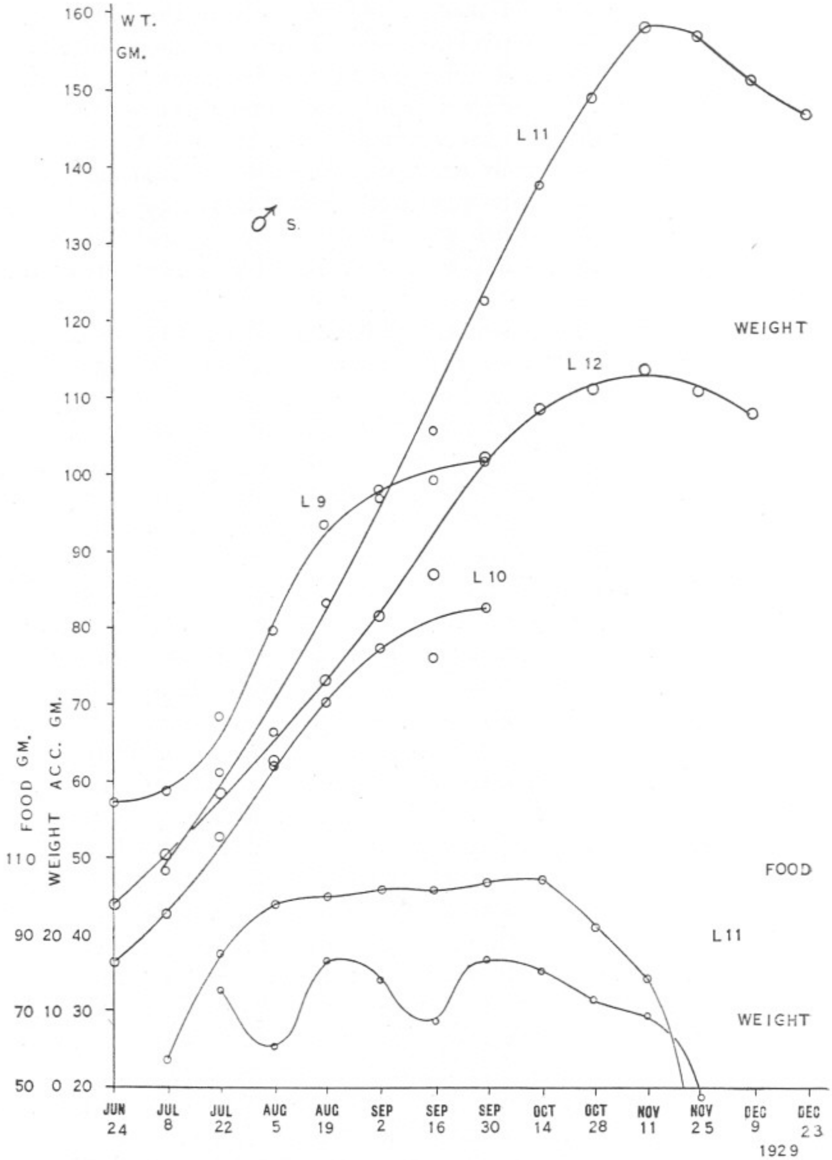

FIG. 13.—Growth curves of weight for the males L9, L10, L11 and L12, together with acceleration curves of food and body-weights. (Lympstone.)

Maximum growth in weight occurred during September, although growth was also rapid during August. The efficiency of the fish varied considerably, and was high during early August and late September. During the latter period the general condition was at its best. The curve of growth is shown in Fig. 13.

Among the females, L15 progressed well. The final weight at the point of inflexion of the growth curve was $4\frac{1}{2}$ times the initial weight, and approximately 10·7 times the body-weight of food had been taken. Growth in weight was most rapid during August, but almost as rapid during September and October (Table 46). Appetite was greatest during late September and early October, when efficiency was highest.

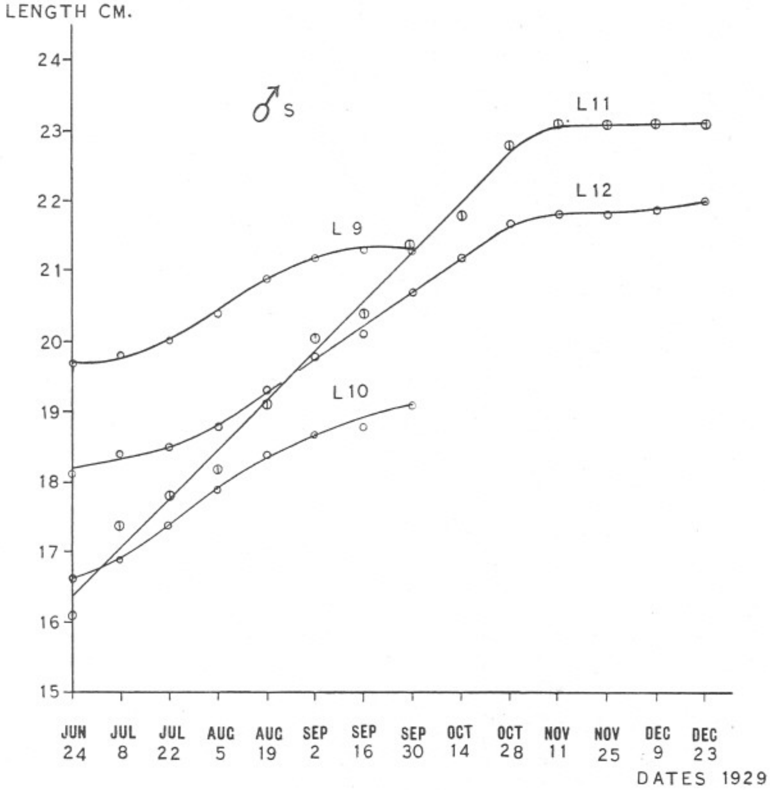

Fig. 14.—Growth curves of length for the males L9, L10, L11 and L12. (Lympstone.)

The efficiency of L16 was consistently high, its lowest during growth being 10·2 gm. of food per gm. of fish, and the appetite was similarly very great. No other fish took as much as 8·9 gm. of food per day, which quantity this fish consumed consistently for a month, from September 16th to October 14th, during which period the body-weight was increased by 38·6 gm., the greatest increase recorded for any two consecutive fortnightly periods. During this period of rapid growth the highest value for the weight/length³ ratio recorded for these experiments was reached (Table 47). The growth curve of weight is shown in Fig. 15.

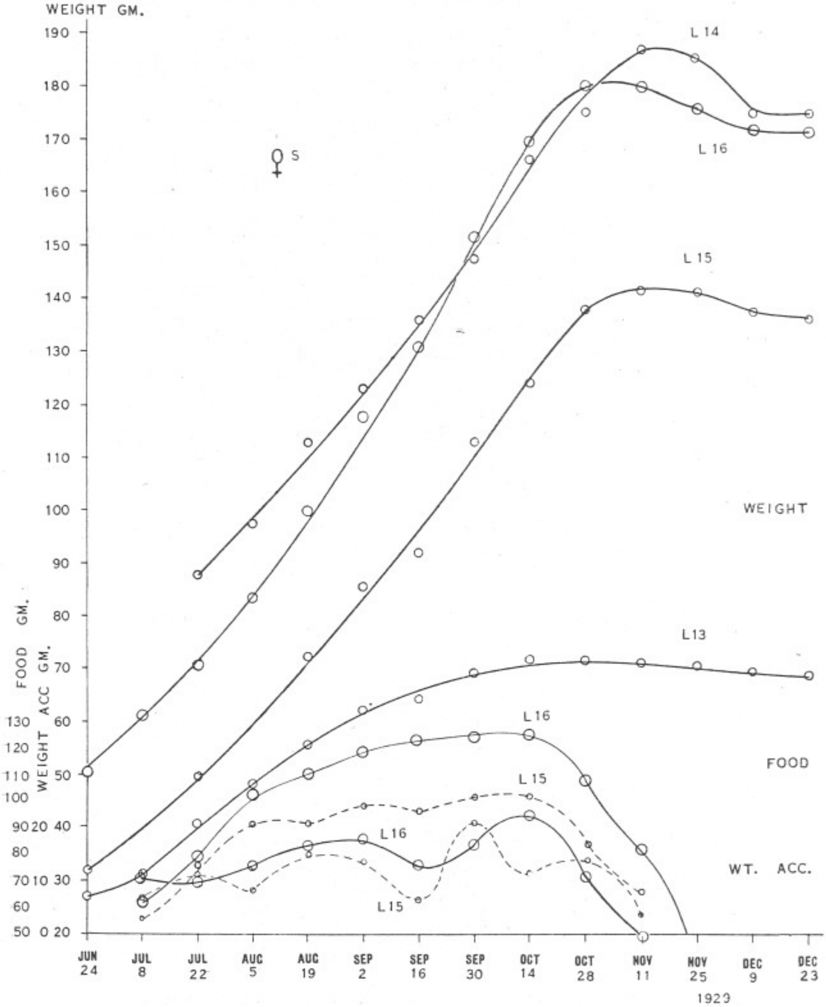

FIG. 15.—Growth curves of weight for the females L13, L14, L15 and L16, together with acceleration curves of food and body-weights for L15 and L16. (Lympstone).

The growth-rate of the female fish L13 was very slow, an increase in weight of 9·5 gm. during July being the greatest for any fortnightly period during the course of the experiment. The efficiency of the fish was low, especially after July, and the general condition ceased to improve. It seems probable that inhibition of growth took place during August (Table 48 and Fig. 15).

The female L14 is probably a 3-year old fish, and it is interesting to compare it with L16. For both fishes alike, maximum growth for any two consecutive periods occurs during late September and early October, when appetite is greatest, efficiency relatively high and the general condition at its best (Tables 49 and 47). The smaller fish took more food, however, and eventually reached to within 9 gm. of the final weight of the larger.

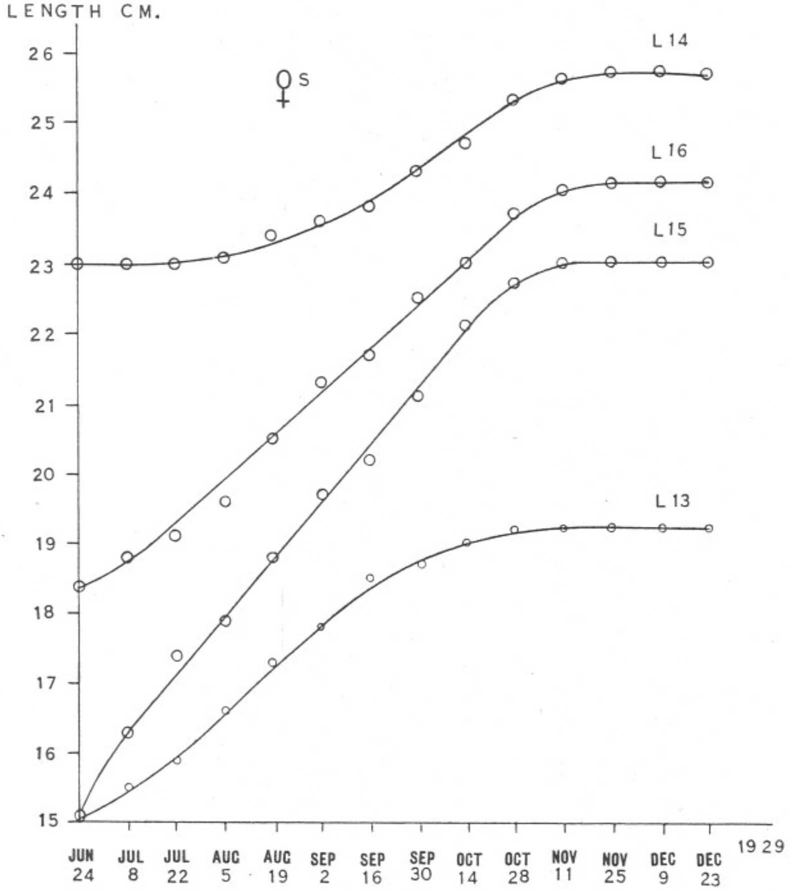

FIG. 16.—Growth curves of length for the females L13, L14, L15 and L16. (Lympstone.)

A characteristic feature of growth of the Lympstone fishes is the abruptness of a retardation of the process and the loss in weight incurred immediately after growth inhibition, during late November and December. Appetite diminishes very considerably when the maximum temperature approaches 10° C. and is lost altogether when this temperature sinks below 10° C. During the growth season there does not appear to be any simple relation between the quantity of food taken per any fortnightly period and the increment of growth in weight for the period. The acceleration curve for food taken is an unbroken one for several consecutive periods, while that of added increments of weight is broken and shows two or three peaks (Fig. 13—♂ and Fig. 15—♀). The efficiency of any fish appears to vary considerably from period to period.

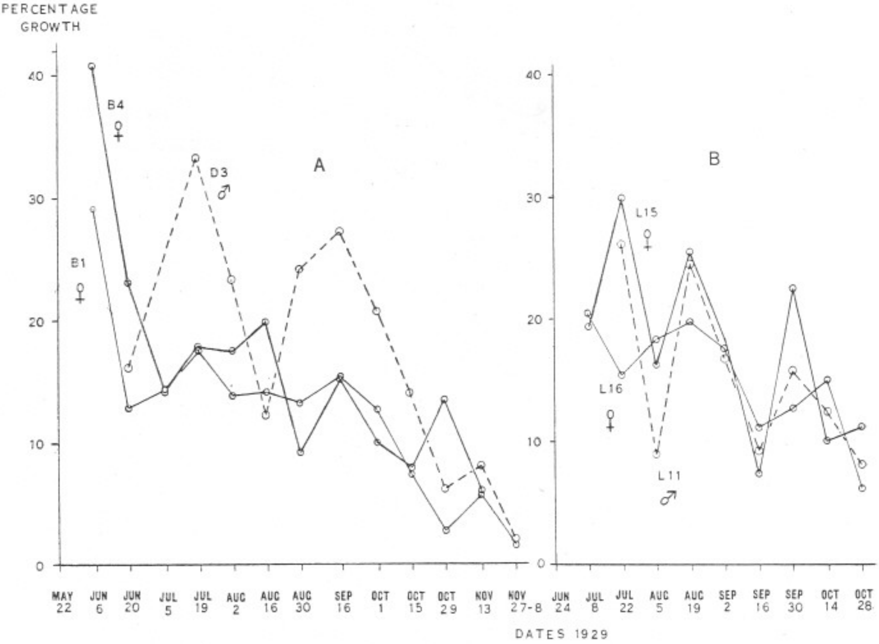

Fig. 17.—Graph showing percentage growth during specified periods for certain maximum fed fish. [A] B1 and B4 (♀'s) and D3 (♂), Cawsand, [B], L11 and L16 (♀'s), and L15 (♂), Lympstone.

Growth in length of maximum-fed male and female fishes is shown graphically in Figs. 14 and 16, and it is readily seen that considerable variation occurs in different individuals, especially in the case of males. In the cases of fish of either sex showing any considerable growth, a straight line curve is obtained from July to October. Table 50 (B) and Fig. 17 (B) attempts to show how the percentage growth in weight varies from period to period in both sexes. A coincidence is seen in the fluctuations in percentage growth of the male L11 and the female L15, which suggests that a factor which operates to modify the growth-rate from period to period influences both sexes. From August 5th to the close of the experiments, L16 (♀) shows some degree of coincidence also. A corresponding curve of percentage growth is shown for the Cawsand fish (Fig. 17 [A]), the data for which is given in Table 50 (A). Similar periodic fluctuations are seen to obtain, but not altogether independently of sex. It is readily seen by comparison of (A) and (B) sections of Fig. 17 that the percentage growth is greater in the case of Cawsand males, but smaller in the case of females.

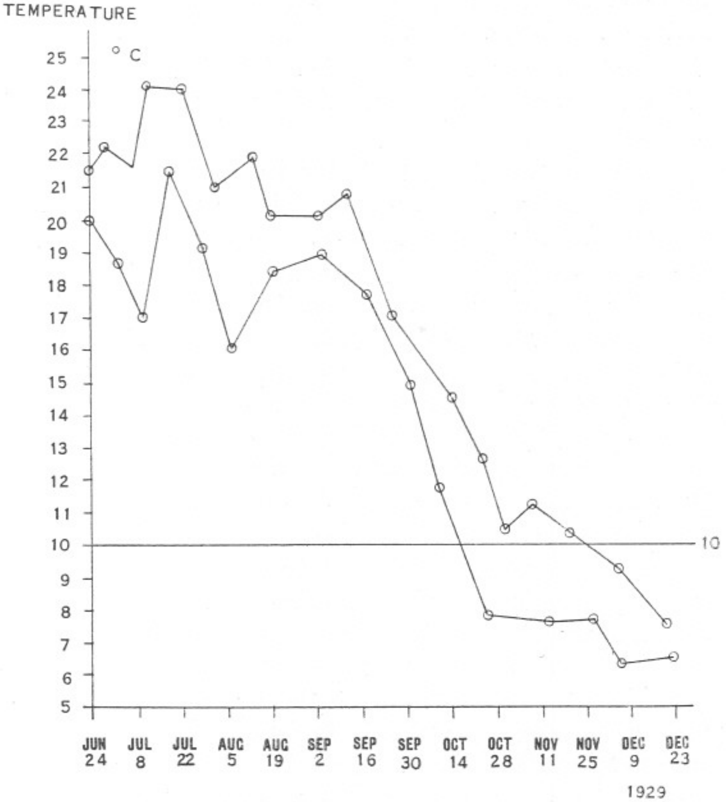

Fig. 18.—Graph of maximum and minimum temperatures at Lympstone (1929).

In Fig. 18 is shown a graph of maximum and minimum temperatures of the tank recorded at Lympstone. The temperatures at Lympstone are seen to be consistently much higher from June to September than those obtaining at Cawsand. This fact in part explains the increased appetite and growth of the maximum fish as compared with those at Cawsand and also the slightly higher values of maintenance rations.

4. CONCLUSIONS DRAWN FROM THE EXPERIMENTS OF 1929 (LYMPSTONE).

(1) Between 0·90 gm. and 0·95 gm. food per day is necessary in order to maintain constant the body-weight of a 50-gm. male fish (L1).

(2) About 1·4 gm. of food per day is necessary in order to maintain constant the body-weight of a 130-gm. male fish. The maintenance requirements of fish 50 gm. to 130 gm. in weight range from 0·9 gm. to 1·4 gm. of food per day.

(3) For female fish 60 gm. to 114 gm. in weight, from 0·8 gm. to 1·5 gm. of food per day is required in order to maintain the weight constant.

(4) The ratio of food required per day for purposes of maintenance/average body-weight of a fish diminishes as the weight of the fish increases, in male and female alike.

(5) Maximum growth for the experiments with male plaice was displayed by L11, which, during a period of 140 days from June 24th, 1929, increased its length from 16·1 cm. to 23·1 cm., its weight from 23·2 gm. to 158·6 gm. It consumed 926 gm. of food, an average of 6·6 gm. per day, and for the whole period, 6·8 gm. of food produced 1·0 gm. of fish. Maximum growth, appetite and efficiency obtained during the same period, September 16th to October 14th.

(6) The female plaice L15 increased its length from 15·1 cm. to 23·0 cm. during 126 days from June 24th, its weight from 31·9 gm. to 141·1 gm. Maximum growth, appetite and efficiency obtained synchronously during late September. The female L16 increased its length from 18·4 cm. to 24·0 cm. during a period of 140 days, its weight from 50·5 gm. to 179·3 gm. From September 16th to October 14th, a period of 28 days, the fish took roughly 250 gm. of food and increased its weight by 38·6 gm., 26 per cent of the weight on September 16th.

(7) Growth of both males and females is abruptly retarded when the maximum temperature of the sea-water approaches 10° C. Growth ceases and loss of weight is incurred when the maximum temperature falls below 10° C.

VI. GENERAL DISCUSSION OF RESULTS.

It was seen that during the preliminary experiments of 1928, the average quantity of food required daily for purposes of maintenance by a mean male fish 44 gm. in weight is approximately 0·6–0·7 gm. But it was suggested that because the decline of a fish which probably failed to obtain food, the value obtained was undoubtedly a low one, and that in all likelihood 0·7–0·8 gm. per day is a more accurate value. Shown as a ratio of the body-weight the value ranges between 0·017 and 0·019, and was suggested as being approximately constant for this fish at 0·018 (Table 1).

In Table 51 the average daily food ration of the above mean male fish of the 1928 experiments is shown to November 30th. For a fish of average weight 42·1 gm. the daily ration is 0·7 gm., or 0·017 of the average weight. Data are also shown in this table which enable us to compare the above result with the results obtained under more refined conditions during 1929 at Cawsand and at Lympstone. The mean A fish of 1928 best compares with C6a (1929) as regards weight, and close conformity is obtained between the observed values for a daily maintenance ration. It is conclusively shown that for a 42 gm. male fish, i.e. a fish commencing its third season of growth, 0·7 gm. of food or 0·017 of the body-weight, per day is sufficient to maintain the body-weight constant.

For a smaller fish a smaller daily ration is required of course, but the decrease in value of this ration is not directly proportional to the decrease in weight of the fish. Thus, C5a, which is 30 gm. in weight, requires 0·6 gm. of food per day, or 0·019 of the body-weight (Table 51), while the mean C fish of 1929, which is much smaller, weighing 17·6 gm., requires 0·4 gm., or 0·024 of the body-weight of food per day. It is thus rendered clear from comparisons afforded by the results of the Cawsand experiments alone, that the value of the maintenance ratio, i.e. the ratio of food required per day to body-weight, decreases as the weight of the fish increases in the case of males. And this interesting result receives support from the results of the Lympstone experiments with male fish. Thus L1, which weighs 52 gm., requires 0·9 gm. or 0·017 of the body-weight of food per day, while L2, which weighs 130 gm., requires 1·4 gm. or 0·011 of the body-weight of food daily. It is clear that considerable variation in the value of the maintenance ratio must occur during the third growth season of a plaice. If the initial and final weights are, say, 18 gm. and 130 gm., the fraction of the body-weight required as daily ration steadily decreases from 0·024 towards 0·011, the actual weight of food per day increasing from 0·4 gm. to 1·4 gm. In Table 51 several intermediate values are shown, while in Fig. 19 a graph of the variation in maintenance rations with size is shown, as given with the data of the results of Cawsand and Lympstone experiments. As was suggested, the curve is not a straight line one, although the Lympstone data alone gave such a curve. The curve would approximate more closely to a straight line, however, if the temperatures at Lympstone and at Cawsand were identical. The higher temperatures obtaining at Lympstone presumably cause the maintenance requirements to be higher there than at Cawsand.

Comparing the results of the three sets of experiments for the females, it is seen that, as in the case of males, the fraction of the body-weight of food required daily for purposes of maintenance decreases as the weight of the fish increases. Thus a Cawsand female fish of 22 gm. requires 0·4 gm. of food per day, a similar fish of 42 gm. requires 0·6 gm. per day, while a Lympstone fish of 103 gm. requires 1·3 gm. per day ; 0·019, 0·015 and 0·013 of the body-weight respectively (Table 52). The maintenance requirements of several fish of various sizes between 22 gm. and 114 gm. in weight are also shown in Table 52, and a curve showing the relationship between the daily maintenance ration and size of fish is presented in Fig 19. The curve is open to the same objections as that for the males, but gives an approximation of some value. From the evidence obtained, it appears that the maintenance requirements of females are slightly less than those of males, for any fish below 100 gm. in weight.

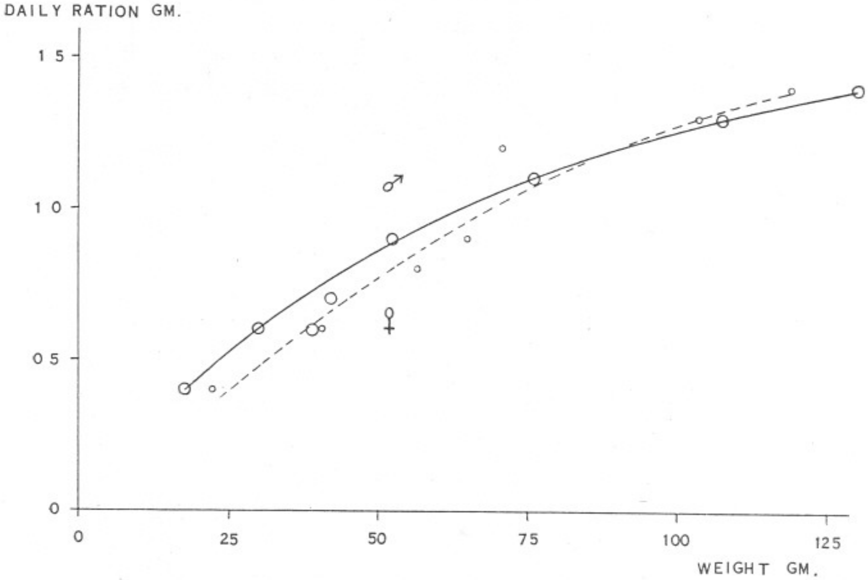

Fig. 19.—Graph showing relationship between daily maintenance ration and size of fish. Based upon Cawsand and Lympstone experiments of 1929.

It must be remembered in spite of the generalisations made above, that the maintenance requirements of any fish appear to vary in an irregular manner from one fortnightly period to another. This obtains for Cawsand and Lympstone fish alike. Examples have been given in the general description of the results and merely is it intended here to emphasise the fact that such variations do occur, although it is not possible to account for them.

One fact stands out clearly when one compares the maximum requirements and efficiency of male fish used in the Cawsand experiments of 1928 and 1929, that the maximum requirements of 1928 were much greater, the efficiency much smaller than in the following year (Table 53). The mean male fish of 1928 took 1129 gm. of food, while D3, the most rapidly growing male fish of 1929, took only rather more than half this quantity and yet increased its weight more substantially. The values obtained from the refined experiments of 1929 are undoubtedly more accurate than those from the experiments of the previous year, and the efficiency of the fish is much greater than the experiments of 1928 indicated. Over a period of 175 days, D3 increased its weight by 1·0 gm. for every 6·5 gm. of food it consumed, and took an average of 3·3 gm. of food per day. At Lympstone, where a higher temperature obtained, growth and appetite were greater, while efficiency was slightly lower. The male fish L11 took 953 gm. of food during a period of 154 days, giving an average of 6·2 gm. per day, and increased its weight by 1·0 gm. for every 7·1 gm. of food taken. It can be inferred, therefore, that the efficiency of a fully growing male fish during its third season of growth lies between 6·5 gm. and 7·1 gm. of food per gm. increase in weight. The fish D3 took 9·75 times the average body-weight for the season of food, while L11 took 10·5 times this weight over a slightly shorter period.

Similar results obtain in the case of female fish. The growth rates of males and females in the Cawsand experiments of 1929 are approximately equal as is appetite in the two sexes [cp. D3 (♂), Table 53, and B4 and B1 (♀s), Table 54]. The males show a rather more rapid growth-rate than the females at Lympstone, while at Cawsand in 1928 the reverse was the case. In the females as in the males, growth and appetite were greater at Lympstone than at Cawsand during the season of 1929, and similarly the efficiency was lower. L15 and L16 took 8·1 gm. and 8·5 gm. of food respectively per gm. increase in weight, while B4 and B1 took only 7·2 gm. and 7·6 gm. for a corresponding increase in weight. The efficiency of the male fish is greater than that of the female at Cawsand and Lympstone alike, and the efficiency of any fish is greater than was indicated by the results of the experiments of 1928 (Tables 53 and 54). The Cawsand fish B4 and B1 took 10 times and 9·5 times the average body-weight for the period respectively of food, the Lympstone fish L15 and L16, 10·3 times and 9·4 times this weight of food respectively, which figures correspond closely to those obtained for the males.

It is seen from Tables 53 and 54 that the growth-rate of different individuals varies considerably. It is difficult to understand why such variations occur. The Cawsand fish were trawled, and it might be argued that the treatment they receive during the process has a baneful effect upon certain individuals. But the Lympstone fish were seined and yet the variations are equally well marked here also. It may be that such variations in the growth-rate obtain under truly natural conditions. The fish D3 suffers a retardation of growth during mid-August, and also shows a fall in appetite for food (Fig. 5). There is also a fall in temperature during mid-August (Fig. 11, 1929). The retardation is temporary and is followed by an acceleration at a time when the temperature is rising. The fish D2 shows an almost complete inhibition of growth in weight during mid-August, which is followed by a very great acceleration, while the temperature of the pond is still rising. D4 shows a growth retardation during August and no acceleration follows it. It is not justifiable to assume that because two events occur simultaneously one necessarily acts as a cause to the other, and it may not be the case that growth retardation or inhibition was caused by a fall in temperature of the pond in the above instances, but it is reasonable to assume that the same causes influence different individuals to different degrees and that in the above instances variations in the growth-rate of fish not apparently injured in any way are the outcome of natural causes, rather than the results of accident during the process of trawling or seining. It is thus rendered necessary to ascertain the variations in the growth-rate occurring under truly natural conditions, which task lies outside the scope of this work.

The question of the relationship existing between the quantity of food taken and growth in weight remains unanswered. Over a period of 150–175 days the efficiency of fish showing a markedly rapid growth-rate varies but slightly. But that of different individuals varies very considerably. Even in the same fish, good, bad or indifferent, it varies considerably from time to time. In this connexion it is important to note the measure of efficiency for each period for D3 (Table 20), B1 (Table 23), B4 (Table 24), L11 (Table 42), L15 (Table 46), and L16 (Table 47), which may all be taken as " normal " fish showing typical growth curves of length and weight. The variations in weight increments added from period to period in these " normal " fish are well beyond reach of the error of the experiments. It is seen in the results of the Cawsand experiments, however, that the acceleration curves for food and weight increments show an approximate degree of correlation (Figs. 5 and 7) which suggests that the efficiency of these fish varies fairly closely about a mean. Thus, for B1, a female fish, the efficiency from May 22nd to October 1st, 1929, varies between 5·2 gm. and 7·1 gm. of food per gm. increase in weight of the fish. That of the male D3 to October 15th varies between 4·8 gm. and 9·8 gm. of food per gm. of fish. Such correlation is not found in the Lympstone results (Figs 13 and 15), where appetite is seen to be maintained irrespective of growth acceleration or retardation. Thus, the efficiency of L11 to October 14th varies between 2·3 gm. and 17·8 gm. of food per gm. of fish, while for the same period and the same measure of efficiency being understood, the figures for L15 range from 4·9 to 15·1, those for

L16 from 5·7 to 9·4 (the growth-rate here being uniformly rapid). Thus it is not possible to postulate even an approximately constant index of efficiency for any short period during the growth season.

ACKNOWLEDGMENT.

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TABLE 1.

Data Obtained from the Preliminary Experiment on Maintenance Requirements of Male Plaice.

Date. (1928)	Fish Nos., Lengths and Weights.												No. of days since previous weighing.	Total average food per fish per period (gm.).	Food per fish per day during period (gm.).	Mean fish (neglecting No. 1.).		Total average quantity of food per fish (of 5). gm.	Food per Fish per day (neglecting No. 1). gm.	Ratio food per day body wt.
	A1.		A2.		A3		A4.		A5.		A6.		Mean A fish.							
	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.				Lth.	Wt.			
July 16	16·8	44·0	16·2	47·0	16·5	45·0	16·1	43·0	14·4	28·0	16·4	45·0	16·1	42·0	—	—	—	15·9	41·6	—	—	—
,, 30	16·7	42·0	16·2	48·0	16·7	48·0	16·4	43·0	14·4	27·0	16·6	43·0	16·2	41·8	14	7·0	0·5	16·1	41·8	8·4	0·6	0·014
Aug. 14	16·9	38·0	16·4	45·0	17·0	50·0	16·4	48·0	14·4	25·0	16·6	40·0	16·3	41·0	15	6·5	0·4	16·2	41·6	7·8	0·5	0·012
,, 27	16·9	37·0	16·5	41·0	17·0	50·0	16·7	52·0	14·4	23·0	16·6	39·0	16·3	40·3	13	9·0	0·7	16·2	41·0	10·8	0·8	0·019
Sept. 10	16·7	35·0	16·4	42·0	17·0	51·0	16·9	54·0	14·4	22·0	16·6	39·0	16·3	40·5	14	9·0	0·6	16·3	41·6	10·8	0·8	0·019
,, 26	16·7	34·0	16·5	41·0	16·9	55·0	16·9	50·0	14·4	21·0	16·6	40·0	16·3	40·2	16	9·0	0·6	16·3	41·4	10·8	0·7	0·017
Oct. 12	16·8	31·0	16·6	44·0	16·9	54·0	16·9	48·0	14·5	21·0	16·7	42·0	16·4	40·0	16	9·7	0·6	16·3	41·8	11·7	0·7	0·017
Nov. 1	16·8	29·0	16·8	48·0	17·1	54·0	16·9	48·0	14·4	22·0	17·0	43·0	16·5	40·7	20	12·7	0·6	16·4	43·0	15·3	0·8	0·019
,, 16	16·8	26·0	16·8	44·0	17·2	53·0	16·9	47·0	14·5	18·0	16·9	40·0	16·5	38·0	15	9·7	0·6	16·5	40·4	11·7	0·8	0·019
,, 30	Dead		16·9	48·0	17·2	55·0	17·0	48·0	14·5	20·0	16·8	42·0	16·5	42·6	14	9·7	0·7	16·5	42·6	10·2	0·7	0·017
Dec. 20			17·1	50·0	17·3	57·0	17·2	52·0	14·6	22·0	16·9	45·0	16·6	45·2	20	11·2	0·6	16·6	45·2	11·2	0·6	0·014
1929 Jan. 8			17·3	52·0	17·4	59·0	17·4	52·0	14·6	25·0	17·0	46·0	16·7	46·8	19	13·8	0·7	16·7	46·8	13·8	0·7	0·015

TABLE 2.

DATA OBTAINED FROM THE PRELIMINARY EXPERIMENT ON THE MAINTENANCE REQUIREMENTS OF FEMALE PLAICE.

Date. (1928)	Fish Nos., Lengths and Weights.														Days in each period.	Average quantity of food per fish per period (gm.).	Food per fish per day (gm.).	Ratio food per day / average body-wt. (for period)
	B1.		B2.		B3.		B4.		B5.		B6.		Mean fish.					
	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.				
July 16	15·7	35·0	12·3	21·0	13·4	24·5	12·8	21·0	12·6	18·5	13·7	26·0	13·4	24·3	—	—	—	—
„ 30	15·7	35·0	12·8	24·0	13·8	29·0	12·8	20·0	12·7	15·5	14·0	27·5	13·6	25·2	14	7·0	0·5	0·020
Aug. 14	15·7	33·0	13·2	27·0	14·0	30·0	12·8	18·0	12·6	15·0	14·3	29·0	13·8	25·3	15	6·5	0·4	0·016
„ 27	15·7	31·0	13·8	33·0	14·5	33·0	12·9	17·0	12·7	15·0	14·6	[? 29·0] 39·0	14·0	? 26·7	13	9·0	0·7	0·027
Sept. 10	15·8	29·0	14·4	36·0	14·6	34·0	12·7	16·0	12·6	15·0	14·8	32·0	14·1	27·0	14	9·0	0·6	0·022
„ 26	15·7	29·0	14·7	36·0	14·9	37·0	12·8	17·0	12·7	14·0	15·3	35·0	14·3	28·0	16	9·0	0·6	0·022
Oct. 12	15·6	29·0	15·0	35·0	14·9	39·0	12·9	15·0	12·7	14·0	15·5	37·0	14·4	28·3	16	9·7	0·6	0·021
Nov. 1	15·7	28·0	15·0	38·0	15·4	45·0	12·7	15·0	Dead		15·6	40·0	14·9	33·2	20	12·7	0·6	0·020
„ 16	Dead		15·1	39·0	15·4	34·0	12·9	17·0			15·9	40·0	14·8	32·5	15	9·7	0·6	0·018
„ 30			15·4	38·0	15·8	38·0	13·2	19·0			15·6	45·0	15·0	35·0	14	9·7	0·7	0·021
Dec. 20			15·6	41·0	16·1	41·0	13·4	23·0			15·8	47·0	15·2	38·0	20	11·2	0·6	0·016
1929 Jan. 8			15·8	44·0	16·4	44·0	13·8	25·0			16·3	51·0	15·6	41·0	19	12·7	0·7	0·018

TABLE 3.

Data Obtained from an Experiment on Maximum Feeding and Growth in Male Plaice.

Date. (1928)	Fish Nos., Lengths and Weights.																						
	C1.		C2.		C3.		C4.		C5.		C6.		Mean C fish.		Mean growth per period		No. of days since previous weighing.	Average weight of food per fish per period	Maintenance allowance per period (=Bdy.-Wt.×M ×days)	Food per period available for growth	Food available for growth (cumulative)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.		(gm.).	(gm.).	(gm.).	(to 1 gm.).	Lth.	Wt.
July 16	16·8	46·0	15·6	36·0	16·2	37·0	15·4	30·0	16·4	42·0	15·9	42·0	16·0	38·8	—		—	—	—	—	—	—	
,, 30	16·9	53·0	16·5	39·0	16·9	42·0	15·8	38·0	17·2	50·0	16·2	42·0	16·6	44·0	0·6	5·2	14	71·7	7·6	64·1	64	0·6	5·2
Aug. 14	18·1	69·0	16·7	42·0	17·1	53·0	16·2	43·0	18·2	62·0	17·2	45·0	17·2	52·3	0·6	8·3	15	65·0	7·9	57·1	121	1·2	13·5
,, 27	19·6	96·0	17·2	53·0	17·8	58·0	16·5	47·0	19·0	73·0	17·9	52·0	18·0	63·2	0·8	10·9	13	90·0	12·9	77·1	198	2·0	24·4
Sept. 10	21·0	115·0	18·0	60·0	18·6	70·0	16·8	48·0	19·7	80·0	18·1	55·0	18·7	71·3	0·7	8·1	14	90·0	16·8	73·2	271	2·7	32·5
,, 26	22·4	137·0	18·8	66·0	19·8	84·0	17·2	55·0	20·3	86·0	18·5	62·0	19·5	81·7	0·8	10·4	16	90·0	19·4	70·6	342	3·5	42·9
Oct. 12	—		—		20·1	87·0	—		20·9	95·0	18·5	59·0	19·5	80·2	—	—	16	97·5	22·2	75·3	—	—	—
Nov. 1					21·2	101·0			21·1	100·0	18·8	59·0	20·4	86·7	0·9	6·5	20	127·5	30·5	97·0	97	0·9	6·5
,, 16					21·7	116·0			21·4	101·0	19·4	68·0	20·8	95·0	0·4	8·3	15	97·5	24·7	72·4	169	1·3	14·8
,, 30					22·6	128·0			21·8	104·0	19·8	76·0	21·4	102·7	0·6	7·7	1 4	97·5	22·6	74·9	244	1·9	22·5
Dec. 20					23·5	151·0			22·1	115·0	20·6	88·0	22·1	118·0	0·7	15·3	20	133·5	28·8	104·7	349	2·6	37·8
1929 Jan. 8					24·1	158·0			22·6	117·0	21·0	95·0	22·6	123·3	0·5	5·3	19	169·0	33·6	135·4	484	3·1	43·1
															3·5	42·9						3·5	42·9
														Totals	3·1	43·1	176	1129·2	227·4			3·1	43·1

TABLE 4.

DATA OBTAINED FROM AN EXPERIMENT ON MAXIMUM FEEDING AND GROWTH IN FEMALE PLAICE.

Date. (1928)	Fish Nos., Lengths and Weights.												Mean D fish.		Mean growth per period.		No. of days since previous weighing.	Average weight of food per fish per period (gm.).	Average weight of food per fish per day (gm.).
	D1.		D2.		D3.		D4.		D5.		D6.								
	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Ltd.	Wt.	Lth.	Wt.	Lth.	Wt.			
July 16	16·4	48·0	15·2	38·0	16·6	43·0	15·6	44·0	16·7	50·0	16·1	37·0	16·1	43·3	—	—	—	—	
,, 30	17·5	62·5	16·4	50·0	17·4	57·0	16·5	54·0	17·7	68·0	16·7	44·5	17·0	56·0	0·9	12·7	14	71·7	5·1
Aug. 14	18·8	80·0	17·3	57·0	18·8	76·0	17·7	66·0	18·9	81·0	17·3	50·0	18·1	68·3	1·1	12·3	15	65·0	4·4
,, 27	19·8	95·0	18·8	64·0	19·6	88·0	18·5	79·0	19·9	96·0	18·0	54·0	19·1	79·3	1·0	11·0	13	90·0	6·9
Sept. 10	20·6	100·0	19·1	79·0	20·5	105·0	19·7	95·0	21·0	116·0	18·7	63·0	19·9	93·0	0·8	13·7	14	90·0	6·4
,, 26	21·0	113·0	19·4	88·0	21·0	118·0	20·5	112·0	22·4	137·0	19·4	77·0	20·6	107·5	0·7	14·5	16	90·0	5·6
Oct. 12	21·5	127·0	20·5	103·0	21·7	131·0	21·3	111·0	23·2	155·0	20·1	83·0	21·4	118·3	0·8	10·8	16	97·5	6·1
Nov. 1	22·7	150·0	21·1	101·0	22·8	150·0	21·9	122·0	23·8	165·0	20·8	91·0	22·2	129·8	0·8	11·5	20	127·5	6·4
,, 16	22·9	157·0	21·2	100·0	23·1	149·0	22·1	124·0	24·3	175·0	21·0	102·0	22·4	134·5	0·2	4·7	15	97·5	6·5
,, 30	23·3	164·0	21·5	104·0	23·1	150·0	22·1	123·0	24·7	197·0	21·2	103·0	22·6	140·2	0·2	5·7	14	97·5	7·0
Dec. 20	23·8	176·0	22·3	114·0	23·5	155·0	22·6	128·0	25·2	205·0	21·2	104·0	23·1	147·0	0·5	6·8	20	133·5	6·7
1929 Jan. 8	24·1	186·0	22·6	121·0	23·4	157·0	22·9	128·0	25·6	203·0	21·3	112·0	23·3	151·2	0·2	4·2	19	169·0	8·9
													Totals		7·2	107·9	176	1129·2	

TABLE 5.

Data Obtained from an Experiment on Intermediate Feeding and Growth in Male Plaice.

Date. (1928)	Fish Nos., Lengths and Weights. E1. Lth.	E1. Wt.	E2. Lth.	E2. Wt.	E3. Lth.	E3. Wt.	E4. Lth.	E4. Wt.	E5. Lth.	E5. Wt.	E6. Lth.	E6. Wt.	Mean E fish. Lth.	Mean E fish. Wt.	Mean growth per period. Lth.	Mean growth per period. Wt.	No. of days since previous weighing.	Average weight of food per fish per period (gm.).	Average weight of food per fish per day (gm.).
July 16	17·2	53·0	14·0	25·0	17·0	54·0	16·6	45·0	15·8	41·0	15·7	37·0	16·0	42·5	—		—	—	—
,, 30	17·9	71·0	13·9	24·0	18·5	72·0	17·0	49·0	16·9	55·0	15·9	37·0	16·7	51·3	0·7	8·8	14	34·9	2·5
Aug. 14	19·0	81·0	14·0	23·0	19·7	91·0	17·0	48·0	17·9	65·0	15·8	45·0	17·2	58·8	0·5	7·5	15	32·5	2·2
,, 27	19·7	89·0	14·0	20·0	20·4	98·0	17·1	48·0	18·2	68·0	16·2	42·0	17·6	60·8	0·4	2·0	13	30·0	2·3
Sept. 10	20·4	100·0	13·8	22·0	21·0	99·0	17·1	48·0	18·7	73·0	16·7	49·0	17·9	65·2	0·3	4·4	14	30·0	2·1
,, 26	20·9	112·0	14·0	20·0	21·2	104·0	17·3	56·0	18·9	75·0	17·0	48·0	18·2	69·1	0·3	3·9	16	30·0	1·9
Oct. 12	21·3	120·0	13·9	19·0	21·5	110·0	18·1	66·0	19·0	74·0	17·1	48·0	18·5	72·8	0·3	3·7	16	32·5	2·0
Nov. 1	21·8	123·0	13·8	20·0	22·1	120·0	19·0	74·0	19·2	80·0	17·1	47·0	18·8	77·3	0·3	4·5	20	42·5	2·1
,, 16	22·0	130·0	13·9	15·0	22·3	120·0	19·6	86·0	19·6	88·0	17·1	48·0	19·1	81·2	0·3	3·9	15	32·5	2·2
,, 30	22·5	134·0	14·3	21·0	22·4	133·0	19·9	86·0	—	—	17·1	45·0	19·2	83·8	0·1	2·6	14	32·5	2·3
Dec. 20	22·5	142·0	14·5	27·0	22·8	129·0	20·3	95·0			17·1	47·0	19·4	88·0	0·2	4·2	20	45·0	2·2
1929 Jan. 8	22·9	149·0	15·0	32·0	22·8	134·0	21·0	106·0			17·1	47·0	19·8	93·6	0·4	5·6	19	51·0	2·7
													Totals		3·8	51·1	176	393·4	

TABLE 6.

Data Obtained from an Experiment on Intermediate Feeding and Growth in Female Plaice.

Date. (1928)	Fish Nos., Lengths and Weights.														Mean growth per period.		No. of days since previous weighing.	Average weight of food per fish per period (gm.).	Average weight of food per fish per day (gm.).
	F1.		F2.		F3.		F4.		F5.		F6.		Mean F fish.						
	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.	Ltd.	Wt.	Lth.	Wt.	Lth.	Wt.			
July 16	17·1	50·0	16·0	39·0	16·7	46·0	16·9	47·0	15·8	39·0	15·1	30·0	16·3	41·8	—		—	—	—
,, 30	18·0	61·0	17·0	52·0	17·1	54·0	17·4	54·0	16·0	37·0	15·4	33·0	16·8	48·5	0·5	6·7	14	35·8	2·6
Aug. 14	18·2	64·0	17·5	58·0	18·3	62·0	18·5	62·0	16·1	35·0	15·8	36·0	17·4	52·8	0·6	4·3	15	32·5	2·2
,, 27	18·3	69·0	17·9	66·0	18·4	67·0	18·4	61·0	16·4	43·0	15·9	37·0	17·5	57·2	0·1	4·4	13	30·0	2·3
Sept. 10	19·0	71·0	18·5	73·0	19·0	69·0	18·5	62·0	17·0	52·0	16·1	39·0	18·0	61·0	0·5	3·8	14	30·0	2·1
,, 26	19·3	84·0	19·1	75·0	19·0	74·0	18·2	61·0	17·7	63·0	16·3	42·0	18·3	66·5	0·3	5·5	16	30·0	1·9
Oct. 12	19·9	88·0	19·2	75·0	19·1	74·0	18·6	71·0	18·3	58·0	16·4	46·0	18·6	68·7	0·3	2·2	16	32·5	2·0
Nov. 1	20·6	100·0	19·6	78·0	19·5	75·0	19·2	81·0	18·3	59·0	16·7	46·0	19·0	73·2	0·4	4·5	20	42·5	2·1
,, 16	20·9	106·0	19·9	82·0	19·6	75·0	19·7	86·0	18·3	59·0	16·8	47·0	19·2	75·8	0·2	2·6	15	32·5	2·2
,, 30	21·3	115·0	19·9	83·0	20·1	89·0	20·0	93·0	18·5	60·0	16·9	50·0	19·4	81·7	0·2	5·9	14	32·5	2·3
Dec. 20	21·8	118·0	20·3	91·0	20·4	93·0	20·6	104·0	18·5	61·0	17·0	51·0	19·8	86·3	0·4	4·6	20	37·5	1·9
1929 Jan. 8	22·3	126·0	20·7	95·0	21·1	103·0	21·5	110·0	19·1	74·0	17·4	56·0	20·3	94·0	0·5	7·7	19	38·5	2·0
													Totals		4·0	52·2	176	374·3	

TABLE 7.

Data Obtained from the Preliminary Experiments.

Showing initial and final values for length and weight of the mean fish in each group and also the corresponding increases. Total quantities of food supplied are shown, as is a measure of the efficiency of each mean fish, in terms of gm. of food effecting 1·00 gm. increase in fish weight.

	Males. Minimum Fed.	Males. Maximum Fed.	Males. Inter-mediate Fed.	Females. Minimum Fed.	Females. Maximum Fed.	Females. Inter-mediate Fed.
Initial length (cm.)	16·1	16·0	16·0	13·4	16·1	16·3
Final length	16·7	22·6	19·8	15·6	23·3	20·3
Growth in length	0·6	6·6	3·8	2·2	7·2	4·0
Initial weight (gm.)	42·0	38·8	42·5	24·3	43·3	41·8
Final weight	46·8	123·3	93·6	41·0	151·2	94·0
Growth in weight	4·8	84·5	51·1	16·7	107·9	52·2
Total food consumed (gm.)	107	1129	393	106	1129	374
Gm. of food per 1·0 gm. increase in fish weight	[22·3]	13·4	7·7	[6·37]	10·5	7·2

TABLE 8.

Data Obtained from Experiments on the Maintenance Requirements of Male and Female Plaice.

The experiments extended over a period of 44 days, from May 22nd to July 5th, 1929.

Fish No.	Sex.	Initial size. Lth.	Initial size. Wt.	Final size. Lth.	Final size. Wt.	Growth for period. Lth.	Growth for period. Wt.	Total food per the period (44 days).	Average weight of food per day. gm.	Ratio food per day. / Average body-wt. (for period)
C1	♂	12·8	17·5	13·2	21·5	0·4	4·0	18·6	0·42	0·022
C2	♂	12·6	16·5	13·3	20·5	0·7	4·0	18·3	0·42	0·023
C3	♂	12·7	18·0	12·9	18·0	0·2	nil	18·6	0·42	0·023
C4	♂	12·8	18·5	12·9	15·5	0·1	– 3·0	19·0	0·43	0·025
C5	♂	12·3	15·0	12·8	18·0	0·5	3·0	18·3	0·42	0·025
C6	♂	12·8	14·5.	12·9	17·0	0·1	2·5	18·3	0·42	0·027
Mean fish	♂	12·7	16·7	13·0	18·4	0·3	1·7^{5}	18·5	0·42	0·024
A1	♀	13·4	20·5	13·6	22·0	0·2	1·5	18·3	0·42	0·020
A2	♀	13·5	22·5	13·8	24·0	0·3	1·5	18·3	0·42	0·018
A3	♀	13·5	21·0	13·8	22·0	0·3	1·0	18·6	0·42	0·020
A4	♀	13·7	21·0	13·9	22·0	0·2	1·0	18·6	0·42	0·020
A5	♀	13·8	23·5	14·3	23·5	0·5	nil	18·6	0·42	0·018
A6	♀	13·8	24·0	13·9	22·0	0·1	– 2·0	18·9	0·43	0·019
Mean fish	♀	13·6	22·1	13·9	22·6	0·3	0·5	18·5^{5}	0·42	0·019

TABLES 9–11

DATA OBTAINED FROM THE EXPERIMENT ON THE MAINTENANCE REQUIREMENTS OF MALE FISH

TABLE 9: C5A.

Date (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
July 5	14·4	30·5	—		—	—	—	—	—	—	—	
,, 19	14·4	26·0	nil	– 4·5	4·75	14	0·34	4·75	14	0·34	nil.	– 4·5
Aug. 2	14·5	25·0	0·1	– 1·0	5·4	14	0·39	10·15	28	0·36	0·1	– 5·5
,, 16	14·5	23·5	nil	– 1·5	8·25	14	0·59	18·40	42	0·44	0·1	– 7·0
,, 30	14·5	25·5	nil	2·0	9·00	14	0·64	27·40	56	0·49	0·1	– 5·0
Sept. 16	14·5	27·0	nil	1·5	11·25	17	0·66	38·65	73	0·53	0·1	– 3·5
Oct. 1	14·7	28·0	0·2	1·0	12·0	15	0·80	50·65	88	0·58	0·3	– 2·5
,, 15	14·7	29·0	nil	1·0	10·0	14	0·71	60·65	102	0·59	0·3	– 1·5
,, 29	14·8	30·0	0·1	1·0	8·0	14	0·57	68·65	116	0·59	0·4	– 0·5
Nov. 13	14·8	29·5	nil	– 0·5	7·5	15	0·50	76·15	131	0·58	0·4	– 1·0
,, 28	14·8	29·5	nil	nil	5·5	15	0·4	81·65	146	0·56	0·4	– 1·0

TABLE 10: C4a.

July 12	15·6	36·0	—		—	—	—	—	—	—	—	
,, 19	15·6	34·5	nil	– 1·5	1·7	7	0·24	1·7	7	0·24	nil	– 1·5
Aug. 2	15·5	33·0	– 0·1	– 1·5	3·4	14	0·24	5·1	21	0·24	– 0·1	– 3·0
,, 16	15·6	33·5	0·1	0·5	6·0	14	0·43	11·1	35	0·32	nil	– 2·5
,, 30	15·7	34·0	0·1	0·5	12·0	14	0·86	23·1	49	0·47	0·1	– 2·0
Sept. 16	15·7	35·0	nil	1·0	12·5	17	0·74	35·6	66	0·54	0·1	– 1·0
Oct. 1	15·8	38·0	0·1	3·0	12·5	15	0·83	48·1	81	0·60	0·2	2·0
,, 15	16·0	39·0	0·2	1·0	10·0	14	0·71	58·1	95	0·61	0·4	3·0
,, 29	16·2	40·0	0·2	1·0	8·5	14	0·61	66·6	109	0·61	0·6	4·0
Nov. 13	16·2	42·0	nil	2·0	8·2	15	0·55	74·8	124	0·60	0·6	6·0

TABLE 11: C6A.

July 12	16·3	41·5	—		—	—	—	—	—	—	—	
,, 19	16·4	40·0	0·1	– 1·5	1·8	7	0·26	1·8	7	0·26	0·1	– 1·5
Aug. 2	16·4	38·0	nil	– 2·0	8·0	14	0·57	9·8	21	0·47	0·1	– 3·5
,, 16	16·5	40·0	0·1	2·0	12·3	14	0·88	22·1	35	0·63	0·2	– 1·5
,, 30	16·5	39·5	nil	– 0·5	13·0	14	0·93	35·1	49	0·72	0·2	– 2·0
Sept. 16	16·6	40·5	0·1	1·0	15·0	17	0·88	50·1	66	0·76	0·3	– 1·0
Oct. 1	16·8	41·0	0·2	0·5	12·5	15	0·83	62·6	81	0·77	0·5	– 0·5
,, 15	16·8	43·0	nil	2·0	12·0	14	0·86	74·6	95	0·79	0·5	1·5
,, 29	16·9	44·0	0·1	1·0	8·0	14	0·57	82·6	109	0·76	0·6	2·5
Nov. 13	17·0	45·0	0·1	1·0	8·0	15	0·53	90·6	124	0·73	0·7	3·5
,, 28	17·0	44·5	nil	– 0·5	5·5	15	0·37	96·1	139	0·69	0·7	3·0

TABLE 12.

DATA OBTAINED FROM THE EXPERIMENTS ON THE MAINTENANCE REQUIREMENTS OF THE MALE PLAICE, C5A, C4A, AND C6A.

		30·5	**C5a**	29·5	36·0	**C4a**	42·0	41·5	**C6a**	44·5
Date. (1929)	No. of days in period.	Increase in wt. per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).‡	Increase in wt. per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in wt. per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).
July 5*	—	—	—	—	—	—	—	—	—	—
,, 19	14†	– 4·5	0·012	0·012	– 1·5	0·007	0·007	– 1·5	0·006	0·006
Aug. 2	14	– 1·0	0·015	0·013	– 1·5	0·007	0·007	– 2·0	0·015	0·012
,, 16	14	– 1·5	0·024	0·016	0·5	0·013	0·009	2·0	0·023	0·015
,, 30	14	2·0	0·026	0·017	0·5	0·026	0·013	– 0·5	0·023	0·018
Sept. 16	17	1·5	0·025	0·018	1·0	0·021	0·015	1·0	0·022	0·019
Oct. 1	15	1·0	0·029	0·020	3·0	0·023	0·016	0·5	0·020	0·019
,, 15	14	1·0	0·025	0·020	1·0	0·018	0·016	2·0	0·020	0·019
,, 29	14	1·0	0·019	0·020	1·0	0·015	0·016	1·0	0·013	0·018
Nov. 13	15	– 0·5	0·017	0·019	2·0	0·013	0·015	1·0	0·012	0·017
,, 28	15	nil	0·014	0·019	—	—	—	– 0·5	0·008	0·016

* July 12th in cases of C4a and C6a.

† Seven days in cases of C4a and C6a.

‡ By mid body-weight is meant the mid value between the initial and final body-weights.

TABLES 13–15.

DATA OBTAINED FROM THE EXPERIMENT ON THE MAINTENANCE REQUIREMENTS OF FEMALE FISH.

TABLE 13: A4A.

Date (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Total wt. of food to date. (gm.)	No. of days. since commencement of expt.	Average. wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
July 5	15·8	39·0	—		—	—	—	—	—	—	—	
,, 19	15·8	32·0	nil	– 7·0	5·7	14	0·40	5·7	14	0·40	nil	– 7·0
Aug. 2	15·9	33·0	0·1	1·0	9·8	14	0·70	15·5	28	0·55	0·1	– 6·0
,, 16	16·0	34·5	0·1	1·5	10·0	14	0·71	25·5	42	0·61	0·2	– 4·5
,, 30	16·1	35·0	0·1	0·5	10·5	14	0·75	36·0	56	0·64	0·3	– 4·0
Sept. 16	16·2	37·0	0·1	2·0	12·5	17	0·74	48·5	73	0·66	0·4	– 2·0
Oct. 1	16·3	38·0	0·1	1·0	12·0	15	0·80	60·5	88	0·69	0·5	– 1·0
,, 15	16·5	40·0	0·2	2·0	10·5	14	0·75	71·0	102	0·70	0·7	1·0
,, 29	16·7	40·5	0·2	0·5	8·0	14	0·57	79·0	116	0·68	0·9	1·5
Nov. 13	16·8	42·0	0·1	1·5	8·5	15	0·57	87·5	131	0·67	1·0	3·0
,, 27	16·8	42·0	nil	nil	5·5	14	0·39	93·0	145	0·64	1·0	3·0

Table 14: A6a.

Date (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day. (gm.)	Total wt. of food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
July 5	15·7	38·0	—		—	—	—	—	—	—	—	
,, 19	15·8	34·5	0·1	– 3·5	5·6^{5}	14	0·40	5·6	14	0·40	0·1	– 3·5
Aug. 2	15·8	36·5	nil	2·0	8·7	14	0·62	14·3	28	0·51	0·1	– 1·5
,, 16	15·9	37·0	0·1	0·5	9·5^{5}	14	0·68	23·9	42	0·57	0·2	– 1·0
,, 30	16·0	38·0	0·1	1·0	10·5	14	0·75	34·4	56	0·61	0·3	nil
Sept. 16	16·2	37·0	0·2	– 1·0	12·5	17	0·73	46·9	73	0·64	0·5	– 1·0
Oct. 1	16·4	41·0	0·2	4·0	11·0	15	0·73	57·9	88	0·66	0·7	3·0
,, 15	16·6	42·0	0·2	1·0	10·0	14	0·71	67·9	102	0·67	0·9	4·0
,, 29	16·7	43·5	0·1	1·5	8·0	14	0·57	75·9	116	0·65	1·0	5·5
Nov. 13	16·9	45·0	0·2	1·5	8·0	15	0·53	83·9	131	0·64	1·2	7·0
,, 27	16·9	46·0	nil	1·0	5·5	14	0·39	89·4	145	0·62	1·2	8·0

Table 15: A3a.

July 12	17·6	55·0	—		—	—	—	—	—	—	—	
,, 19	17·6	54·5	nil	– 0·5	3·0	7	0·43	3·0	7	0·43	nil	– 0·5
Aug. 2	17·8	54·0	0·2	– 0·5	9·8	14	0·70	12·8	21	0·61	0·2	– 1·0
,, 16	18·0	54·5	0·2	0·5	13·5	14	0·96	26·3	35	0·75	0·4	– 0·5
,, 30	17·9	55·0	– 0·1	0·5	12·0	14	0·86	38·3	49	0·78	0·3	nil
Sept. 16	17·8	55·0	– 0·1	nil	13·5	17	0·80	51·8	66	0·78	0·2	nil
Oct. 1	17·8	57·5	nil	2·5	12·0	15	0·80	63·8	81	0·79	0·2	2·5
,, 15	17·9	60·0	0·1	2·5	19·5	14	1·39	83·3	95	0·88	0·3	5·0
,, 29	17·9	58·5	nil	– 1·5	14·5	14	1·04	97·8	109	0·90	0·3	3·5
Nov. 13	17·9	60·0	nil	1·5	10·0	15	0·67	107·8	124	0·87	0·3	5·0
,, 27	17·9	58·0	nil	– 2·0	5·5	14	0·39	113·3	138	0·82	0·3	3·0

TABLE 16.

Data Obtained from the Experiments on the Maintenance Requirements of the Female Plaice A4a, A6a, and A3a.

		39·0	**A4a**	42·0	38·0	**A6a**	46·0	55·0	**A3a**	58·0
Date. (1929)	No. of days in period.	Increase in wt. per period. (gm.)	Food per day/ /average body-wt. (for each period).	Food per day/ /mid body-wt. (to date).	Increase in wt. per period. (gm.)	Food per day/ /average body-wt. (for each period).	Food per day/ /mid body-wt. (to date).	Increase in wt. per period. (gm.)	Food per day/ /average body-wt. for each period).	Food per day/ /mid body-wt. (to date).
July 5*	—	—	—	—	—	—	—	—	—	—
,, 19	14†	– 7·0	0·011	0·011	– 3·5	0·011	0·011	– 0·5	0·008	0·008
Aug. 2	14	1·0	0·022	0·015	2·0	0·017	0·014	– 0·5	0·013	0·011
,, 16	14	1·5	0·021	0·017	0·5	0·019	0·015	0·5	0·018	0·014
,, 30	14	0·5	0·022	0·017	1·0	0·020	0·016	0·5	0·016	0·014
Sept. 16	17	2·0	0·021	0·017	– 1·0	0·019	0·017	nil	0·015	0·014
Oct. 1	15	1·0	0·021	0·018	4·0	0·019	0·017	2·5	0·014	0·014
,, 15	14	2·0	0·019	0·018	1·0	0·017	0·017	2·5	0·024	0·015
,, 29	14	0·5	0·014	0·017	1·5	0·013	0·016	– 1·5	0·018	0·016
Nov. 13	15	1·5	0·014	0·017	1·5	0·012	0·015	1·5	0·011	0·015
,, 27	14	nil	0·009	0·016	1·0	0·009	0·015	– 2·0	0·007	0·015

* July 12th in case of A3. † Seven days in case of A3.

TABLE 17.

Summarised Data from the Experiments on Maintenance in the Male Plaice, C5a, C4a, and C6a, and in the Female Plaice, A4a, A6a, and A3a.

Fish No.	Sex.	Initial size. Lth.	Initial size. Wt.	Final size. Lth.	Final size. Wt.	Growth. Lth.	Growth. Wt.	Period. (1929).	Days in period.	Average weight of food per day for period. (gm.).	Ratio Food per day/average body-weight for period.
C5a	♂	14·4	30·5	14·8	29·5	0·4	−1·0	July 5th to Nov. 28th	146	0·56	0·019
C4a	♂	15·6	36·0	16·2	42·0	0·6	6·0	July 12th to Nov. 13th	124	0·60	0·015
C6a	♂	16·3	41·5	17·0	44·5	0·7	3·0	July 12th to Nov. 28th	139	0·69	0·016
A4a	♀	15·8	39·0	16·8	42·0	1·0	3·0	July 5th to Nov. 27th	145	0·64	0·016
A6a	♀	15·7	38·0	16·9	46·0	1·2	8·0	July 5th to Nov. 27th	145	0·62	0·015
A3a	♀	17·6	55·0	17·9	58·0	0·3	3·0	July 12th to Nov. 27th	138	0·82	0·015

TABLE 18.

Showing how the Maintenance Requirements of Male and Female Plaice vary with the size of Fish and how these Requirements Diminish During late November.

1929.		October 1st–November 13th (43 days).									November 13th–27th (14 days)								
		Initial size.		Final size.		Growth.		Total weight of food per period. (gm.)	Average weight of food per day for period. (gm.)	Ratio food per day / average body-wt. (for period)	Initial size.		Final size.		Growth.		Total weight of food per period. (gm.)	Average weight of food per day for period. (gm.)	Ratio food per day / average body-wt. (for period)
Fish No.	Sex.	Lth.	Wt.	Lth.	Wt.	Lth.	Wt.				Lth.	Wt.	Lth.	Wt.	Lth.	Wt.			
C2a	♂	19·6	65·0	19·5	64·0	– 0·1	– 1·0	30·0	0·70	0·011	19·5	64·0	19·4	65·0	– 0·1	1·0	6·0	0·43	0·007
C6a	♂	16·8	41·0	17·0	45·0	0·2	4·0	28·0	0·65	0·015	17·0	45·0	17·0	44·5*	nil	– 0·5	5·5†	0·37	0·008
C4a	♂	15·8	38·0	16·2	42·0	0·4	4·0	26·7	0·62	0·015	—		—		—		—	—	—
C5a	♂	14·7	28·0	14·8	29·5	0·1	1·5	25·5	0·59	0·021	14·8	29·5	14·8	29·5*	nil	nil	5·5†	0·37	0·013
A2a	♀	19·7	71·5	19·8	77·0	0·1	5·5	43·0	1·00	0·013	19·8	77·0	19·7	72·5	– 0·1	– 4·5	5·5	0·39	0·005
A1a	♀	18·8	60·0	18·9	60·0	0·1	nil	35·5	0·83	0·014	18·9	60·0	18·9	60·0	nil	nil	5·5	0·39	0·006
A3a	♀	17·8	57·5	17·9	60·0	0·1	2·5	44·0	1·02	0·017	17·9	60·0	17·9	58·0	nil	– 2·0	5·5	0·39	0·007
A6a	♀	16·4	41·0	16·9	45·0	0·5	4·0	26·0	0·60	0·014	16·9	45·0	16·9	46·0	nil	1·0	5·5	0·39	0·009
A4a	♀	16·3	38·0	16·8	42·0	0·5	4·0	27·0	0·63	0·016	16·8	42·0	16·8	42·0	nil	nil	5·5	0·39	0.009

* November 28th. † Period of 15 days.

TABLE 19.

SUMMARISED DATA CONCERNING MAXIMUM REQUIREMENTS AND GROWTH IN MALE AND FEMALE PLAICE.

Fish No.	Sex.	Period.	No. of days in period.	Initial size.		Final size.		Growth.		Total food per the period. (gm.).	Average weight of food per day for period. (gm.).
				Lth.	Wt.	Lth.	Wt.	Lth.	Wt.		
D1	♂	May 22–Oct. 29	160	12·2	14·0	15·9	40·5	3·7	26·5	420	2·6
D2	♂	May 22–Nov. 13	175	12·2	15·0	17·9	64·0	5·7	49·0	471	2·7
D3	♂	June 6–Nov. 28	175	12·0	15·5	21·0	105·0	9·0	89·5	585	3·3
D4	♂	June 6–Nov. 28	175	12·0	13·0	17·3	56·5	5·3	43·5	475	2·7
D5	♂	May 22–Nov. 28	190	11·9	14·5	15·8	38·0	3·9	23·5	417	2·2
D6	♂	May 22–Nov. 13	175	12·0	17·0	14·5	24·0	2·5	7·0	361	2·1
B1	♀	May 22–Nov. 27	189	13·2	24·0	21·0	105·5	7·8	81·5	618	3·3
B2	♀	May 22–Nov. 27	189	12·7	17·0	16·9	51·0	4·2	34·0	438	2·3
B3	♀	June 6–Nov. 27	174	12·6	18·0	14·5	32·0	1·9	14·0	379	2·2
B4	♀	May 22–Nov. 27	189	13·2	18·5	21·3	103·5	8·1	85·0	613	3·3
B5	♀	May 22–Sept. 16	117	12·3	15·0	13·3	20·0	1·0	5·0	190	1·6
B5a	♀	Sept. 17–Nov. 27	71	17·9	54·0	20·1	86·0	2·2	32·0	290	4·1
B6	♀	May 22–Nov. 27	189	12·0	16·0	16·7	51·0	4·7	35·0	448	2·4

TABLES 20–22.

MAXIMUM REQUIREMENTS AND GROWTH OF MALE PLAICE.

TABLE 20: D3.

Date. (1929)	Size of fish.		Wt./Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date from June 6 (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth.	Wt.		Lth.	Wt.					Lth.	Wt.		
June 6	12·0	15·5	0·009	—		—	—	—	—	—		—	—
,, 20	12·2	18·0	0·010	0·2	2·5	22·0	8·8	14	1·6	0·2	2·5	22	8·8
July 5	13·1	22·5	0·010	0·9	4·5	26·0	5·8	15	1·7	1·1	7·0	48	6·9
,, 19	14·1	30·0	0·011	1·0	7·5	36·0	4·8	14	2·6	2·1	14·5	84	5·8
Aug. 2	15·0	37·0	0·011	0·9	7·0	41·4	5·9	14	3·0	3·0	21·5	125	5·8
,, 16	15·9	41·5	0·010	0·9	4·5	44·2	9·8	14	3·1	3·9	26·0	170	6·5
,, 30	16·6	51·5	0·011	0·7	10·0	53·2	5·3	14	3·8	4·6	36·0	223	6·2
Sept. 16	17·8	65·5	0·012	1·2	14·0	68·5	4·9	17	4·0	5·8	50·0	291	5·8
Oct. 1	18·9	79·0	0·012	1·1	13·5	65·2	4·8	15	4·3	6·9	63·5	356	5·6
,, 15	19·7	90·0	0·012	0·8	11·0	76·5	7·0	14	5·5	7·7	74·5	433	5·8
,, 29	20·3	95·5	0·011	0·6	5·5	63·0	11·5	14	4·5	8·3	80·0	496	6·2
Nov. 13	20·7	103·0	0·012	0·4	7·5	50·0	6·7	15	3·3	8·7	87·5	546	6·2
,, 28	21·0	105·0	0·011	0·3	2·0	39·0	19·5	15	2·6	9·0	89·5	585	6·5

TABLE 21: D2.

May 22	12·2	15·0	0·008	—		—	—	—	—	—		—	—
June 6	12·6	19·5	0·010	0·4	4·5	40·0	8·9	15	2·7	0·4	4·5	40	8·9
,, 20	12·9	21·0	0·010	0·3	1·5	22·0	14·7	14	1·6	0·7	6·0	62	10·3
July 5	13·1	22·0	0·010	0·2	1·0	26·0	26·0	15	1·7	0·9	7·0	88	12·6
,, 19	13·9	27·0	0·010	0·8	5·0	33·9	6·8	14	2·4	1·7	12·0	122	10·2
Aug. 2	14·6	32·0	0·010	0·7	5·0	38·4	7·7	14	2·7	2·4	17·0	160	9·4
,, 16	15·3	32·5	0·009	0·7	0·5	43·1	86·2	14	3·1	3·1	17·5	203	11·6
,, 30	15·8	33·0	0·008	0·5	0·5	47·0	94·0	14	3·4	3·6	18·0	250	13·9
Sept. 16	16·6	49·0	0·010	0·8	16·0	58·4	3·6	17	3·4	4·4	34·0	309	9·1
Oct. 1	16·9	53·5	0·011	0·3	4·5	56·6	12·6	15	3·8	4·7	38·5	365	9·5
,, 15	17·4	58·0	0·011	0·5	4·5	42·5	9·4	14	3·0	5·2	43·0	408	9·5
,, 29	17·6	60·5	0·011	0·2	2·5	39·0	15·6	14	2·8	5·4	45·5	447	9·8
Nov. 13	17·9	64·0	0·011	0·3	3·5	24·0	6·9	15	1·6	5·7	49·0	471	9·6
,, 28	17·9	63·0	0·011	nil	−1·0	23·0−	—	15	1·5−	5·7	48·0	494	10·+

TABLE 22: D4.

June 6	12·0	13·0	0·008	—		—	—	—	—	—		—	—
,, 20	12·1	14·0	0·008	0·1	1·0	22·0	22·0	14	1·6	0·1	1·0	22	22·0
July 5	12·8	19·5	0·009	0·7	5·5	26·0	4·7	15	1·7	0·8	6·5	48	7·4
,, 19	13·5	24·0	0·010	0·7	4·5	33·5	7·4	14	2·4	1·5	11·0	81	7·4
Aug. 2	14·2	29·0	0·010	0·7	5·0	42·5	8·5	14	3·0	2·2	16·0	124	7·7
,, 16	14·7	32·5	0·010	0·5	3·5	42·0	12·0	14	3·0	2·7	19·5	166	8·5
,, 30	15·1	36·0	0·010	0·4	3·5	47·5	13·5	14	3·4	3·1	23·0	213	9·3
Sept. 16	15·6	40·0	0·011	0·5	4·0	59·9	15·0	17	4·0	3·6	27·0	273	10·1
Oct. 1	16·2	47·0	0·011	0·6	7·0	51·0	7·3	15	3·4	4·2	34·0	324	9·5
,, 15	16·7	51·0	0·011	0·5	4·0	51·5	12·9	14	3·7	4·7	38·0	376	9·9
,, 29	17·0	55·0	0·011	0·3	4·0	46·0	11·5	14	3·3	5·0	42·0	422	10·0
Nov. 13	17·3	57·0	0·011	0·3	2·0	30·5	15·2	15	2·0	5·3	44·0	452	10·3
,, 28	17·3	56·5	0·011	nil	−0·5	23−	—	15	1·5−	5·3	43·5	475−	10·9

TABLES 23–27.

Maximum Requirements and Growth of Female Plaice.

Table 23: B1.

Date. (1929)	Size of fish.		Wt./Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date from May 22 (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth.	Wt.		Lth.	Wt.					Lth.	Wt.		
May 22	13·2	24·0	0·010	—		—	—	—	—	—	—	—	—
June 6	14·0	31·0	0·011	0·8	7·0	40·0	5·7	15	2·7	0·8	7·0	40	5·7
,, 20	14·7	35·0	0·011	0·7	4·0	22·0	5·5	14	1·6	1·5	11·0	62	5·6
July 5	15·4	40·0	0·011	0·7	5·0	26·0	5·2	15	1·7	2·2	16·0	88	5·5
,, 19	16·2	47·0	0·011	0·8	7·0	38·0	5·4	14	2·7	3·0	23·0	126	5·5
Aug. 2	16·8	53·5	0·011	0·6	6·5	44·3	6·8	14	3·2	3·6	29·5	170	5·8
,, 16	17·5	61·0	0·011	0·7	7·5	46·2	6·2	14	3·3	4·3	37·0	216	5·8
,, 30	18·2	69·0	0·011	0·7	8·0	57·0	7·1	14	4·1	5·0	45·0	273	6·1
Sept. 16	19·0	79·5	0·012	0·8	10·5	69·0	6·6	17	4·1	5·8	55·5	342	6·2
Oct. 1	19·8	89·5	0·012	0·8	10·0	66·9	6·7	15	4·5	6·6	65·5	409	6·2
,, 15	20·2	96·0	0·012	0·4	6·5	63·0	9·7	14	4·5	7·0	72·0	472	6·6
,, 29	20·5	98·5	0·011	0·3	2·5	49·0	19·6	14	3·5	7·3	74·5	521	7·0
Nov. 13	20·8	104·0	0·012	0·3	5·5	54·0	9·8	15	3·6	7·6	80·0	575	7·2
,, 27	21·0	105·5	0·011	0·2	1·5	43 –	28·7	14	3·1 –	7·8	81·5	618	7·6
Dec. 11	21·0	105·5	0·011	nil	nil	28·5 –	—	14	2·0 –	7·8	81·5	646	—

Table 24: B4.

May 22	13·2	18·5	0·008	—		—	—	—	—	—	—	—	—
June 6	13·9	26·0	0·009	0·7	7·5	40·0	5·3	15	2·7	0·7	7·5	40	5·3
,, 20	14·7	32·0	0·010	0·8	6·0	22·0	3·6	14	1·6	1·5	13·5	62	4·6
July 5	15·3	36·5	0·010	0·6	4·5	26·0	5·8	15	1·7	2·1	18·0	88	4·9
,, 19	16·1	43·0	0·010	0·8	6·5	36·5	5·6	14	2·6	2·9	24·5	124	5·1
Aug. 2	16·9	50·5	0·010	0·8	7·5	48·7	6·5	14	3·5	3·7	32·0	173	5·4
,, 16	17·7	60·5	0·011	0·8	10·0	51·4	5·1	14	3·7	4·5	42·0	224	5·3
,, 30	18·4	66·0	0·011	0·7	5·5	54·3	9·9	14	3·9	5·2	47·5	279	5·9
Sept. 16	19·0	76·0	0·011	0·6	10·0	65·5	6·5	17	3·9	5·8	57·5	344	6·0
Oct. 1	19·6	83·5	0·011	0·6	7·5	55·2	7·4	15	3·7	6·4	65·0	400	6·2
,, 15	20·2	90·0	0·011	0·6	6·5	59·0	9·1	14	4·2	7·0	71·5	459	6·4
,, 29	20·7	102·0	0·011	0·5	12·0	63·0	5·2	14	4·5	7·5	83·5	522	6·3
Nov. 13	21·2	108·0	0·011	0·5	6·0	52·5	8·7	15	3·5	8·0	89·5	574	6·4
,, 27	21·3	103·5	0·011	0·1	– 4·5	38·5 –	—	14	2·7	8·1	85·0	613	7·2

Table 25: B5a.

Sept. 17	17·9	54·0	0·009	—		—	—	—	—	—	—	—	—
Oct. 1	18·1	59·0	0·010	0·2	5·0	42·2	8·4	14	3·0	0·2	5·0	42	8·4
,, 15	18·9	72·5	0·011	0·8	13·5	77·5	5·7	14	5·5	1·0	18·5	120	6·5
,, 29	19·7	86·0	0·011	0·8	13·5	76·5	5·7	14	5·5	1·8	32·0	196	6·1
Nov. 13	20·1	89·0	0·011	0·4	3·0	57·5	19·2	15	3·8	2·2	35·0	254	7·3
,, 27	20·1	86·0	0·011	nil	– 3·0	37 –	—	14	2·6	2·2	32·0	291 –	9·1

TABLE 26: B2.

Date. (1929)	Size of fish.		Wt. / Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date from May 22 (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth.	Wt.		Lth.	Wt.					Lth.	Wt.		
May 22	12·7	17·0	0·008	—		—	—	—	—	—	—	—	—
June 6	13·3	23·0	0·010	0·6	6·0	40·0	6·7	15	2·7	0·6	6·0	40	6·7
,, 20	14·0	27·0	0·010	0·7	4·0	22·0	5·5	14	1·6	1·3	10·0	62	6·2
July 5	14·2	27·0	0·009	0·2	nil	26·0	—	15	1·7	1·5	10·0	88	8·8
,, 19	14·5	28·5	0·009	0·3	1·5	23·0	15·3	14	1·6	1·8	11·5	111	9·7
Aug. 2	14·8	30·0	0·009	0·3	1·5	30·2	20·1	14	2·2	2·1	13·0	141	10·8
,, 16	14·9	30·5	0·009	0·1	0·5	29·7	59·4	14	2·1	2·2	13·5	171	12·7
,, 30	15·2	34·0	0·010	0·3	3·5	37·8	10·8	14	2·7	2·5	17·0	209	12·3
Sept. 16	15·5	36·5	0·010	0·3	2·5	45·6	18·2	17	2·7	2·8	19·5	254	13·0
Oct. 1	15·7	39·5	0·010	0·2	3·0	45·3	15·1	15	3·0	3·0	22·5	300	13·3
,, 15	15·8	40·0	0·010	0·1	0·5	42·0	84·0	14	3·0	3·1	23·0	342	14·9
,, 29	16·3	45·0	0·010	0·5	5·0	42·5	8·5	14	3·0	3·6	28·0	384	13·7
Nov. 13	16·7	49·5	0·011	0·4	4·5	29·5	6·6	15	2·0	4·0	32·5	414	12·7
,, 27	16·9	51·0	0·011	0·2	1·5	24·5 –	16·3	14	1·7	4·2	34·0	438 –	12·9

TABLE 27: B6.

May 22	12·0	16·0	0·009	—		—	—	—	—	—	—	—	—
June 6	12·7	23·0	0·011	0·7	7·0	40·0	5·7	15	2·7	0·7	7·0	40	5·7
,, 20	13·3	25·0	0·011	0·6	2·0	22·0	11·0	14	1·6	1·3	9·0	62	6·8
July 5	13·8	28·0	0·011	0·5	3·0	26·0	8·7	15	1·7	1·8	12·0	88	7·3
,, 19	14·5	29·0	0·010	0·7	1·0	34·0	34·0	14	2·4	2·5	13·0	122	9·4
Aug. 2	15·1	36·0	0·010	0·6	7·0	31·6	4·5	14	2·3	3·1	20·0	154	7·7
,, 16	15·2	37·0	0·011	0·1	1·0	34·0	34·0	14	2·4	3·2	21·0	188	9·0
,, 30	15·4	38·5	0·011	0·2	1·5	36·5	24·3	14	2·6	3·4	22·5	224	10·0
Sept. 16	15·7	41·5	0·011	0·3	3·0	47·1	15·7	17	2·8	3·7	25·5	271	10·6
Oct. 1	15·9	44·0	0·011	0·2	2·5	44·0	17·6	15	2·9	3·9	28·0	315	11·2
,, 15	16·4	49·0	0·011	0·5	5·0	47·5	9·5	14	3·4	4·4	33·0	363	11·0
,, 29	16·5	50·0	0·011	0·1	1·0	38·5	38·5	14	2·7	4·5	34·0	401	11·8
Nov. 13	16·7	53·5	0·011	0·2	3·5	23·0	6·6	15	1·5	4·7	37·5	424	11·3
,, 27	16·7	51·0	0·011	nil	– 2·5	24 –	—	14	1·7 –	4·7	35·0	448	12·8

TABLES 28–31.

MAINTENANCE REQUIREMENTS OF MALE PLAICE.

TABLE 28: L1.

Date. (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average wt. of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
Aug. 22	17·0	50·3	—		—	—	—	—	—	—	—	
Sept. 2	17·0	49·0	nil	– 1·3	8·2	11	0·74	8·2	11	0·74	nil	– 1·3
,, 16	17·0	47·7	nil	– 1·3	11·9	14	0·85	20·1	25	0·80	nil	– 2·6
,, 30	17·0	49·9	nil	2·2	13·3	14	0·95	33·4	39	0·86	nil	– 0·4
Oct. 14	17·2	53·1	0·2	3·2	13·4	14	0·96	46·8	53	0·88	0·2	2·8
,, 28	17·6	52·7	0·4	– 0·4	12·7	14	0·91	59·5	67	0·89	0·6	2·4
Nov. 11	17·6	54·5	nil	1·8	13·2	14	0·94	72·7	81	0·90	0·6	4·2
,, 25	17·6	54·1	nil	– 0·4	12·6	14	0·90	85·3	95	0·90	0·6	3·8
Dec. 9	17·6	54·4	nil	0·3	8·3	14	0·59	93·6	109	0·86	0·6	4·1
,, 23	17·6	53·7	nil	– 0·7	10·5	14	0·75	104·1	123	0·85	0·6	3·4

TABLE 29 : L4a ABOVE, L4b BELOW.

Date. (1929)	Size of fish. Lth.	Size of fish. Wt.	Growth per period. Lth.	Growth per period. Wt.	Weight of food per period. (gm.)	No. of days in period.	Average wt. of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth. Lth.	Cumulative growth. Wt.
Aug. 19	20·8	84·7	—		—	—	—	—	—	—	—	
Sept. 2	20·8	83·0	nil	− 1·7	11·9	14	0·85	11·9	14	0·85	nil	− 1·7
,, 16	20·8	83·7	nil	0·7	12·3	14	0·88	24·2	28	0·86	nil	− 1·0
Sept. 30	20·8	75·1	—		—	—	—	—	—	—	—	
Oct. 14	20·9	77·7	0·1	2·6	14·0	14	1·00	14·0	14	1·0	0·1	2·6
,, 28	20·9	75·1	nil	− 2·6	10·6	14	0·76	24·6	28	0·88	0·1	nil
Nov. 11	21·0	77·2	0·1	2·1	19·6	14	1·40	44·2	42	1·05	0·2	2·1
,, 25	21·0	76·9	nil	− 0·3	18·2	14	1·30	62·4	56	1·11	0·2	1·8
Dec. 9	21·0	77·2	nil	0·3	11·9	14	0·85	74·3	70	1·06	0·2	2·1
,, 23	21·0	78·0	nil	0·8	16·2	14	1·16	90·5	84	1·08	0·2	2·9

TABLE 30 : L3.

Sept. 8	21·4	105·3	—		—	—	—	—	—	—	—	
,, 16	21·4	102·5	nil	− 2·8	10·4	8	1·30	10·4	8	1·30	nil	− 2·8
,, 30	21·5	104·2	0·1	1·7	21·1	14	1·51	31·5	22	1·43	0·1	− 1·1
Oct. 14	21·6	108·2	0·1	4·0	21·1	14	1·51	52·6	36	1·46	0·2	2·9
,, 28	21·7	106·0	0·1	− 2·2	16·5	14	1·16	69·1	50	1·38	0·3	0·7
Nov. 11	22·0	110·2	0·3	4·2	19·4	14	1·39	88·5	64	1·38	0·6	4·9
,, 25	22·0	109·4	nil	− 0·8	14·8	14	1·06	103·3	78	1·32	0·6	4·1
Dec. 9	22·0	110·4	nil	1·0	12·1	14	0·86	115·4	92	1·25	0·6	5·1
,, 23	22·1	111·9	0·1	1·5	18·9	14	1·35	134·3	106	1·27	0·7	6·6

TABLE 31 : L2.

Aug. 19	22·8	129·9	—		—	—	—	—	—	—	—	
Sept. 2	22·8	129·1	nil	− 0·8	17·5	14	1·25	17·5	14	1·25	nil	− 0·8
,, 16	22·8	123·3	nil	− 5·8	17·6	14	1·26	35·1	28	1·25	nil	− 6·6
,, 30	22·8	126·7	nil	3·4	23·4	14	1·67	58·5	42	1·39	nil	− 3·2
Oct. 14	22·9	129·7	0·1	3·0	23·5	14	1·68	82·0	56	1·46	0·1	− 0·2
,, 28	23·0	123·2	0·1	− 6·5	16·8	14	1·20	98·8	70	1·41	0·2	− 6·7
Nov. 11	23·0	130·5	nil	7·3	24·3	14	1·74	123·1	84	1·47	0·2	0·6
,, 25	23·1	129·4	0·1	− 1·1	18·1	14	1·29	141·2	98	1·44	0·3	− 0·5
Dec. 9	23·1	130·7	nil	1·3	12·9	14	0·92	154·1	112	1·38	0·3	0·8
,, 23	23·1	130·9	nil	0·2	20·4	14	1·46	174·5	126	1·38	0·3	1·0

TABLE 32.

MAINTENANCE IN THE MALE PLAICE, L2A AND L1A.

Fish No.	Date. (1929)	Size of fish. Lth.	Size of fish. Wt.	Growth per period. Lth.	Growth per period. Wt.	Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day during each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of exp.	Average weight of food per day to date. (gm.)	Cumulative growth. Lth.	Cumulative growth. Wt.
	July 8	15·2	22·3	—		—	—	—	—	—	—	—	
L2a	,, 22	15·2	21·1	nil	− 1·2	9·8	14	0·70	9·8	14	0·70	nil	− 1·2
	Aug. 5	15·2	20·9	nil	− 0·2	10·2	14	0·73	20·0	28	0·71	nil	− 1·4
	July 8	21·2	62·5	—		—	—	—	—	—	—	—	
L1a	,, 22	21·2	61·0	nil	− 1·5	9·4	14	0·67	9·4	14	0·67	nil	− 1·5
	Aug. 5	21·2	61·0	nil	nil	10·2	14	0·73	19·6	28	0·70	nil	− 1·5
	,, 19	21·2	61·5	nil	0·5	11·2	14	0·80	30·8	42	0·73	nil	− 1·0

Fish No.	Lth.	Wt.	Period.	No. of days in period.	Increase in weight per period (gm.)	Average weight of food per day (gm.)	Food per day / average body weight (for period).
L2a	22·3	20·9	July 8th to Aug. 5th	28	− 1·4	0·71	0·033
L1a	62·5	61·5	July 8th to Aug. 19th	42	− 1·0	0·73	0·012

TABLE 33.

Maintenance in the Male Plaice, L1, L4b, L3, and L2.

		50·3	**L1**	53·7	75·1	**L4B**	78·0	105·3	**L3**	111·9	129·9	**L2**	130·9
Date. (1929)	No. of days in period.	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).
Aug. 19*	—	—	—	—	—	—	—	—	—	—	—	—	—
Sept. 2†	14	– 1·3	0·015	0·015	—	—	—	—	—	—	– 0·8	0·010	0·010
„ 16	14	– 1·3	0·018	0·016	—	—	—	– 2·8	0·013	0·013	– 5·8	0·010	0·010
„ 30	14	2·2	0·019	0·017	—	—	—	1·7	0·015	0·014	3·4	0·013	0·011
Oct. 14	14	3·2	0·019	0·017	2·6	0·013	0·013	4·0	0·014	0·014	3·0	0·013	0·011
„ 28	14	– 0·4	0·017	0·017	– 2·6	0·010	0·012	– 2·2	0·011	0·013	– 6·5	0·009	0·011
Nov. 11	14	1·8	0·018	0·017	2·1	0·018	0·014	4·2	0·013	0·013	7·3	0·014	0·011
„ 25	14	– 0·4	0·017	0·017	– 0·3	0·017	0·015	– 0·8	0·010	0·012	– 1·1	0·010	0·011
Dec. 9	14	0·3	0·011	0·016	0·3	0·011	0·014	1·0	0·008	0·013	1·3	0·007	0·011
„ 23	14	– 0·7	0·014	0·016	0·8	0·015	0·014	1·5	0·012	0·012	0·2	0·011	0·011

* August 22nd for L1. † September 8th for L3.

TABLES 34–37.

MAINTENANCE IN FEMALE PLAICE.

TABLE 34 : L5.

Date. (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average wt. of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
Aug. 8	18·5	62·8	—		—	—	—	—	—	—	—	
,, 19	18·5	60·5	nil	− 2·3	8·8	11	0·80	8·8	11	0·80	nil	− 2·3
Sept. 2	18·5	59·3	nil	− 1·2	11·8	14	0·84	20·6	25	0·82	nil	− 3·5
,, 16	—		—		13·2	14	0·94	33·8	39	0·87	—	
,, 30	18·4	62·2	− 0·1	2·9	13·2	14	0·94	47·0	53	0·89	− 0·1	− 0·6
Oct. 14	18·4	65·7	nil	3·5	15·3	14	1·09	62·3	67	0·93	− 0·1	2·9
,, 28	18·5	65·3	0·1	− 0·4	11·1	14	0·79	73·4	81	0·91	nil	2·5
Nov. 11	18·6	65·6	0·1	0·3	11·3	14	0·81	84·7	95	0·89	0·1	2·8
,, 25	18·6	66·9	nil	1·3	11·3	14	0·81	96·0	109	0·88	0·1	4·1
Dec. 9	18·7	67·0	0·1	0·1	6·2	14	0·44	102·2	123	0·83	0·2	4·2
,, 23	18·7	67·5	nil	0·5	10·4	14	0·74	112·6	137	0·82	0·2	4·7

TABLE 35 : L6.

Date. (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average wt. of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
Sept. 16	19·2	71·2	—		—	—	—	—	—	—	—	
,, 30	19·2	70·5	nil	− 0·7	15·4	14	1·10	15·4	14	1·10	nil	− 0·7
Oct. 14	19·2	73·5	nil	3·0	17·8	14	1·27	33·2	28	1·19	nil	2·3
,, 28	19·2	70·3	nil	− 3·2	13·3	14	0·95	46·5	42	1·11	nil	− 0·9
Nov. 11	19·2	71·7	nil	1·4	17·3	14	1·24	63·8	56	1·14	nil	0·5
,, 25	19·3	70·1	0·1	− 1·6	19·6	14	1·40	83·4	70	1·19	0·1	− 1·1
Dec. 9	19·3	69·9	nil	− 0·2	11·0	14	0·79	94·4	84	1·12	0·1	− 1·3
,, 23	19·3	70·4	nil	0·5	18·0	14	1·29	112·4	98	1·15	0·1	− 0·8

TABLE 36 : L7.

Date. (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average wt. of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
Sept. 4	22·3	104·8	—		—	—	—	—	—	—	—	
,, 16	22·3	100·1	nil	− 4·7	15·6	12	1·30	15·6	12	1·30	nil	− 4·7
,, 30	22·4	97·5	0·1	− 2·6	18·2	14	1·30	33·8	26	1·30	0·1	− 7·3
Oct. 14	22·4	99·2	nil	1·7	19·6	14	1·40	53·4	40	1·33	0·1	− 5·6
,, 28	22·4	94·4	nil	− 4·8	16·4	14	1·17	69·8	54	1·29	0·1	− 10·4
Nov. 11	22·5	99·5	0·1	5·1	20·5	14	1·46	90·3	68	1·33	0·2	− 5·3
,, 25	22·7	100·6	0·2	1·1	17·7	14	1·26	108·0	82	1·32	0·4	− 4·2
Dec. 9	22·7	99·8	nil	− 0·8	10·6	14	0·76	118·6	96	1·24	0·4	− 5·0
,, 23	22·7	100·0	nil	0·2	16·6	14	1·19	135·2	110	1·23	0·4	− 4·8

TABLE 37 : L8.

Date. (1929)	Size of fish.		Growth per period.		Weight of food per period. (gm.)	No. of days in period.	Average wt. of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of expt.	Average wt. of food per day to date. (gm.)	Cumulative growth.	
	Lth.	Wt.	Lth.	Wt.							Lth.	Wt.
Aug. 22	21·9	102·0	—		—	—	—	—	—	—	—	
Sept. 2	22·0	102·1	0·1	0·1	14·3	11	1·30	14·3	11	1·30	0·1	0·1
,, 16	22·0	102·8	nil	0·7	18·2	14	1·30	32·5	25	1·30	0·1	0·8
,, 30	22·1	104·5	0·1	1·7	19·0	14	1·36	51·5	39	1·32	0·2	2·5
Oct. 16	23·0	114·0	—		—	—	—	—	—	—	—	
,, 28	23·1	111·3	0·1	− 2·7	16·8	12	1·40	16·8	12	1·40	0·1	− 2·7
Nov. 11	23·2	114·0	0·1	2·7	23·4	14	1·67	40·2	26	1·55	0·2	nil
,, 25	23·3	113·6	0·1	− 0·4	20·2	14	1·44	60·4	40	1·51	0·3	− 0·4
Dec. 9	23·3	114·2	nil	0·6	13·4	14	0·96	73·8	54	1·37	0·3	0·2
,, 23	23·3	116·5	nil	2·3	20·8	14	1·49	94·6	68	1·39	0·3	2·5

TABLE 38.

MAINTENANCE IN THE FEMALE PLAICE, L5, L6, L7, AND L8 (a & b).

		62·8	**L5**	67·5	71·2	**L6**	70·4	104·8	**L7**	100·0	102·0 114·0	**$L8^{a}_{b}$**	104·5 116·5
Date. (1929)	No. of days in period.	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).	Increase in weight per period. (gm.)	Food per day/ /average body-wt. (for period).	Food per day/ /mid body-wt. (to date).
Aug. 8	—				—			—			—		
,, 19†	11	− 2·3	0·013	0·013							—		
Sept. 2*	14	− 1·2	0·014	0·013				—			0·1	0·013	0·013
,, 16	14	—	—	—	—			− 4·7	0·013	0·013	0·7	0·013	0·013
,, 30	14	2·9	0·015	0·014	− 0·7	0·016	0·016	− 2·6	0·013	0·013	1·7	0·013	0·013
Oct. 14‡	14	3·5	0·017	0·014	3·0	0·018	0·016	1·7	0·014	0·013	—		
,, 28	14	− 0·4	0·012	0·014	− 3·2	0·013	0·016	− 4·8	0·012	0·013	− 2·7	0·012	0·012
Nov. 11	14	0·3	0·012	0·014	1·4	0·017	0·016	5·1	0·015	0·013	2·7	0·015	0·014
,, 25	14	1·3	0·012	0·014	− 1·6	0·020	0·017	1·1	0·013	0·013	− 0·4	0·013	0·013
Dec. 9	14	0·1	0·007	0·013	− 0·2	0·011	0·016	− 0·8	0·008	0·012	0·6	0·008	0·012
,, 23	14	0·5	0·011	0·013	0·5	0·018	0·016	0·2	0·012	0·012	2·3	0·013	0·012

* September 4th for L7. † August 22nd for L8. ‡ October 16th for L8.

TABLE 39.

MAINTENANCE IN THE FEMALE PLAICE, L6a, L5a, L8c, AND L7a.

Fish No.	Date. (1929)	Size of fish. Lth.	Size of fish. Wt.	Growth per period. Lth.	Growth per period. Wt.	Weight of food per period. (gm.)	No. of days in period.	Average weight of food per day for each period. (gm.)	Total food to date. (gm.)	No. of days since commencement of exp.	Average weight of food per day to date. (gm.)	Cumulative growth. Lth.	Cumulative growth. Wt.
L6a	June 24	15·2	22·9	—		—	—	—	—	—	—	—	
	July 8	15·2	21·7	nil	− 1·2	7·6	14	0·54	7·6	14	0·54	nil	− 1·2
	,, 22	15·3	21·8	0·1	0·1	9·1	14	0·65	16·7	28	0·60	0·1	− 1·1
L5a	June 24	17·0	35·5	—		—	—	—	—	—	—	—	
	July 8	17·1	34·0	0·1	−1·5	8·1	14	0·58	8·1	14	0·58	0·1	− 1·5
	,, 22	17·1	33·7	nil	− 0·3	9·0	14	0·64	17·1	28	0·61	0·1	− 1·8
L8c	July 8	18·5	40·9	—		—	—	—	—	—	—	—	
	,, 22	18·5	37·3	nil	− 3·6	9·4	14	0·67	9·4	14	0·67	nil	− 3·6
	Aug. 5	18·6	37·9	0·1	0·6	11·2	14	0·80	20·6	28	0·74	0·1	− 3·0
	,, 19	18·6	38·0	nil	0·1	11·0	14	0·79	31·6	42	0·75	0·1	− 2·9
L7a	July 22	19·7	57·8	—		—	—	—	—	—	—	—	
	Aug. 5	19·7	57·0	nil	− 0·8	10·9	14	0·78	10·9	14	0·78	nil	− 0·8
	,, 19	19·7	54·9	nil	− 2·1	10·9	14	0·78	21·8	28	0·78	nil	− 2·9
	Sept. 2	19·7	55·2	nil	0·3	11·7	14	0·84	33·5	42	0·80	nil	− 2·6

TABLE 40.

MAINTENANCE IN THE FEMALE PLAICE, L6a, L5a, L8c, AND L7a.

Fish No.	Period.	No. of days in period.	Initial weight. (gm.)	Final weight. (gm.)	Increase in weight. (gm.)	Food per period. (gm.)	Average weight of food per day. (gm.)	Food per day/ /average body-wt. (for period).
L6a	June 24–July 22	28	22·9	21·8	− 1·1	16·7	0·60	0·027
L5a	,, ,,	28	35·5	33·7	− 1·8	17·1	0·61	0·018
L8c	July 22–Aug. 19	28	37·3	38·0	0·7	22·2	0·79	0·021
L7a	July 22–Sept. 2	42	57·8	55·2	− 2·6	33·5	0·80	0·014

TABLE 41.

Maximum Requirements and Growth.

Fish No.	Sex.	Period. (1929)	No. of days in period.	Initial size.		Final size.		Growth.		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.	Wt.	Lth.	Wt.	Lth.	Wt.			
L11	♂	June 24–Nov. 25	154	16·1	23·2	23·1	157·4	7·0	134·2	953	6·2	7·1
L10	♂	June 24–Sept. 30	98	16·6	36·2	19·1	82·8	2·5	46·6	536	5·5	11·5
L12	♂	June 24–Nov. 25	154	18·1	44·0	21·8	111·4	3·7	67·4	758	4·9	11·2
L9	♂	June 24–Sept. 30	98	19·7	57·5	21·3	102·6	1·6	45·1	676	6·9	15·0
L13	♀	June 24–Nov. 25	154	15·1	27·0	19·2	70·4	4·1	43·4	626	4·1	14·4
L15	♀	June 24–Nov. 25	154	15·1	31·9	23·0	140·7	7·9	108·8	883	5·7	8·1
L16	♀	June 24–Nov. 25	154	18·4	50·5	24·1	175·0	5·7	124·5	1060	6·9	8·5
L14	♀	July 15–Nov. 25	133	23·0	90·1	25·7	184·8	2·7	94·7	905	6·8	9·6

TABLES 42–45.

MAXIMUM REQUIREMENTS AND GROWTH OF MALE PLAICE.

TABLE 42 : L11.

Date. (1929)	Size of fish.		Wt./ /Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date. (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth. (cm.)	Wt. (gm.)		Lth. (cm.)	Wt. (gm.)					Lth.	Wt.		
June 24	16·1	23·2	0·006	—		—	—	—	—	—		—	—
July 8	17·4	48·5	0·009	1·3	25·3	57·2	2·3	14	4·1	1·3	25·3	57	2·3
,, 22	17·8	61·2	0·011	0·4	12·7	85·0	6·7	14	6·1	1·7	38·0	142	3·7
Aug. 5	18·2	66·7	0·011	0·4	5·5	98·0	17·8	14	7·0	2·1	43·5	240	5·5
,, 19	19·2	83·1	0·012	1·0	16·4	100·4	6·1	14	7·2	3·1	59·9	340	5·7
Sept. 2	20·0	97·1	0·012	0·8	14·0	102·3	7·3	14	7·3	3·9	73·9	443	6·0
,, 16	20·4	106·0	0·012	0·4	8·9	102·0	11·5	14	7·3	4·3	82·8	545	6·6
,, 30	21·3	122·8	0·013	0·9	16·8	104·4	6·2	14	7·5	5·2	99·6	649	6·5
Oct. 14	21·8	138·0	0·013	0·5	15·2	105·3	6·9	14	7·5	5·7	114·8	755	6·6
,, 28	22·8	149·2	0·013	1·0	11·2	92·0	8·2	14	6·6	6·7	126·0	847	6·7
Nov. 11	23·1	158·6	0·013	0·3	9·4	79·1	8·4	14	5·6	7·0	135·4	926	6·8
,, 25	23·1	157·4	0·013	nil	– 1·2	26·6	—	14	1·9	7·0	134·2	953	7·1
Dec. 9	23·1	151·6	0·012	nil	– 5·8	4·6	—	14	0·3	7·0	128·4	958	7·5
,, 23	23·1	147·2	0·012	nil	– 4·4	5·9	—	14	0·4	7·0	124·0	963	7·8

TABLE 43 : L10.

Date. (1929)	Size of fish.		Wt./ /Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date. (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth. (cm.)	Wt. (gm.)		Lth. (cm.)	Wt. (gm.)					Lth.	Wt.		
June 24	16·6	36·2	0·008	—		—	—	—	—	—	—	—	—
July 8	16·9	42·8	0·009	0·3	6·6	52·2	7·9	14	3·7	0·3	6·6	52	7·9
,, 22	17·4	52·8	0·010	0·5	10·0	69·7	7·0	14	5·0	0·8	16·6	122	7·3
Aug. 5	17·9	62·0	0·011	0·5	9·2	84·0	9·1	14	6·0	1·3	25·8	206	8·0
,, 19	18·4	70·3	0·011	0·5	8·3	90·7	10·9	14	6·5	1·8	34·1	297	8·7
Sept. 2	18·7	77·5	0·012	0·3	7·2	94·0	13·1	14	6·7	2·1	41·3	391	9·5
,, 16	18·8	76·2	0·011	0·1	– 1·3	77·6	—	14	5·5	2·2	40·0	468	11·7
,, 30	19·1	82·8	0·012	0·3	6·6	67·9	10·3	14	4·8	2·5	46·6	536	11·5

TABLE 44. : L9.

Date. (1929)	Size of fish.		Wt./ /Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date. (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth. (cm.)	Wt. (gm.)		Lth. (cm.)	Wt. (gm.)					Lth.	Wt.		
June 24	19·7	57·5	0·008	—		—	—	—	—	—	—	—	—
July 8	19·8	59·0	0·008	0·1	1·5	58·2	38·8	14	4·2	0·1	1·5	58	38·8
,, 22	20·0	68·9	0·009	0·2	9·9	82·5	8·3	14	5·9	0·3	11·4	141	12·4
Aug. 5	20·4	79·8	0·009	0·4	10·9	102·3	9·4	14	7·3	0·7	22·3	243	10·4
,, 19	20·9	93·6	0·010	0·5	13·8	102·7	7·4	14	7·3	1·2	36·1	346	9·6
Sept. 2	21·2	98·3	0·010	0·3	4·7	110·0	23·4	14	7·9	1·5	40·8	456	11·2
,, 16	21·3	99·4	0·010	0·1	1·1	107·1	97·4	14	7·0	1·6	41·9	563	13·4
,, 30	21·3	102·6	0·011	nil	3·2	113·1	35·3	14	2·5	1·6	45·1	676	15·0

TABLE 45 : L12.

Date. (1929)	Size of fish.		Wt./ /Lth.^{3}	Growth per period.		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.)	Cumulative growth.		Total food to date. (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth. (cm.)	Wt. (gm.)		Lth. (cm.)	Wt. (gm.)					Lth.	Wt.		
June 24	18·1	44·0	0·007	—		—	—	—	—	—	—	—	—
July 8	18·4	50·3	0·008	0·3	6·3	57·7	9·2	14	4·1	0·3	6·3	58	9·2
,, 22	18·5	58·7	0·009	0·1	8·4	73·0	8·7	14	5·2	0·4	14·7	131	8·9
Aug. 5	18·8	62·7	0·009	0·3	4·0	76·3	19·1	14	5·4	0·7	18·7	207	11·1
,, 19	19·3	73·3	0·010	0·5	10·6	78·6	7·4	14	5·6	1·2	29·3	286	9·8
Sept. 2	19·8	81·6	0·011	0·5	8·3	82·8	10·0	14	5·9	1·7	37·6	368	9·8
,, 16	20·1	87·1	0·011	0·3	5·5	83·7	15·2	14	6·0	2·0	43·1	452	10·5
,, 30	20·7	102·5	0·012	0·6	15·4	86·4	5·6	14	6·2	2·6	58·5	538	9·2
Oct. 14	21·2	109·0	0·011	0·5	6·5	87·2	13·4	14	6·2	3·1	65·0	626	9·6
,, 28	21·7	111·7	0·011	0·5	2·7	73·8	27·3	14	5·3	3·6	67·7	699	10·3
Nov. 11	21·8	114·7	0·011	0·1	3·0	50·0	16·7	14	3·6	3·7	70·7	749	10·6
,, 25	21·8	111·4	0·011	nil	– 3·3	8·4	—	14	0·6	3·7	67·4	758	11·2
Dec. 9	21·9	108·7	0·010	0·1	– 2·7	1·9	—	14	0·1	3·8	64·7	760	11·7
,, 23	22·0	104·5	0·010	0·1	– 4·2	2·7	—	14	0·2	3·9	60·5	763	12·6

TABLES 46–49.

MAXIMUM REQUIREMENTS AND GROWTH OF FEMALE PLAICE.

TABLE 46: L15.

Date. (1929)	Size of fish.		Wt./Lth.^{3}	Growth per period.		Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Food per day during each period. (gm.)	Cumulative growth.		Total food to date from June 24 (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
	Lth.	Wt.		Lth.	Wt.					Lth.	Wt.		
June 24	15·1	31·9	0·009	—		—	—	—	—	—		—	—
July 8	16·8	38·1	0·008	1·7	6·2	55·7	9·0	14	4·0	1·7	6·2	56	9·0
,, 22	17·4	49·5	0·009	0·6	11·4	77·2	6·8	14	5·5	2·3	17·6	133	7·6
Aug. 5	17·9	57·5	0·010	0·5	8·0	91·0	11·4	14	6·5	2·8	25·6	224	8·7
,, 19	18·8	72·2	0·011	0·9	14·7	91·2	6·2	14	6·5	3·7	40·3	315	7·8
Sept. 2	19·7	85·5	0·011	0·9	13·3	97·6	7·3	14	7·0	4·6	53·6	413	7·7
,, 16	20·2	91·8	0·011	0·5	6·3	95·4	15·1	14	6·8	5·1	59·9	507	8·5
,, 30	21·1	112·5	0·012	0·9	20·7	101·1	4·9	14	7·2	6·0	80·6	608	7·5
Oct. 14	22·1	123·8	0·011	1·0	11·3	101·3	9·0	14	7·2	7·0	91·9	709	7·7
,, 28	22·7	137·6	0·012	0·6	13·8	83·2	6·0	14	5·9	7·6	105·7	792	7·5
Nov. 11	23·0	141·1	0·012	0·3	3·5	65·4	18·4	14	4·7	7·9	109·2	858	7·9
,, 25	23·0	140·7	0·012	nil	– 0·4	24·8	—	14	1·8	7·9	108·8	883	8·1
Dec. 9	23·0	137·0	0·011	nil	– 3·7	4·6	—	14	0·3	7·9	105·1	888	8·4
,, 23	23·0	135·5	0·011	nil	– 1·5	8·0	—	14	0·6	7·9	103·6	896	8·6

TABLE 47. : L16.

June 24	18·4	50·5	0·008	—		—	—	—	—	—		—	—
July 8	18·8	61·1	0·009	0·4	10·6	61·2	5·8	14	4·4	0·4	10·6	61	5·8
,, 22	19·1	70·5	0·010	0·3	9·4	81·5	8·6	14	5·8	0·7	20·0	143	7·1
Aug. 5	19·6	83·4	0·011	0·5	12·9	102·2	7·9	14	7·3	1·2	32·9	245	7·4
,, 19	20·5	99·9	0·012	0·9	16·5	109·5	6·6	14	7·8	2·1	49·4	354	7·2
Sept. 2	21·3	117·5	0·012	0·8	17·6	118·5	6·7	14	8·5	2·9	67·0	473	7·1
,, 16	21·7	130·5	0·013	0·4	13·0	122·3	9·4	14	8·7	3·3	80·0	595	7·4
,, 30	22·5	147·1	0·013	0·8	16·6	124·0	7·5	14	8·9	4·1	96·6	719	7·4
Oct. 14	23·0	169·1	0·014	0·5	22·0	124·7	5·7	14	8·9	4·6	118·6	844	7·1
,, 28	23·7	179·6	0·014	0·7	10·5	107·6	10·2	14	7·7	5·3	129·1	951	7·4
Nov. 11	24·0	179·3	0·013	0·3	– 0·3	81·9	—	14	5·8	5·6	128·8	1033	8·0
,, 25	24·1	175·0	0·012	0·1	– 4·3	26·6	—	14	1·9	5·7	124·5	1060	8·5
Dec. 9	24·1	171·1	0·012	nil	– 3·9	6·4	—	14	0·5	5·7	120·6	1066	8·8
,, 23	24·1	170·8	0·012	nil	– 0·3	10·6	—	14	0·8	5·7	120·3	1077	8·9

TABLE 48: L13.

June 24	15·1	27·0	0·008	—		—	—	—	—	—		—	—
July 8	15·5	31·1	0·008	0·4	4·1	36·7	9·0	14	2·6	0·4	4·1	37	9·0
,, 22	15·9	40·6	0·010	0·4	9·5	70·0	7·4	14	5·0	0·8	13·6	107	7·9
Aug. 5	16·6	48·1	0·011	0·7	7·5	81·4	10·9	14	5·8	1·5	21·1	188	8·9
,, 19	17·3	55·6	0·011	0·7	7·5	68·8	9·2	14	4·9	2·2	28·6	257	9·0
Sept. 2	17·8	61·9	0·011	0·5	6·3	67·6	10·7	14	4·8	2·7	34·9	324	9·3
,, 16	18·5	64·0	0·010	0·7	2·1	69·9	33·3	14	5·0	3·4	37·0	394	10·6
,, 30	18·7	69·0	0·011	0·2	5·0	70·3	14·1	14	5·0	3·6	42·0	464	11·0
Oct. 14	19·0	71·8	0·010	0·3	2·8	70·0	25·0	14	5·0	3·9	44·8	534	11·9
,, 28	19·2	71·4	0·010	0·2	– 0·4	48·4	—	14	3·5	4·1	44·4	583	13·1
Nov. 11	19·2	71·0	0·010	nil	– 0·4	36·3	—	14	2·6	4·1	44·0	619	14·1
,, 25	19·2	70·4	0·010	nil	– 0·6	7·2	—	14	0·5	4·1	43·4	626	14·4
Dec. 9	19·2	69·1	0·010	nil	– 1·3	3·7	—	14	0·3	4·1	42·1	630	15·0
,. 23	19·2	68·5	0·010	nil	– 0·6	5·1	—	14	0·4	4·1	41·5	635	15·3

TABLE 49: L14.

Date. (1929)	Size of fish. Lth.	Size of fish. Wt.	Wt. / Lth.^{3}	Growth per period. Lth.	Growth per period. Wt.	Total food per period. (gm.)	Gm. of food per 1·0 gm. increase in weight of fish.	No. of days in period.	Food per day during each period. (gm.)	Cumulative growth. Lth.	Cumulative growth. Wt.	Total food to date from June 24 (gm.)	Gm. of food per 1·0 gm. increase in wt. of fish to date.
July 15	23·0	90·1	0·007	—		—	—	—	—	—		—	—
,, 22	23·0	87·6	0·007	nil	− 2·5	31·7	—	7	4·5	nil	− 2·5	32	—
Aug. 5	23·1	97·3	0·008	0·1	9·7	96·7	10·0	14	6·9	0·1	7·2	128	17·8
,, 19	23·4	112·5	0·009	0·3	15·2	105·9	7·0	14	7·6	0·4	22·4	234	10·4
Sept. 2	23·6	122·6	0·009	0·2	10·1	110·7	11·0	14	7·9	0·6	32·5	345	10·6
,, 16	23·8	135·7	0·010	0·2	13·1	113·3	8·6	14	8·1	0·8	45·6	458	10·0
,, 30	24·3	151·2	0·011	0·5	15·5	115·2	7·4	14	8·2	1·3	61·1	573	9·4
Oct. 14	24·7	165·7	0·011	0·4	14·5	114·4	7·9	14	8·2	1·7	75·6	687	9·1
,, 28	25·3	174·5	0·011	0·6	8·8	94·3	10·7	14	6·7	2·3	84·4	782	9·3
Nov. 11	25·6	186·5	0·011	0·3	12·0	85·5	7·1	14	6·1	2·6	96·4	867	9·0
,, 25	25·7	184·8	0·011	0·1	− 1·7	37·7	—	14	2·7	2·7	94·7	905	9·6
Dec. 9	25·7	179·2	0·011	nil	− 5·6	7·8	—	14	0·6	2·7	89·1	913	10·3
,, 23	25·7	179·1	0·011	nil	− 0·1	12·5	—	14	0·9	2·7	89·0	926	10·4

TABLE 50.

SHOWING PERCENTAGE GROWTH IN WEIGHT OF SPECIFIED MALE AND FEMALE PLAICE FOR EACH PERIOD AT CAWSAND AND LYMPSTONE.

	[A] *Cawsand.*				[B] *Lympstone.*		
Date [1929]	B1 ♀	B4 ♀	D3 ♂	Date [1929]	L15 ♀	L16 ♀	L11 ♂
May 22	—	—	—				
June 6	29·2	40·5	—				
20	12·9	23·1	16·1	June 24	—	—	—
July 5	14·3	14·1	25·0	July 8	19·4	21·0	—
19	17·5	17·8	33·3	22	30·0	15·4	26·2
Aug. 2	13·8	17·4	23·3	Aug. 5	16·2	18·3	9·0
16	14·0	19·8	12·2	19	25·6	19·8	24 6
30	13·1	9·1	24·1	Sept. 2	18·4	17·6	16·8
Sept. 16	15·2	15·1	27·2	16	7·4	11·1	9·2
Oct. 1	12·6	9·9	20·6	30	22·5	12·7	15·8
15	7·3	7·8	13·9	Oct. 14	10·0	15·0	12·4
29	2·6	13·3	6·1	28	11·1	6·2	8·1
Nov. 13	5·6	5·9	7·9				
27	1·4	—	1·9				

TABLE 51.

MAINTENANCE OF MALE PLAICE AT CAWSAND (1928 AND 1929) AND AT LYMPSTONE (1929). SUMMARISED DATA.

Exp.	Fish No.	Average length (cm.).	Average weight (gm.).	Average daily ration (gm.).	Food per day/ /average body-wt.	Tables for reference.	Period to date given below.
C. 1928	Mean A	16·2	42·3	0·7	0·017	1	Nov. 30
C. 1929	Mean C	12·8	17·6	0·4	0·024	8	July 5
,,	C5a	14·6	30·0	0·6	0·019	9 & 12	Nov. 28
,,	C4a	15·9	39·0	0·6	0·015	10 & 12	Nov. 13
,,	C6a	16·7	43·0	0·7	0·016	11 & 12	Nov. 28
L. 1929	L1	17·3	52·2	0·9	0·017	28 & 33	Nov. 25
,,	L4b	20·9	76·0	1·1	0·015	29 & 33	,,
,,	L3	21·7	107·3	1·3	0·012	30 & 33	,,
,,	L2	22·9	129·7	1·4	0·011	31 & 33	,,

TABLE 52.

MAINTENANCE OF FEMALE PLAICE AT CAWSAND (1928 AND 1929) AND AT LYMPSTONE (1929). SUMMARISED DATA.

Exp.	Fish No.	Average length (cm.).	Average weight (gm.).	Average Daily ration (gm.).	Food per day/ /average body-wt.	Tables for reference.	Period to date given below.
C. 1928	Mean B	14·2	29·6	0·6	0·021	2	Nov. 30
,,	Suggested mean B	—	25	0·4 to 0·5	0·016 to 0·020	—	,,
C. 1929	Mean A	13·7	22·3	0·4	0·019	8	July 5
,,	A4a	16·3	40·5	0·6	0·016	13 & 16	Nov. 27
,,	A6a	16·3	42·0	0·6	0·015	14 & 16	,,
,,	A3a	17·7	56·5	0·8	0·015	15 & 16	,,
L. 1929	L5	18·5	64·8	0·9	0·014	34 & 38	Nov. 25
,,	L6	19·2	70·6	1·2	0·017	35 & 38	,,
,,	L7	22·5	102·7	1·3	0·013	36 & 38	,,
,,	L8a	22·0	103·2	1·3	0·013	37 & 38	Sept. 30
,,	L8b	23·1	113·8	1·4	0·013	37 & 38	Nov. 25

TABLE 53.

MAXIMUM REQUIREMENTS AND GROWTH OF CAWSAND AND LYMPSTONE MALE PLAICE.

Exp.	Fish No.	Initial size.		Final size.		Growth.		Total No. of days.	Total food taken. (gm.)	Average weight of food per day. (gm.)	Food per 1·0 gm. increase in weight of fish. (gm.)
		Lth.	Wt.	Lth.	Wt.	Lth.	Wt.				
C. 1928	Mean C	16·0	38·8	22·6	123·3	6·6	84·5	176	1129	6·4	13·3
C. 1929	D3	12·0	15·5	21·0	105·0	9·0	89·5	175	585	3·3	6·5
,,	D2	12·2	15·0	17·9	64·0	5·7	49·0	175	471	2·7	9·6
,,	D4	12·0	13·0	17·3	56·5	5·3	43·5	175	475	2·7	11·7
,,	D1	12·2	14·0	15·9	40·5	3·7	26·5	160	420	2·6	15·8
,,	D5	11·9	14·5	15·8	38·0	3·9	23·5	190	424	2·2	18·0
L. 1929	L11	16·1	23·2	23·1	157·4	7·0	134·2	154	953	6·2	7·1
,,	L12	18·1	44·0	21·8	111·4	3·7	67·4	154	758	4·9	11·2
,,	L10	16·6	36·2	19·1	82·8	2·5	46·6	98	536	5·5	11·5
,,	L9	19·7	57·5	21·3	102·6	1·6	45·1	98	676	6·9	15·0

TABLE 54.

MAXIMUM REQUIREMENTS AND GROWTH OF CAWSAND AND LYMPSTONE FEMALE PLAICE.

Exp.	Fish No.	Initial size.		Final size.		Growth.		Total No. of days.	Total food taken. (gm.)	Average weight of food per day. (gm.)	Food per 1·0 gm. increase in weight of fish. (gm.)
		Lth.	Wt.	Lth.	Wt.	Lth.	Wt.				
C. 1928	Mean D	16·1	43·3	23·3	151·2	7·2	107·9	176	1129	6·4	10·5
C. 1929	B4	13·2	18·5	21·3	103·5	8·1	85·0	189	613	3·3	7·2
,,	B1	13·2	24·0	21·0	105·5	7·8	81·5	189	618	3·3	7·6
,,	B5a	17·9	54·0	20·1	86·0	2·2	32·0	71	291	4·1	9·1
,,	B6	12·0	16·0	16·7	51·0	4·7	35·0	189	448	2·4	12·8
L. 1929	L16	18·4	50·5	24·1	175·0	5·7	124·5	154	1060	6·9	8·5
,,	L15	15·1	31·9	23·0	140·7	7·9	108·8	154	883	5·7	8·1
,,	L14	23·0	90·1	25·7	184·8	2·7	94·7	133	907	6·8	9·6
,,	L13	15·1	27·0	19·2	70·4	4·1	43·4	154	626	4·1	14·4

The Larvæ of the Plymouth Galatheidæ. I. *Munida banffica, Galathea strigosa* and *Galathea dispersa.*

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With 1 Text-Figure and Plates 1–3.

In the Plymouth district there are five or six species belonging to the Galatheidæ, one Munida, and four or five Galathea. The species occurring are the following:—

Munida banffica (Pennant).
Galathea strigosa L.
Galathea dispersa Kinahan.
Galathea nexa Embledon.
Galathea squamifera Leach.
Galathea intermedia Lilljeborg.

Of the Galathea species, it is a disputed point as to whether *Galathea dispersa* and *G. nexa* are separate species. Both occur in our outside waters, the *dispersa* form being exceedingly common, the *nexa* form rare. Selbie (1914), who discusses the question in detail, regards the *nexa* form, which is more spiny and has shorter claws, merely as an old male of *dispersa*, giving them both the earlier name of *nexa*. Crawshay (1912) found both forms occurring on the outer grounds beyond the Eddystone and states that the males and females of *nexa* both had these characteristics and were easily distinguished from *dispersa*. Unfortunately I have been able only to examine one *nexa* but many *dispersa*, and the *nexa* form was quite different in appearance. It was a small male, probably not fully grown, but its claws were much shorter and more spiny than the males of *dispersa* of the same size. No live specimens of *nexa* have been available recently and therefore no berried females from which to obtain larvæ. The larvæ of *dispersa* have been hatched from the egg and it has been seen clearly that these are by far the commonest Galathea larvæ in the plankton of the outside waters and occasionally inshore. The larvæ of *Galathea strigosa* are frequently found with those of *dispersa* outside and also occur inside with those of

G. squamifera, which is almost exclusively an inshore form. Those of *G. intermedia* occur occasionally both outside and inside.

These four larvæ are easily distinguishable and are the only Galatheas to be found after careful search in the outside plankton, usually taken beyond the Eddystone. It does not follow, however, that there may not be another larva occurring still farther out, which may belong to *nexa*. It is regarded here as probable that the two species are distinct and therefore the species called *nexa* by Selbie (*loc. cit.*), and also by G. O. Sars (1890) when describing the larva, is here called *dispersa*, and it is presumed that the five species of Galathea occur in the district. Of these the larva of *G. nexa* is not yet known. *Munida banffica*, only recognised recently as present in the Plymouth fauna, but now found to be abundant, has been followed through all its larval stages and hatched from the egg. The larvæ agree in all respects with those of Sars (*loc. cit.*) who described and figured them as *Munida rugosa*. *Galathea strigosa* and *Galathea dispersa* have also been followed through the whole of their life-histories and hatched from the egg, *G. strigosa* for the first time, and *G. dispersa* agreeing with Sars' description of that species, described as *G. nexa*. *Galathea squamifera*, the common shore species, has not yet been hatched from the egg, but has been followed through all its larval stages until the young Galathea emerged from the last larva. *Galathea intermedia*, not nearly so common, has been found in all the larval stages, except the second, and has been kept until the last larva turned into the young Galathea. The last two species have also been described by Sars (*loc. cit.*) to a certain extent. They are reserved for a later paper in the hopes of hatching them from the egg. It is possible to recognise all these four larvæ, particularly when alive, as the colouring in each is characteristic, but they can also be recognised when preserved, by other characters as will be shown in the following notes :—

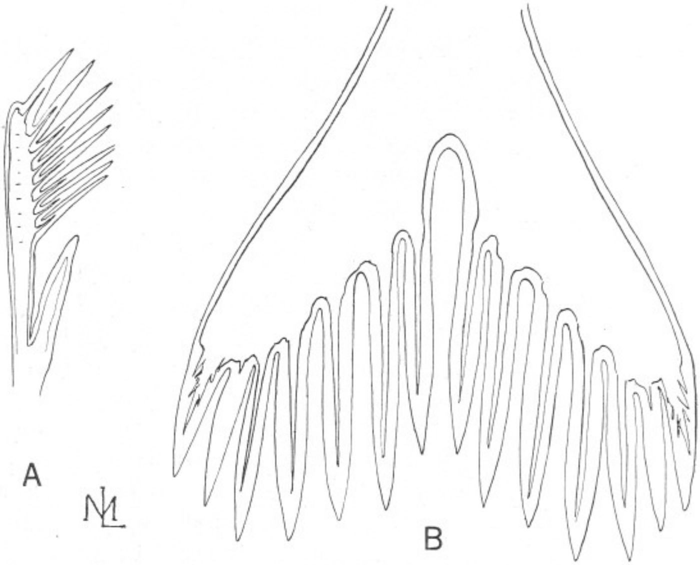
The general form of the larval galatheid is well known, Sars having described the general life-history of Munida and of Galathea with details of the appendages. Munida is easy to distinguish from Galathea, but the species of Galathea have hitherto been difficult to separate from one another. In an attempt to differentiate all species of the decapod larvæ from Plymouth it has been possible to distinguish these four distinct Galathea larvæ.

Munida banffica, *Galathea strigosa* and *Galathea dispersa* all occur fairly commonly on the outside grounds, *G. dispersa* being much the most numerous. *G. strigosa* and occasionally *G. dispersa* also occur inshore, but Munida is always outside. All occur in berry at least from autumn to spring and probably (certainly in the case of *G. dispersa*) all the year round, and the larvæ are fairly abundant in the plankton, particularly the two Galathea species.

Munida can be distinguished at once from Galathea by its elongated form, long spines and aciculate antennal scales. *Galathea strigosa* can be distinguished from the other Galathea larvæ by its longer spines and larger size, except in the last stage of *G. dispersa*, which is much the same size but easily separated by having spines on the fifth abdominal segment and not on the fourth. *G. squamifera* and *G. intermedia* are much smaller and although *squamifera* has spines on the fourth abdominal segments, they are much shorter than in *strigosa* and the other spines altogether smaller. *G. intermedia*, having spines on the fifth abdominal segment only, is so much smaller than any of the others that there is no mistaking it. All four can be separated when alive by their colour.

The common features of Munida and Galathea larvæ are the following: four or five larval stages; very transparent body with orange-red pigment in certain areas, rarely a little brown, yellow or crimson; long rostrum; carapace produced into a spine posteriorly at each side, the margin of the carapace toothed behind laterally and on the hind margin; eyes very conspicuous; antennules with long base ending in two short branches, the inner with a long seta at its tip, which later disappears, and one on the inner side of the base takes its place, the outer with æsthetes and spines; antenna with inner flagellum unjointed in all stages, the scale ending in a long apical spine and bearing several setæ internally, mandible with a simple palp in later stages; first maxilla with two inner lobes and either a one- or two-jointed palp; second maxilla with four inner lobes, an unjointed palp, and a conspicuous external plate. Only two pairs of maxillipedes functional in the first larva with swimming exopodites and jointed endopodites, the third pair rudimentary and only functional in the second stage. Abdominal segments denticulate, or with two spines dorsally on the hind margins, with lateral spines on the fourth and fifth segments, or on the fifth only. Telson deeply forked, armed at the end with seven spines on each side in the first stage, eight in the second; the second spine from the outside being hair-like, the fourth becoming the longest. In the first and second stage the telson is a simple plate fused with the sixth segment, and with the outer spine the longest; in the third, fourth and fifth (if present) uropods appear, and the telson is cut off from the sixth segment. In the third stage the telson is long and narrow, uropods are formed but their base is not cut off and there are no setæ on the inner branch, the outer branch bearing several setæ. In the fourth stage (usually the last) the inner branch is setose and the base is cut off from the uropods. The legs appear gradually until at the last stage the first is large and chelate and bulges out from the body, but no legs are functional. Pleopods appear as small knobs in the third stage and are long but unjointed in the last stage. Four larval stages appear to be the usual number, but in *Galathea dispersa* there are four or five, five being the most frequent. By keeping the third and fourth larvæ of all the species it was found that the young Galathea emerged from the fourth larva in Munida, *Galathea strigosa*, *G. squamifera*, and *G. intermedia*, but although *G. dispersa* sometimes emerged as a young Galathea from the fourth stage, there was in this species a fifth stage which seemed to be usual. The fourth larva was seen emerging from the third in all the species.

The embryonic cuticle is cast off just before hatching. It corresponds to the pre-zoea of the Brachyura. It is very interesting, for in the telson seven fully developed long spines cover the seven setæ of the first larva (Text-Fig. 1B), the second, which in the larva is represented by a hair, having quite a normal large spine covering it. The antennal scale is covered by a sheath with eight large spines on the inside corresponding to the eight setæ in the first larva (Text-Fig. 1A).



TEXT-FIG. 1.—*Munida banffica.* A, embryonic antenna ; B, embryonic telson.

Sars (*loc. cit.*) has described and figured the appendages very fully both in Munida and Galathea ; it is therefore unnecessary to figure them again, but the chief differences and the general aspect of the larvæ are given below. The red colouring of the first larva is indicated in the figures of the plates by black. The same scheme occurs through all the larvæ of each species, but intensified in the later stages.

Genus MUNIDA.

Munida banffica (Pennant).

(Plate 1).

Larvæ described by Sars (1890) as *M. rugosa*. Four larval stages (no fifth stage seen), the fourth changing to a young Munida. First larva from egg, second larva from first from plankton, third from second from plankton, fourth from third from plankton, first young stage from fourth from plankton.

Eggs 0·80 mm. by 0·64 mm. when nearly ready to hatch; at first orange-red, then becoming brown.

Larvæ very transparent, orange-red dorsally under the carapace in two distinct streaks and a small patch each side, two streaks on each side of the abdominal segments and at the base of the telson. Length of first larva from tip of rostrum to end of telson 6·24 mm. (Plate 1, Figs. A and B), growing rapidly so that each successive stage is conspicuously larger than the last. The size varies to some extent and a third larva of one brood may be smaller than a second larva of another brood. Rostrum very long, prickly, base of antennule long, antennal scale aciculate with long drawn-out prickly spine at the tip, carapace usually covering the first segment and sometimes part of the second, with long lateral posterior spines. Second to fifth abdominal segments with two dorsal spines on the hind margin, dwindling in size in the later stages; conspicuous lateral spines on segments four and five. In the third and fourth stages a large central spine on the hind margin of the sixth segment. Outer branch of uropods with a long apical prickly spine. Outer spine of telson very long and armed with thick spines in the early stages, dwindling later; second spine hair-like, fourth becoming the longest. In the third stage there are five smaller spines on each side internal to the fourth, and in the fourth stage there are six, making ten in all on each side; unlike Galathea which has only eight on each side. Palp of second maxilla one-jointed (two-jointed in Galathea). Gills conspicuous in last stage.

Genus GALATHEA.

All the larvæ of Galathea differ from Munida in being much shorter with non-aciculate antennal scales, although the scale ends in a long point, the rostrum and spines of carapace not so long. The second to the fifth abdominal segments are armed on the posterior margin with a row of minute denticles. No central spine on sixth segment. Telson with outer spine in early stages not so long, in later stages with eight spines on each side. Second maxilla with two-jointed palp. Otherwise much like Munida.

Galathea strigosa L.

(Plate 2).

Four larval stages (no fifth seen), the fourth changing to a young Galathea. First larva from egg, second from first from plankton, third from second from plankton, fourth from third from plankton, young Galathea from fourth from plankton.

Eggs 0·88 mm. by 0·76 mm. when ready to hatch. At first orange-red, then brownish.

Larvæ very transparent but with more colour than Munida. Orange-red on base of antennules on side of eyes, on exopodite of maxillipedes, at base of rostrum and a large mass in the thoracic region. Two large streaks on the abdomen from the fourth segment to the base of telson. Tip of rostrum and carapace spines becoming pinkish in later stages, not prickly. Length of first larva *ca.* 3·5 mm., second *ca.* 4·96 mm., third *ca.* 5·36 mm., fourth (last) *ca.* 6·88 mm. Much less elongated than Munida, rostrum and spines of carapace and antennular scale not so long. Fourth and fifth abdominal segments with conspicuous lateral spines. Hind margin of segments two to five denticulate, the denticles dwindling and almost disappearing in the later stages. Telson a wide triangular plate in the first and second stages, having seven spines on each side posteriorly in the first stage, eight in the other stages ; second spine hair-like. In the later stages the telson gradually narrows and the fourth spine becomes much the longest. Nine or ten spines in the inner uropods on the fourth (last) stage. This stage emerges from the third stage with no spines on the inner uropods.

Galathea dispersa Kinahan.

(Plate 3).

Larva described by Sars (1890) as *G. nexa*. It differs from *G. strigosa* in its smaller early stages, absence of lateral spines on the fourth abdominal segment, narrower telson, and in its pigmentation.

Four or five larval stages. Five is probably normal, but the young Galathea has been seen to emerge from the fourth stage, and the normally fifth stage has been seen to emerge from the third stage with no spines on the inner branch of the uropods ; thus the fourth or fifth stage may be omitted.

Eggs measure 0·64 mm. by 0·48 mm. when nearly ready to hatch. At first orange-red, then brownish.

Larvæ very transparent, first obtained from egg, second from first from plankton, third from second from plankton, fourth from third from plankton, fifth from fourth or occasionally from third from plankton, young Galathea from fourth or normally from fifth from plankton.

Orange-red on base of antennules, on maxillipedes, at base of rostrum, much on thorax, on first, second and third abdominal segments (not always on third), on the fifth and at the base of the telson in two streaks. In the later stages there is a good deal of yellow in the thorax. Rostrum and carapace spines becoming pinkish, smooth. First larva *ca.* 2·5 mm., second *ca.* 3·1 mm., third *ca.* 3·9 mm., fourth *ca.* 5 mm., fifth *ca.* 6·56–6·8 mm.

The young stages of Galathea from the last larva are much alike, but Munida is easily recognised by its three-pronged rostrum (Plate 1, Fig. F), the long central spine having a small tooth each side near the tip. The first young stage of *Galathea strigosa* and *G. dispersa* closely resemble the figure of *G. intermedia* given by Sars. All have a fairly long pointed rostrum with three prominent teeth on each side and usually with one or two smaller teeth at the base, and five prominent teeth at the sides of the carapace, usually with smaller teeth in between. The legs bear many spines and hairs but external specific characters are hardly apparent. *Galathea dispersa* (Plate 3, Fig. J) has a longer rostrum and more prominent teeth on the carapace than *G. strigosa*. Both are of a yellowish colour with red, no blue being apparent as yet in *G. strigosa*.

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EXPLANATION OF PLATES.

(All drawn to same scale.)

PLATE 1.

Munida banffica.

A, B. 1st larva from egg, 6·24 mm. long.
C. 2nd larva from first from plankton.
D. Posterior end of 3rd larva from plankton.
E. Posterior end of 4th larva from plankton.
F. Carapace of 1st juv. from last larva from plankton.

PLATE 1.

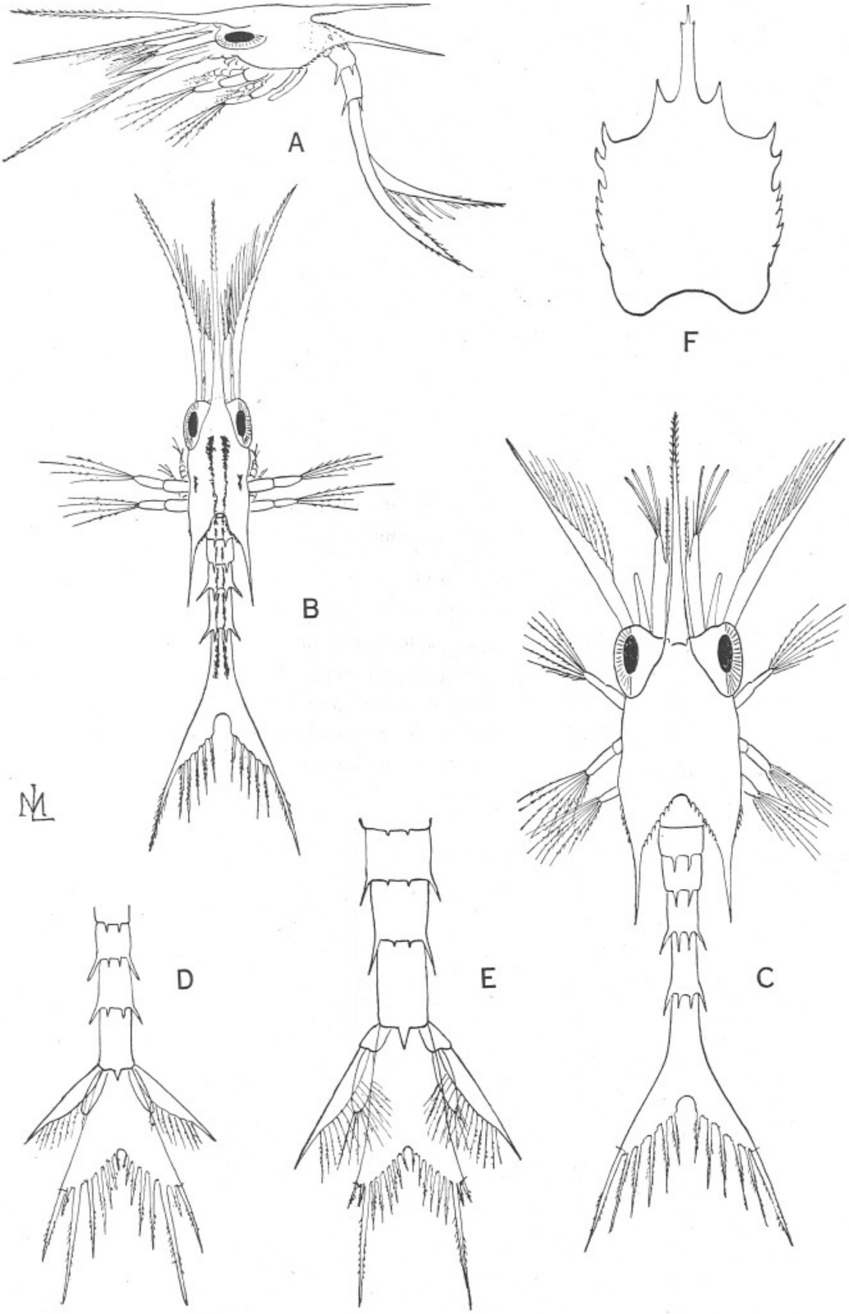


PLATE 2.

Galathea strigosa.

A, B. 1st larva from egg, 3·5 mm. long.
C. 2nd larva from plankton, 4·96 mm. long.
D. 3rd larva from plankton, 5·36 mm. long.
E. 4th larva from plankton, 6·88 mm. long.
F. Carapace of 1st juv. from last larva from plankton.

PLATE 2.

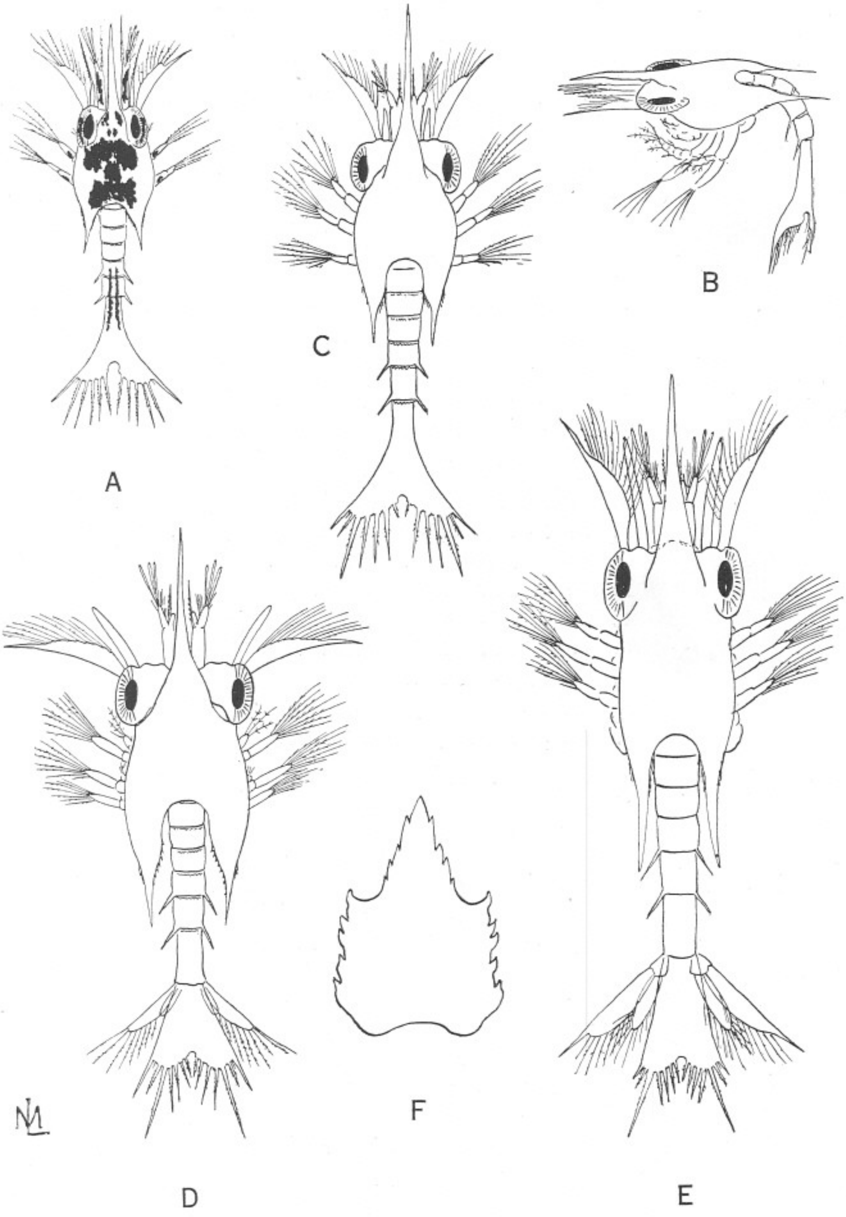
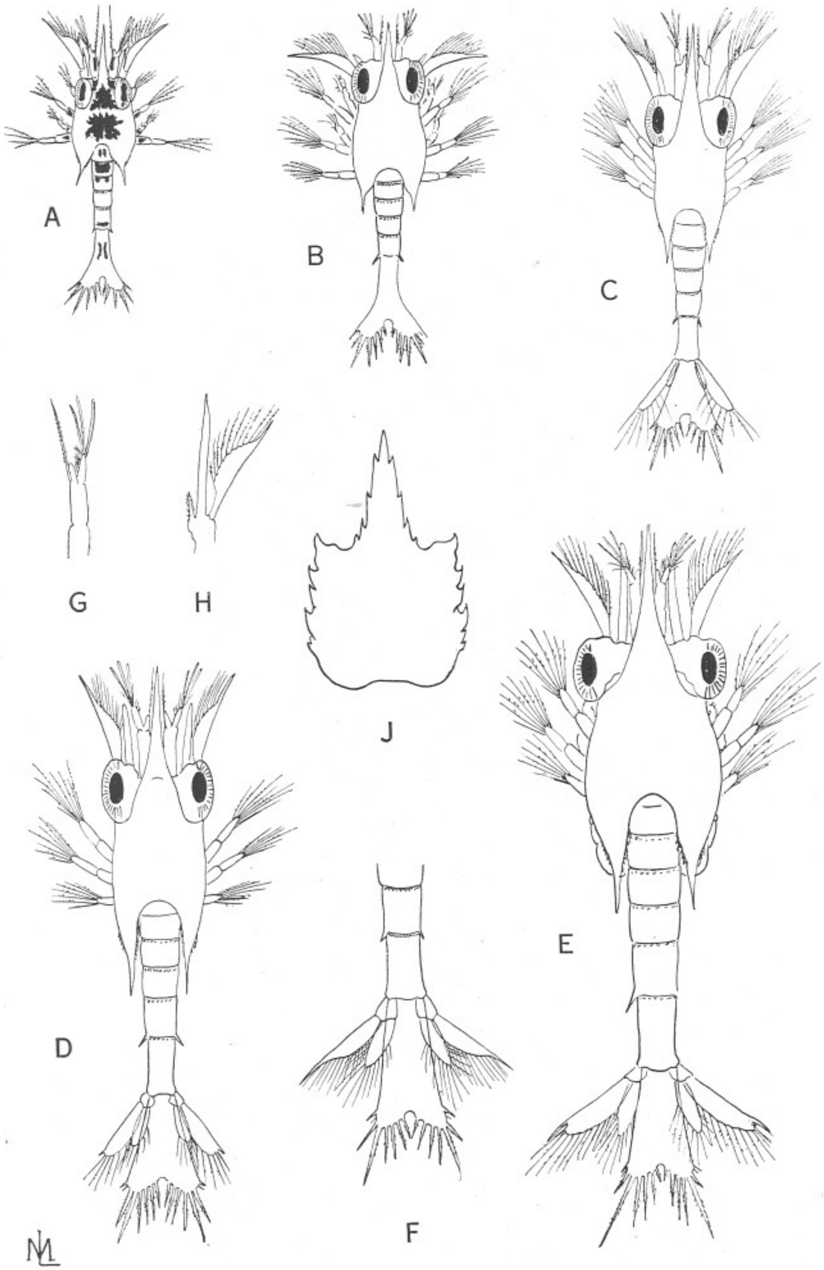


PLATE 3.

Galathea dispersa.

A. 1st larva from egg, 2·5 mm. long.
B. 2nd larva from plankton, 3·12 mm. long.
C. 3rd larva from plankton, 3·9 mm. long.
D. 4th larva from third, 5 mm. long.
E. 5th larva from fourth, 6·56 mm. long.
F. Posterior end of a larger fifth larva.
G. Antennule of same.
H. Antenna of same.
J. Carapace of 1st juv. from last larva.

PLATE 3.



Some New Eye-Colour Changes in *Gammarus chevreuxi* Sexton. Part I.

By

E. W. Sexton, A. R. Clark and G. M. Spooner.

With Plate VIII.

1. INTRODUCTION.

SUMMARY OF MUTANT STOCKS GIVING RED EYES.

THE eye-colour of the wild *Gammarus chevreuxi* is always black and no variation from the normal Black has ever been observed in the many thousands which have been taken in the native habitat of the species. This, however, does not preclude the possibility that mutations may have arisen in the wild stock and have gone under in the struggle for survival.

The difficulty we have had throughout our work in establishing mutant stocks that have arisen in the Laboratory indicates that the mutations of the type used for genetical study would have but little chance under normal conditions in nature, of survival through the early critical period. Each new mutation has shown greatly lowered vitality during its earlier generations, accompanied by marked abnormalities in breeding.

But once established, the mutants tend to become healthier with each generation, some, such as the Red-eye and the Albino-eye of Mutant Stock I, for example, being able, in time, to hold their own with the normal wild Black-eyed animals in vigour, length of life and number of offspring.

As has been shown before (**5**, p. 46), the black pigment in normal cases starts as bright scarlet in the embryo and passes through various darkening stages from " intermediate red " to " dark red " and then to jet black on hatching.

In all the different mutating stocks there have arisen Red-eyed specimens in which the red colour that normally appears only for a short time in the embryonic stage persists after hatching. It is noteworthy that the Reds from the five stocks with which we work are all genetically distinct from one another, for in whatever way we cross-mated the Reds from different stocks the young have always been born Black-eyed. In other stocks started at the same time as Stock V, in which Red-eyes appeared, none survived to be cross-mated ; the details of their occurrence are given below (p. 00).

The term " Mutant Stock " we apply to the offspring of any one particular Black-eyed pair in which mutations from the normal have developed. They may be summarised briefly.

Mutant Stock I.

One of the pairs brought in from the wild on June 12th, 1912, and kept in laboratory conditions, gave the first Red-eyed young in the F_2 generation from one Black-eyed female only—the Red a bright scarlet (Plate VIII—Normal Red). Other mutations in this stock were, the Albino degenerate eye from a mating of Black with Red, the Irregular Coloured eye, the No-white, the Blind, and the One-eyed. This is the stock with which Mr. E. B. Ford is working at Oxford.

Mutant Stocks II, III, and IV.

These three stocks came from a dredging brought in on September 12th, 1922. Nineteen pairs were set out in an incubator kept as nearly as possible at 21° C. Only two of the pairs gave redness in their offspring (Stocks II and IV), both in the F_2 generation.

Sixteen other pairs were started in laboratory conditions, with the temperature varying through a wide range, from two to six degrees centigrade in the twenty-four hours ; the highest recorded was 27° C. in July, the lowest 5·7° C. one day in January, when the heating apparatus failed. Five of these pairs, one the Mutant Stock III referred to below, gave some redness in the offspring. Of the others, one showed slight reddening in F_1 and F_2, two in F_1 only, and the fourth gave two bright Reds out of a total of 574 offspring.

Mutant Stock II. The Red-eye* in this, as in Stock I, is bright scarlet associated, as in all the stocks, with normal pale-green body-colour. The most striking feature appeared with the Red-eye, in the F_2 generation, viz., the White-body mutation, in which the body and eye are completely devoid of coloured pigment. The eyes connected with it are, the homozygous White-eye, the Changeling White which later develops red-eye and body colour, the Flushed White, and the Purple White eye.

Mutant Stock III differs from the others in that the Red came gradually, some Black-eyed parents becoming Reddish Black and giving different shades of Red-eye in their offspring. This Red is not the bright scarlet of Stock I but a deeper tint, like the New Red figured on Plate VIII. Another point of resemblance with our new mutation, V, is that the eye-colours sometimes change with growth, but with these it is usually only in the one direction, a *lightening* of the colour, e.g., Reddish Black to Dark Red, Dark Red to brighter Red.

The "Mosaic" eye appeared in this stock, i.e. an eye with some of the ommatidia jet-black and some bright red.

In *Mutant Stock IV* also there are different kinds of Red eyes, bright, intermediate, and dark. Like the preceding, the Dark Red lightens in varying degree. The colours are heritable, and an animal hatched Dark Red functions always as Dark Red, however much the colour may alter during its life.

In our new *Mutant Stock V* with which this paper deals there is much greater variation in eye-colour and, particularly, in colour-changes. All intermediate stages between Black and Red have occurred. Changes undergone after birth include both darkening and lightening, as well as either permanent or temporary changes to some shade of purple. Intermediate Reds have been crossed with Reds of Stock I, Stock II, and Stock III and have given a Black F_1 with all.

In comparing these five mutant stocks, it is seen that there are two distinct categories of mutants producing red eye-colour. In one, represented by Stocks I and II, the Red-eye appears as a typical mutation, arising suddenly and persisting as a simple recessive. Its mode of inheritance is comparable with that of other familiar recessives, occurring, for example, in Drosophila or Primula, and interpretable in terms of a change

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* This Red is referred to as "New Red" in "Inheritance in *Gammarus chevreuxi* Sexton" (**3**, p. 119). Since then, we have found that the different Reds of the five stocks fall into two distinct classes of colour—the bright scarlet of Stocks I and II, which we call "Normal Red," and a deeper, more intense shade of red which appears in Stocks III, IV, and V, to which we now confine the term "New Red" (see Plate VIII).

in a single gene. Attention may be called, firstly, to the manner in which the Red-eye of Stock I originated : there were altogether 9 reds in the progeny of a certain black-eyed F_1 female,—2 out of 13 survivors from two broods with a brother, 4 out of 44 from a mating with a freshly captured male, and 3 out of 39 from another mating with the same brother. Since neither of these males threw any red offspring when mated with other females, it suggests that the female parent was in some way responsible for the occurrence of the red mutation in the offspring (**1**, p. 22). Secondly, to the physiological difference between " Black-eye " and " Red-eye " as demonstrated by Ford and Huxley (**4**, p. 115), who showed that when kept at a temperature of 23° C. the red-eyed individuals gradually darken to black, undergoing a process similar to, but much slower than that of normal blacks before hatching. The Red-eye is thus a case in which the rate of deposition of black pigment is very much reduced, in fact indefinitely reduced at normal temperatures. A more precise idea of the action of the gene concerned in the Red mutation is thus obtained. The mutation " Red-eye " is now expressed as a certain degree of retardation of pigment deposition.

In the other category, represented by Stocks III and V, redness emerges somewhat gradually, as described below. Intermediate stages between black and red occur and it seems as though segregation is necessary for the production of a bright red eye. Colour change during the course of life, involving either darkening or lightening, is of usual occurrence and characteristic of these stocks.

The manner in which red eye-colour appears is as follows. A certain number among the offspring from a wild pair are found to develop a reddish tinge and may become " Reddish Black " or even redder. Amongst the next generation, whether derived from these specimens or from unchanged Blacks, there occur individuals born in various stages of redness, i.e. " Reddish Black," " Dark Red," " Intermediate Red " (for explanation of these colours see below, p. 193 and Plate VIII), and bright " Reds " may also appear. Those that survive of the various reds may keep the same colour throughout life, but they are more liable to change, either in the direction of red (lighten) or black (darken). In Stock III lightening was the rule, but in Stock V both darkening and lightening occur. One other point common to the Stocks III and V should be mentioned—namely, that the shade of the red colour in the " New Red " eye is different from that in the original " Normal Red " (see Plate VIII). Examination of specimens in Stock V indicates that this is because the New Red is rendered slightly impure by a dilute deposit of a dark pigment, apparently some form of melanin.

Stock IV holds an interesting intermediate position. The red is evidently a simple recessive to black, but the red may exist in different shades, i.e. bright Red, Intermediate Red, Dark Red, or even Reddish Black. In so far as this stock has been investigated no tendency for the reds to darken has been found,—on the other hand nearly all the darker shades have lightened to red. Among the blacks, there are some which develop a certain degree of redness. It may be supposed that these are heterozygotes showing not quite complete dominance, but, if so, not all heterozygous specimens behave thus. The quality of the red colour is more akin to that of the " New Red " than to that of the " Normal Red."

It is hoped to enter more fully into the comparison of the various red mutants on a future occasion. The present investigation aims at elucidating the mode of inheritance of this second category of eye redness. Owing to its manner of origin there are obvious difficulties in thinking of the "New Red " eye as a simple mutation involving only one gene, however much the action of the latter may be modified by accessory genes. If, on the other hand, a group of genes is involved, then the " New Red " is not a simple, but a multiple recessive. The comparison, therefore, of the " New Red " with the " Normal Red " becomes a matter of considerable interest, and may well throw light on the general problem of the nature of mutations.

THE TYPES OF EYE-COLOUR.

We may now summarise the various shades of eye-colour that have been distinguished and used in description.

The symbols relating to each are inserted below in brackets, and the colours are shown on Plate VIII.

Pure Black (B), the normal wild type ;
Reddish Black (RB) ;
Dark Red (DR) ;
Intermediate Red (Int. in Charts 1–4, I.R. in Table II) ;
Bright Red (R), the " New Red " of this new Mutant Stock V ; the bright Red of Stock I is shown on the Plate as " Normal Red " ;
Purplish Black (PB) ;
Dark Purple (P) ;
and Reddish Purple (Rp).

Red, Intermediate Red, Dark Red, Reddish Black and Black form a series of progressive darkening, such as, for instance, occurs in the embryo of normal Blacks. Purplish Black has roughly the same depth of colour as Reddish Black, and Reddish Purple that of Intermediate Red.

Mr. E. B. Ford, in his work on *Gammarus chevreuxi* at Oxford, has distinguished a series of fourteen stages of darkening in the red eye-colour (**4**, p. 114). A proof of our Plate VIII was sent to him, and he has very kindly compared the eye-colours on the Plate with those in his series.

He allows us to state that his "stage 3, Light Red" is the same as our Intermediate Red, his "stage 6, Brown" is the same as our Dark Red, and his "Chocolate, stage 9" as our Reddish Black.

The selection of these particular colours is purely a matter of convenience. Every gradation, both among the reds and between the reds and purples, has been observed. The standards chosen are sufficiently far apart to be determinable even in a live, wriggling specimen, but they are sufficiently close to indicate any marked change in the colour of the eye.

If a "No-white" eye (i.e. lacking the reticulation of white pigment) were being used no doubt a greater accuracy in differentiation of colour shades (if indeed desirable) could be obtained. In these eyes with the normal white pigmentation, not only is the colour of the pigment cells largely hidden or shaded, but the optical effects of the white pigment when the animal is moving quite clearly give a brighter, redder shade than is seen when the eye is perfectly still. Care has to be taken especially with regard to this latter point. Previous work on eye-colour changes (Ford and Huxley, **4** and **6**) has been carried out upon No-white eyes.

2. HISTORY OF THE EXPERIMENT.

The opportunity for this investigation occurred when a number of wild pairs brought into the Laboratory in January and February, 1928, for temperature experiments, gave offspring which showed a tendency to redden, and an F_2 containing individuals of various shades of red at birth. Altogether thirty-nine pairs were set out in an incubator, thirty-two of these gave offspring and it is noteworthy that in 20 of these stocks this tendency to redness appeared. Whatever mutations are concerned therefore occurred independently in at least 20 cases. It is difficult not to conclude that some common environmental factor was instrumental in inducing them. The change over from the wild conditions in winter to those of the incubator room (starting at a temperature of 20·8° C. and rising in four months to 28° C.) is the obvious possible environmental factor.

Mutant Stock V with which this paper is mainly concerned is descended from one of these pairs.

Before giving the details of the history of the experiment, mention must be made of the many difficulties encountered in the handling of the stock, quite apart from the problems connected with the characters investigated. The broods were usually very small, numbers such as 1 to 10 being often recorded, whereas in the normal stocks the average number hatched is from 30 to 40. Then there was frequent ineffective mating and other irregularities in breeding; the proportion of young surviving to maturity was small; but the greatest difficulty was the cannibalism of the males, which was carried on to such an extent that few of the females died a natural death.* Adults available at the right time for mating were always scarce, and therefore continual cross-matings between members of different families of the stock, often different phenotypically, were necessary in order to keep the stock going, with the consequence that progress in the direction of establishing pure lines has been slow. The mortality after eighteen months in the incubator was so great that a reduction in the temperature was necessitated. The stock has therefore been kept under the more normal laboratory conditions, which has meant that, though its viability has increased, it is no longer subject to a regulated temperature.

The incubator referred to was a small room 10 ft. × 8ft. × 7 ft. high, in which the temperature could be kept approximately constant. It was heated by hot-air pipes, the gas furnishing the hot air being regulated by a Hearson's thermostat placed in the room. Air and water readings were taken daily by means of a thermograph in the air, and Negretti and Zambra's maximum and minimum thermometers immersed in a covered glass dish of water, the difference between the readings for air and water averaging about half a degree centigrade, those in the water being the lower. The broods were always examined in the incubator, so that

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* An instance from one of the F_4 families may be given in illustration of these points. Seventy-six young were hatched, of which only 18 survived to maturity, six males and twelve females. Only one of the females died a natural death, the other eleven were eaten by their mates.

Normally a male pairs with a female towards the end of a reproductive period, some days before her moult is due, mating as soon as this is accomplished. The eggs are laid almost at once; if not laid before the cuticle hardens, that is to say, within about 24 hours of casting the old skin, oviposition becomes impossible till the time for moulting comes again. The term "mating" therefore implies a complete reproductive period. The danger to the females comes during or just after the moult while the cuticle is still soft.

The matings of this family were as follows:—

One female mated, ate the male; mated with another male, same stock, laid eggs which were thrown off, mated again four times with no results; then ate the male; mated twice with a brother, and was eaten.

One male mated with sister female, no results, mated four times with eggs laid and broods hatched, numbering 1, 11, 14, and 21 respectively, then ate the female; mated once again with another female and died.

The second male mated with a sister, female died; mated with another sister, ate her; with a third female, had a brood of 1; mated again, brood of 8, ate the female, and died.

The third male had two matings with a sister, broods of 1 and 3, ate the female; two matings with another female, brood of 1, mated again, ate this female, and another, and then died.

The fourth male mated twice, ate the female, and died.

The fifth had three matings with a female, ate her; mated with another, ate her; mated twice with a third female, ate her; then as it had grown to a large size, it was given a female from the wild. With this one, it has had four broods, numbering 17, 46, 38, and 26 respectively, followed by three matings with no results, and now, after a fourth mating, eggs laid.

The sixth male ate two sisters in the brood bowl; mated three times with a third female, broods of 2, 9, and 8, mated again and ate the female; mated with another, ate her; mated with a female from the wild, ate her; mated with a second one, a brood of 15; mated again, brood of 22, and male was eaten.

they were not subjected to any change of temperature during the examination.

The temperature of the room when the experiment started on February 24th, 1928, was 20·2° C. The heat was gradually and steadily increased until in April it reached a mean of 25·8°* From May 1st to June 11th the mean was 26·8° C. From June 12th to June 26th it stood at 28°. This was found to be the limit of endurance for the species. Only 5 broods were hatched from all the pairs in the incubator, and these were very small numbers, 8, 3, 2, 3, 1,—all died within a few days. An alteration was therefore made, and the heat was lowered to 23·8° C. and kept at this from June 26th to July 6th. It rose again through July, as will be seen by the mean temperature given below for the incubating periods, until on August 16th it was decided to keep it constant at about 23° C. From August 16th, 1928, to June, 1929, it was kept almost constant between 22° and 23° C. In June it rose one degree and was constant through July and August till September 6th when the gas was turned out. The stock had grown so weak that it had to be re-established in healthier conditions.

The heat averaged 18° C. through the rest of September, and 15° through the winter months.

On April 9th, 1930, the bowls were brought out into the Laboratory, temperature averaging 15·7° C. The heating of the Laboratory was stopped on April 30th, and since then the mean was 14·5° for May, rising in June to about 17° C.

The first four generations, with the exception of one F_4 mating were hatched and reared in the heat. The broods hatched since are marked with the symbol † on the Charts.

Mutant Stock V is derived from one of the pairs brought in on February 13th, 1928, and kept at first in laboratory conditions for the females to extrude their young. In this pair, the female extruded her young, and laid eggs on February 16th. They were placed in the incubator on February 24th, the temperature then standing at 20·2° C. On the 28th this brood was extruded and the first batch of eggs to be laid in the heat was deposited.

Twelve Black-eyed F_1 were extruded on March 8th, the mean temperature for the incubation period, 8 days, being 20·8° C. Ten of these reached maturity about six weeks later, 6 males and 4 females, and mated in the brood bowl, but only one pair gave any results. From this pair all the stock is descended. The others mated again and again,

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* At 10.30 every morning the temperature at the time was read, and also the maximum and minimum temperature for the previous 24 hours. It was found that the mean of the temperature readings at 10.30 gave a result which differed only slightly from the mean of the maximum and minimum readings. When considering the temperature over a period we have therefore used the mean of the readings taken at 10.30 a.m.

seven batches of eggs were laid and thrown off, only 1 young, Black-eyed, was hatched and it died. The pair referred to mated and were taken out in a separate bowl on April 27th, and the *first* batch of eggs was laid on April 28th.

The heat was being increased, and the mean temperature for the incubating period was 25·8° C. It was evidently too much for the female, for though she carried the eggs until they showed orange in the pouch, i.e. to within a few hours of hatching, they were thrown off.

The *second* brood, laid on May 5th, was also thrown off.

The *third* brood, laid May 12th, hatched, and 5 young were extruded on May 20th, two Black-eyed and three with a slightly reddish tinge, the first sign of redness in the stock. Four survived, eye-colour unchanged, and two, a male and female, were seen to be mature on July 6th, a period of 47 days. By July 16th both females had eggs.

The matings gave different results, viz. the Black male mated with the Reddish Black female gave 47 Black, 21 Reddish Black, 1 Dark Red, and 10 Intermediate Red; while the other pair, Reddish Black male with Black female, gave 112 Black, 37 Reddish Black, and 16 Intermediate Red.

The *fourth* brood, laid May 20th, extruded May 27th, consisted of 7 Black and 1 Reddish Black. Four survived, three males and one female, maturing in about 40 days, the first eggs, only 2 or 3 in number, being laid on July 6th. The offspring given by this female were 97 Black and 1 Reddish Black.

The *fifth* brood, laid May 27th, and the *sixth* on June 4th were both thrown off—most likely because of the rise in temperature to 26·3° C. The *seventh* brood, laid June 11th, and extruded June 18th, was also a failure, for only 2 young, Black-eyed, were produced and these died almost at once.

The temperature was still rising, the mean from June 12th to June 26th being 28° C. Two batches of eggs were laid during this period, the *eighth* on June 18th, *ninth* on June 26th, but were thrown off, and as it was evident from the mortality in all the stocks that the conditions were too severe, the gas was lowered. The next brood, *tenth*, laid July 5th and extruded on the 12th, with a mean temperature during the incubating of 23·6° C., died before the young could be examined for eye-colour.

New eggs, brood *eleven*, were laid on July 13th, extruded July 20th, the mean for the seven days being 25·3° C.; 15 Black and 1 Reddish Black were hatched, but none reached maturity.

Brood *twelve*, July 21st to July 28th, mean temperature 24·4° C., contained 13 Black, 5 Reddish Black, and 1 Intermediate Red, the first Red-eyed young of this mutation.

Five Black survived, one of which lightened to Reddish Black; five

Reddish Black also, three of them unchanged, while the other two had lightened, one to Intermediate Red, and the other first to Intermediate Red, and still further to bright Red. The one Intermediate Red of the brood, almost normal red at birth, had darkened to Dark Red by August 14th. This is the first instance of lightening and darkening both occurring in the same brood, and noteworthy too for the fact that the changes took place within a comparatively short time after extrusion, 17 days. The young were an exceptional length of time in reaching maturity, the first to be noted, a female, took 65 days to October 1st. Some of the others took 93 days, and others even longer, a period of time comparable with that taken by the young maturing in the open Laboratory.

The *thirteenth* brood, July 29th to August 6th, took eight days hatching in a mean temperature of 23·4° C. Fifteen Black and 3 Reddish Black were extruded, the only survivor, a Black female, mated, eggs thrown off, mated again and was eaten by her mate.

The *fourteenth* brood, laid on August 7th, was extruded on August 14th and 15th, mean temperature for the seven days, 23·4° C. There were 11 Black, 2 Dark Red which darkened, and 1 Intermediate Red which grew up unchanged. The first to mature took 52 days, to October 5th, the first eggs were laid on October 8th.

The male parent of these broods died on August 15th, and the female on August 16th.

3. EYE-COLOURS AND COLOUR CHANGES IN MUTANT STOCK V.

The Appearance of Red Eyes in the Stock.

From the wild pairs brought in during January and February, 1928 (see p. 194), close on 4000 offspring were hatched in the F_1 generation. All were born with black eyes, but of the 432 survivors (representing 32 families), 33 (from 14 families) showed a tendency to redden later in life. Fifteen developed a reddish tinge; fourteen became definitely Reddish Black; and four lightened still further, two to Dark Red, one to Dark Red and then to Intermediate Red, and one still further to Red.

Among the 1890 specimens in the F_2 generation, twenty-eight were born Reddish Black, two Dark Red, ten Intermediate Red, and seven bright Red. Some of these reds were born from parents that had developed a reddish tinge and some from parents that had remained black. Of the four stocks that produced these reds, namely, H. I, VIII, XXV, and XXXI (our Mutant Stock V), one, H. VIII, had shown reddening in the F_1, the other three had not.

In three stocks, H. I, XIII, and XXX in which the F_2 were all born black, subsequent reddening appeared for the first time in the F_2. Only one of these stocks, H. I, was carried on, and in it red-at-birth specimens arrived in the F_3.

Apart from Mutant Stock V, the only survivors of all the specimens which showed any redness at birth, behaved as follows :—

One Reddish Black unchanged,
One Reddish Black became Purplish Black,
Four Reddish Blacks darkened to Black,
One Intermediate Red darkened to Black.

The figures for these stocks are given in Table I.

TABLE I.

TABLE SHOWING SIMULTANEOUS APPEARANCE OF EYE-REDNESS IN THE PROGENY OF 20 WILD PAIRS BROUGHT IN JANUARY AND FEBRUARY, 1928.

N.B.—All the pairs which gave broods are included, except 4 which gave an F_1 of under 50 and went no further, and 3 which gave still smaller F_1 with no survivors.

For explanation of the symbols see p. 193.

Stock No.	Generation.	Colour at Birth.	Survivors.
H. I	F_1	20 B	4 B un.
	F_2	102 B	10 B→**RB**.
	F_3	284B: 5**RB**: 10**Int.**	25B un.: 9 B→slightly **RB**.
	F_4	132 B: 3 slightly **RB**: 2 **Int.**	26 B un.: 4 B→**RB**: 1 B→**PB**. 1 **RB**→B: 1 **RB**→**PB**.
	F_5	26 B: 1 **RB**	4 B un.
H. VIII	F_1	127 B	26 B un.: 2 B→slightly **RB**.
	F_2	282 B: 13 **RB**: 8 **Int.**: 6 **Red**	16 B un. 1 **RB** un.: 3 **RB**→B. 1 **Int.**→B.
	F_3	221 B: 3 **RB**	22 B un.
H. XIV	F_1	55 B	26 B un.: 1 B→**RB**: 1 B→**DR** (?)
	F_2	244 B	9 B un.: 5 B→**RB**: 1 B→**RB**→B.
	F_3	62 B	11 B un.
	F_4	55 B	6 B un.
H. XII	F_1	348 B	37 B un.; 3 B→slightly **RB**.
	F_2	175 B: 2 **RB**	9 B un.
H. II	F_1	264 B	26 B un.: 4 B→**RB**.
	F_2	169 B	6 B un.: 4 B→**RB**.
H. V	F_1	369 B	32 B un.: 1 B→**RB**.
	F_2	167 B	11 B un.: 1 B→slightly **RB**.
H. XXV	F_1	234 B	19 B un.
	F_2	64 B: 1 Red	1 B un.
H. III	F_1	126 B	16 B un.: 3 B→**RB**: 1 B→**RB**→**DR**; 1 B→**DR**→**R**.
H. XLI	F_1	38 B	1 B un.: 1 B→**Int.**
H. VI	F_1	108 B	8 B un.
	F_2	9 B	4 B un.

Stock No.	Generation.	Colour at Birth.	Survivors.
H. VII	F_1	268 B	9 B un.: 2 B→slightly **RB**.
H. X	F_1	297 B	23 B un.: 3 B→**RB**.
	F_2	5 B	4 B un.
H. XI	F_1	232 B	33 B un.
	F_2	55 B	3 B un.
H. XIII	F_1	2 B	2 B un.
	F_2	73 B	9 B un.: 1 B→slightly **RB**.
H. XV	F_1	242 B	12 B un.: 1 B→**RB**.
	F_2	17 B	4 B un.
H. XX	F_1	306 B	15 B un.: 1 B→**RB**.
	F_2	69 B	3 B un.
H. XXI	F_1	141 B	8 B un.
H. XXIII	F_1	178 B	23 B un.
	F_2	65 B	9 B un.
H. XXVI	F_1	230 B	17 B un.
	F_2	41 B	8 B un.
H. XXIX	F_1	16 B	3 B→slightly **RB**.
H. XXX	F_1	23 B	3 B un.
	F_2	33 B	5 B un.: 2 B→**RB**.
H. XXXIII	F_1	33 B	8 B un.
	F_2	160 B	11 B un.: 1 B→**RB**.
H. XXXIV	F_1	43 B	4 B→slightly **RB**.
H. XL	F_1	43 B	9 B un.: 1 B→slightly **RB**.
H. XXXI	F_1	12 B	10 B un.
	F_2	65 B: 13 **RB**: 2 **DR**: 2 **Int.**	12 B un: 1 B→RB. 7 RB un. 1 RB→B. 1 RB→DR. 1 RB→Int. 1 RB→Int.→Red. 2 DR→RB. 1 Int. un. 1 Int.→DR.
	F_3	425 B: 125 **RB**: 60 **DR**: 105 **Int.**: 1 **Red**	43 B un. 3 B→PB. 4 B→RB. 1 B→Rp 1 B→Int. 6 RB un. 1 RB→B→PB. 2 RB→PB 1 RB→PB→P. 1 RB→P. 1 RB→DR: 3 RB→Int.

Stock No.	Generation.	Colour at Birth.	Survivors.
			1 DR un.
			7 DR→Rp.
			1 DR→Rp.→R.
			2 DR→Int.
			1 DR→Int.→Red.
			11 Int. un.
			1 Int.→RB.
			5 Int.→P.
			5 Int.→Rp.
			1 Int.→DR
			6 Int→DR→Rp.
	F_4	397 B : 252 **RB** : 233 **DR** : 131 **Int.** : 2 **Red**	113 B un.
			6 B→PB.
			9 B→RB.
			2 B→Rp.
			1 B→DR.
			2 B→Int.
			1 B→Red.
			26 RB un.
			2 RB→B→PB.
			10 RB→PB.
			1 RB→PB→P.
			1 RB→PB→Int.
			1 RB→P.
			2 RB→Rp.
			3 RB→Rp→Int.
			6 RB→DR.
			2 RB→DR→Int.
			1 RB→DR→Int.→Red.
			9 RB→Int.
			2 RB→Int.→DR.
			2 RB→Int.→Red.
			22 DR un.
			3 DR→PB.
			15 DR→RB.
			4 DR→RB→DR.
			3 DR→P.
			21 DR→Rp .
			1 DR→Int.→Rp.
			10 DR→Int.
			3 DR→Int.→Red.
			1 DR→Red.
			13 Int. un.
			1 Int.→PB.
			11 Int.→RB.
			2 Int.→P.
			1 Int.→P→DR→Rp.
			12 Int.→Rp.
			1 Int.→Rp→Int.
			2 Int.→DR→P.
			1 Int.→DR.
			1 Red→Int.
	F_5	389 B : 225 **RB** : 21 **DR** : 106 **Int.** : 18 **Red**	91 B un.
			2 B→PB.
			3 B→RB→Rp.
			1 B→DR→Int.→Red.

Stock No.	Generation.	Colour at Birth.	Survivors.
			6 RB un.
			18 RB→PB→P.
			11 RB→PB→P→Rp.
			1 RB→PB→P→Rp→Int.
			1 RB→PB.
			1 RB→PB→P→Int.
			5 RB→PB→Rp.
			1 RB→PB→Red.
			1 RB→PB→DR→Int.
			2 RB→PB→Int.→Red.
			12 RB→P.
			1 RB→P→PB.
			5 RB→P→Rp.
			1 RB→P→Rp→Red.
			1 RB→P→Int.
			2 RB→P→Int.→Rp.
			1 RB→P→Red.
			2 RB→Rp→Int.→Red.
			1 RB→Int.
			1 RB→Int.→Rp.
			1 RB→DR→P→DR.
			2 RB→DR→Int.→Red.
			1 DR un.
			1 DR→RB.
			6 DR→Rp.
			2 Int. un.
			4 Int.→PB.
			1 Int.→RB.
			12 Int.→Rp.
			2 Int.→P.
			2 Int.→Rp→Int.
			2 Int.→Rp→Red.
			1 Int.→P→Rp→Red.
			3 Int.→Red.
			4 Int.→Rp→Int.→Rp.
	F_6	97 B : 12 **RB** : 266 **Int.** : 124 **Red**	10 B un. 6 B→RB.
	Still going.		

In Mutant Stock V the 12 F_1 were all Black and remained so. One of the pairs, from which all the rest of the stock are descended, produced an F_2 containing, at birth, 65 Blacks, 13 Reddish Blacks, 2 Dark Reds, and 2 Intermediate Reds (see Chart 1). Of the 2 Intermediate Reds, one remained unchanged and one darkened to Dark Red. Of the 2 Dark Reds both darkened to Reddish Black. Of the 13 Reddish Blacks, two died young, one darkened to Black, one lightened to Dark Red, one to Intermediate Red, and one to Red, seven remained unchanged, but of these two died immature. Of the 13 Black survivors one turned Reddish Black. In this family, therefore, both lightening and darkening occurred.

THE APPEARANCE OF PURPLE EYES IN THE STOCK.

The results of the matings of various members of this family with one another produced, in the F_3, an even greater variety of eye-colour changes, which included not only darkening and lightening but also, for the first time, changes to *purple*. Purple eyes arose from various types of red and from black as well. Three shades of purple were distinguished—" Purplish Black," " Dark Purple " (or simply, " Purple ") and " Reddish Purple " (see Plate VIII).

In no case were young born with purple eyes, the colour in question always coming as a change later in life. Most frequently there was no further colour change after the purple condition had been reached, but this has not been the rule in subsequent generations, in which purple appears as an intermediate stage at one time or another in almost every type of colour change. It is noteworthy, however, that there is no instance at all of an eye purple at birth, the earliest onset of purpling observed up to now being at 14 days, e.g. a number of young hatched Red on April 25th, 1930, darkened to Intermediate Red by April 29th, and by May 9th were all Reddish Purple.

In the companion stocks, nearly all of which, it should be mentioned, were dying out in the F_3, purpling occurred in one family, namely, the F_4 of H. I (see Table I). One Black and one Reddish Black changed to Purplish Black.

CHANGES OF EYE-COLOUR IN INDIVIDUAL ANIMALS.

In Stock V eye-colour changes in the individual animals have occurred in great variety. With very few exceptions they are all in the one direction—either of darkening or of lightening—that is, they do not change over from one direction to the other. Lightening is much commoner and proceeds to greater lengths than darkening, which when it occurs seldom goes beyond one stage. Purple may intervene at any point in the course of a change, as has been particularly evident since the stock was brought out of the incubator room. A glance through the accompanying charts will show the variety of occasions on which Purple eyes have appeared.

In the case of Blacks which have changed, the majority have gone no further than Reddish or Purplish Black, but there have been cases of Blacks giving Dark Red, Purple, Intermediate Red, Reddish Purple, and even Red.

Reddish Blacks have lightened to various extents, in several cases going as far as bright Red. Purple is commonly involved in the changes, especially in certain families. There are only two instances of darkening to Black.

Dark Reds have darkened to Reddish Black and in one case to Black. Of those which have lightened some have gone as far as Red.

Intermediate Reds have lightened to Red, but many more have darkened either to Dark Red or Reddish Black. As in the other types of Reds, a number have remained unchanged, 81 changed to 27 unchanged,—curiously enough, the total proportion of changed to unchanged, taking all the Reds together, gives an actual 3 to 1 ratio, i.e. 288 changed to 96 unchanged.

Only three isolated cases of individuals born bright Red occurred in the earlier generations (F_3 and F_4). Of these two died young and the survivor darkened to Intermediate Red as it grew older. In F_5 and F_6 there have been four families which have produced a number of Reds (see Chart 1), 122 individuals altogether, but the survivors are still immature. The majority have turned Reddish Purple or Intermediate Red. Up to now, therefore, no permanent Reds, such as, e.g. those in Mutant Stocks III and IV, are known from this stock.

The Red eye of Mutant Stock V has thus occurred in two different circumstances. (1) Individuals are born red and subsequently darken or turn purple ; (2) Red occurs as the final result of a process of lightening from any of the darker reds or even black. In no case yet has the red produced by lightening undergone any further change.

4. INTERPRETATION OF COLOURS IN TERMS OF PIGMENTATION.

Darkening and Lightening.

With a view to bringing this work in line with previous work on eye-colour changes (see p. 193), it is now necessary to examine more closely the question of eye-colours and the changes described : to express them, in fact, as far as possible in terms of the pigmentation in the retinal cells. By doing this there is every chance that the problem of the colour changes will be simplified and the manner of action of whatever genes are concerned made more evident. At the least the characters will have been expressed in a less empirical form. Further, some explanation is required on the relation of the purples to other types of colour.

In the normal eye the first pigment to appear in the embryo is red. As the eye grows dark pigment is deposited in increasing quantity, the rate of deposition of red pigment rapidly falls off, and in one to two days the eye is quite black. After extrusion the rate of black pigment deposition keeps pace with the growth of the eye, so that it remains a jet-black. All the time quite probably a certain amount of red pigment is also being formed—in fact it may be a necessary precursor of the black.

The gradation of intermediate stages between the red and the black is more easily observed in cases of Normal Reds which, kept at 23° C., gradually darken during life (Ford and Huxley, **4**).

As the melanin accumulates so the shade of the eye becomes darker and the darkening is an approximate measure of the amount of melanin accumulated. Such fluctuation as may have occurred in the concentration of the red pigment has been evidently unimportant. It should be mentioned that the extent of melanin deposition can, if necessary, be observed directly by placing the specimen in alcohol—the red pigment dissolves out, leaving behind a deposit of the insoluble dark.

In the changes occurring in Mutant Stock V and falling within the series of Black→Red, evidently a reverse process is taking place—the rate of deposition of dark pigment falls off and that of the red increases, or at least fails to decrease. Since there is reason to suppose that dark pigment, once laid down, remains always, dilution can only be caused by the growth of the ommatidia. At any given stage, therefore, there must be sufficient dark pigment to account for any earlier darker stage. Thus a specimen born Black and changing later to Reddish Black should in the latter stage contain sufficient dark pigment to account for the earlier blackness. So unless a Black starts to change early it has little chance of lightening very far. It is in fact found that few lightened Blacks pass beyond the Reddish Black stage. Again, Red individuals which have lightened from darker stages should contain a deposit of melanin. This is precisely what has been found. Several Reds have been preserved in alcohol at death, and have all shown a dilute deposit of dark pigment after the red pigment has dissolved out.

THE INTERPRETATION OF PURPLE.

The explanation of the purple eye-colours has proved a simple matter. It was found, on examining a series of the various stages of red-eyes preserved in spirit, that the colour of the diluted dark pigment deposit which remained after the red had gone was in all cases a chocolate. The intensity of the chocolate colour, of course, varied with the quantity of pigment present, being dark for the darker red eyes and pale for the lighter red. A complete gradation, too, between dark chocolate and jet-black was found, but the quality of the colour was approximately the same all through.

Purple eyes left just the same kind of chocolate colour.

Comparison of Purple eyes in the living animals with Purple eyes preserved in spirit showed that the colour of the two was essentially the same, namely, a shade of chocolate. In fact "Purplish Black" and "Dark Purple" eyes after treatment with alcohol were found to remain unchanged; while "Reddish Purple" eyes became a duller chocolate, losing the redness. These facts go to show that the Purple colour is given by eyes in which diluted dark pigment is not covered over by red pigment. The red element in these eyes is much reduced or entirely negligible; when there is an appreciable quantity present the purple is brightened up.

Purplish Black corresponds to Reddish Black in which the red pigment has disappeared; Dark Purple similarly to Dark Red; while a small admixture of red with a dilute black pigmentation gives Reddish Purple. Reddish Purple merges into Intermediate Red as the concentration of red increases.

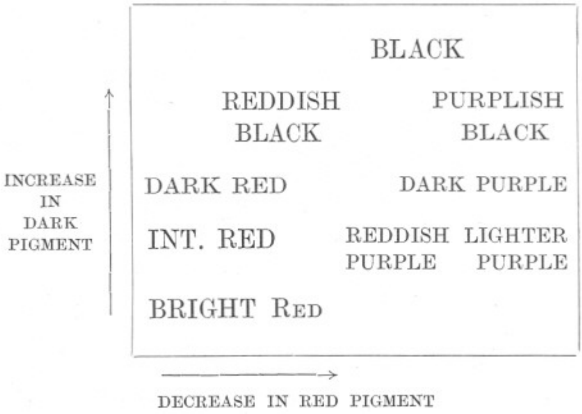
Further examination of the effects of alcohol on different eyes has borne out this conclusion. We are indebted to Mr. E. B. Ford for the loan of spirit specimens of the Normal Red of Stock I in various stages of darkening. These specimens also showed that the dark pigment when diluted is of a chocolate colour.

To sum up, purple colour is produced by eyes in which the red pigment has fallen off without a corresponding increase in dark pigment.

THE RELATION BETWEEN THE VARIOUS EYE-COLOURS.

It is thus possible to express all colour variations occurring in this stock in terms of variations in the concentration of the two pigments present in the normal eye—the red and the black;* and all changes in terms of variations in the rates of deposition of each of these two pigments relative to the rate of growth of the eye (or, rather more precisely, of the ommatidia).

The relations between the various colours may be expressed by the following scheme:—



5. RESULTS OF MATINGS WITHIN MUTANT STOCK V.

GENERAL.

The matings within Stock V have at present reached the eighth filial generation. Difficulties encountered in the behaviour of the stock have already been mentioned; and, when to these are added the complications

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* As a matter of fact, in the original water-colour drawings for the colour series on Plate VIII, all the different shades were obtained by using two tones of red with black.

exhibited by the characters under investigation, it can be realised that progress towards elucidating the mode of inheritance has necessarily been slow.

For the present, therefore, we go no further than setting out the results of the various matings within the stock as they stand, in order to show the sort of results that have been obtained and the data available up to now.

Charts 1 to 4 show the cases in which in-mating within the families has been possible through to the F_8. Certain cross-matings are omitted as well as unproductive matings or matings which produced very small numbers of young. Table II, however, gives a record of every mating that has produced a brood. It is arranged so as to bring together as far as possible, irrespective of the generation, matings of a similar kind.

The known colour changes of the survivors are in all cases given. It should be pointed out that often a long period elapsed, especially in the case of the earlier generations, in between examinations of a specimen for eye-colour. Consequently in cases of colour change intervening stages have been easily overlooked. So, when a certain specimen is designated, for example, B→IR, it is not implied that there is any difference from a case denoted B→RB→DR→IR. It only means that the intervening stages that must have occurred happen to have been missed. In later generations eyes have been examined more frequently.

In each of the charts a special note is made of those families which have been reared since the stock was removed from the incubator room. It is impossible as yet to say what difference this change to a lower temperature has made. Though no doubt it may have affected the *rate* of eye-colour change, yet perhaps after all it has not made much difference to the *kind* of change. It is perhaps worth mentioning that the occurrence of purple seems much more frequent since the stock has been kept in the cool.

CHART 1.

Chart 1 shows the ancestry of the most promising of the F_6 families. Starting with the ancestral F_2 in which reddening and darkening both occur, we pass to an F_3 derived from a mating between a Black and a Reddish Black, both of which showed reddening. At birth this F_3 contained a mixture of Black, Reddish Black, and Intermediate Red of which the survivors either remained unchanged or else turned Purple. One Black changed to Intermediate Red, and there is also an indication of lightening (of the dark pigment) in the Reddish Black which turned from Purplish Black to Purple; darkening is indicated by the five Intermediate Reds which became Dark Red before purpling, and an unusual mixture of darkening and lightening in the RB→B→PB. But it is seen that, with the exception of the one B→Int.R., there is no *reddening* such as occurred in both the parents, and as is conspicuous in subsequent generations.

In contrast to the F_3, in the two families of the F_4 (in production of which purple parents were involved) a strong tendency to redden is shown and no change to purple appeared at all.

The three families of the F_5 are all in many ways similar. Judging from the behaviour of the high proportion of survivors, it looks as though almost every individual was doing its best to redden and turn purple at the same time. Thinking more precisely in terms of concentrations of red and black pigment, one sees that the F_5 specimens almost without exception show a steady dilution of dark pigment, while the red pigment fluctuates independently. The red pigment on the whole diminishes after birth and tends to reappear later in life, by which time the black pigment is dilute enough to produce the Intermediate Red or the bright Red condition. Those born Reddish Black approximate in their behaviour closely to a mean represented by the expression (RB→Purple stages→Int. or Bright Red), and the Intermediate Red to (IR→redder purple stages→Red). What is of main interest is that all the individuals are behaving in very much the same sort of way. This homogeneity is most refreshing.

There are eleven families in the F_6, of which nine are still going and so far have given up to four broods. It is seen that the young at birth are either all Red, or all Intermediate Red; or a mixture of the two. It is hoped that the homogeneous nature of some of these families is a sign that pure lines are in the process of emerging.

The F_2, F_3, and F_4 families were reared under the incubator conditions, and F_5 and F_6 in the cool. It is impossible to say what difference this has made. At any rate the contrast between the F_3 and F_4 cannot be put down to this account.

This chart therefore shows (1) the appearance of Purples in the F_3, and how purple parents may give offspring that show no signs of purple; (2) how more or less homogeneous families are gradually making their appearance in the stock.

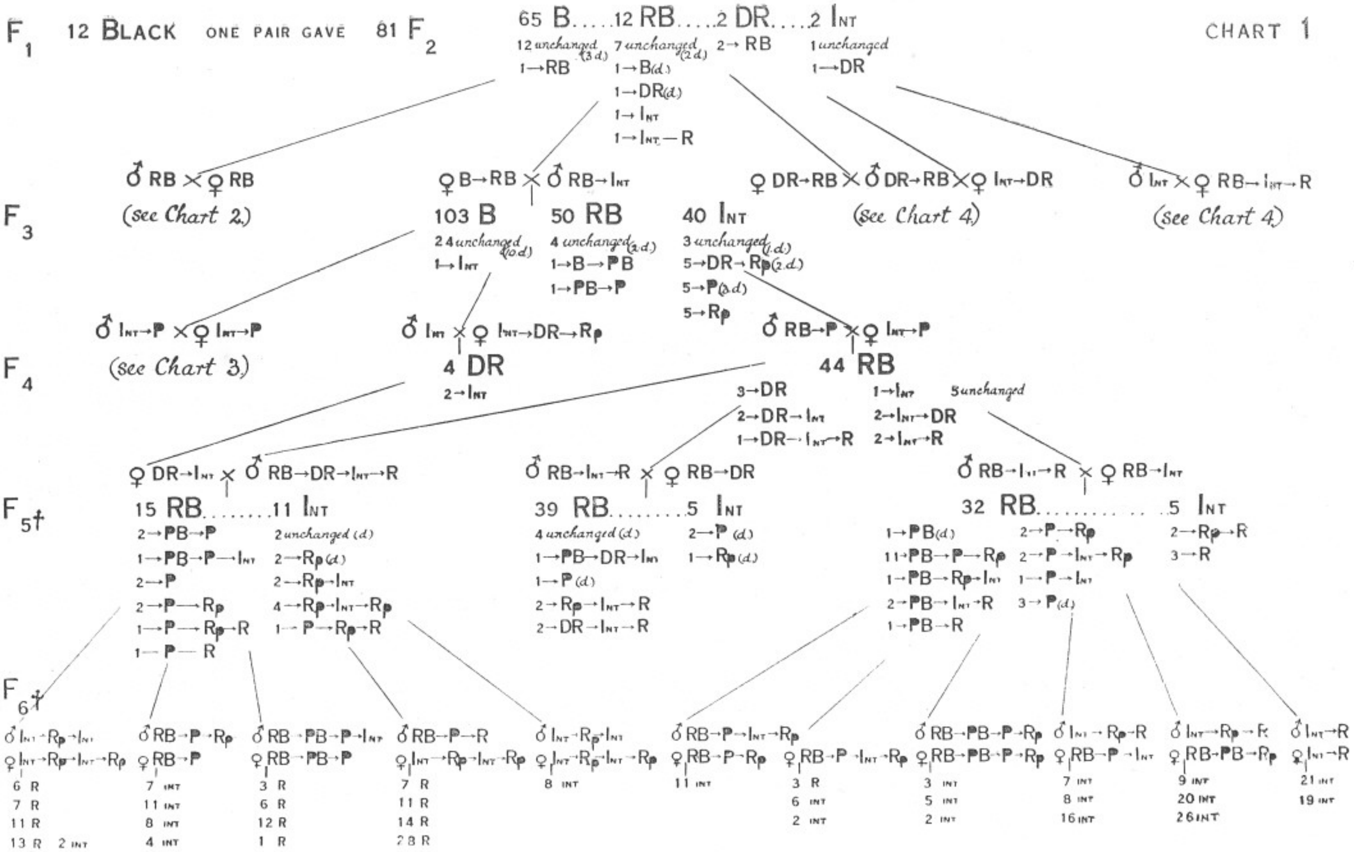
CHART 2.

This shows the stage so far reached in an attempt to establish a pure Black stock from an original pair of F_2 Reddish Blacks. Such other matings as gave any result are also included.

CHART 3.

An early attempt at establishing a Red strain is shown here. It gradually died out. Attention is called to the appearance of Blacks in one of the F_5 families. However, the two survivors did not remain Black; one changed right over to bright Red, the other to Purplish Black.

CHART 1



† Broods hatched after the heat was turned off.

CHART 2

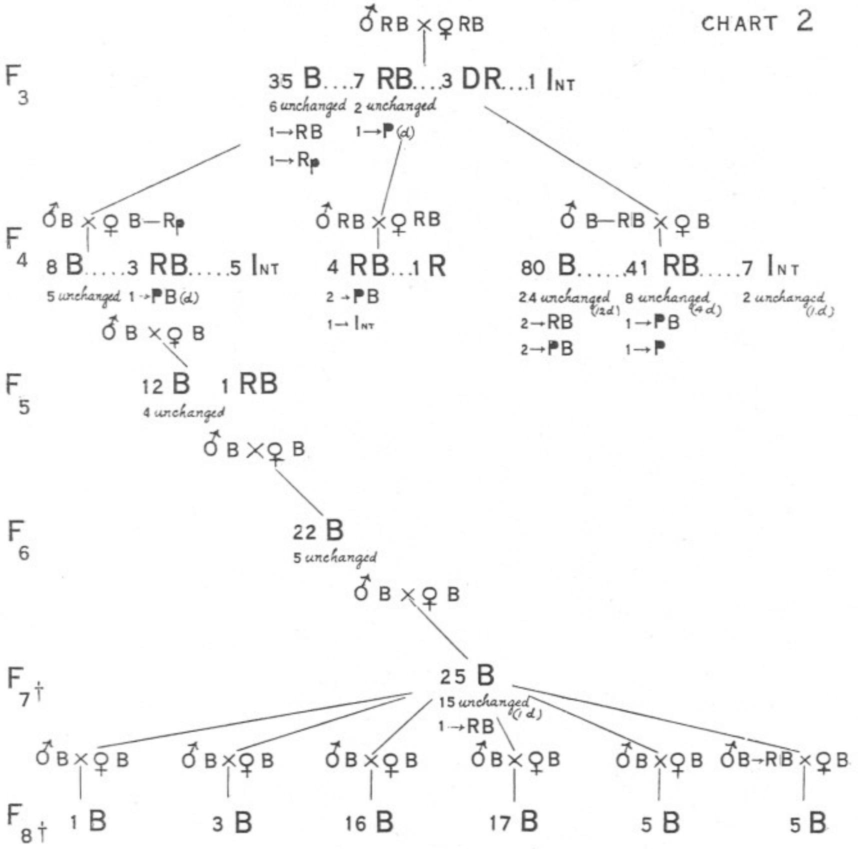
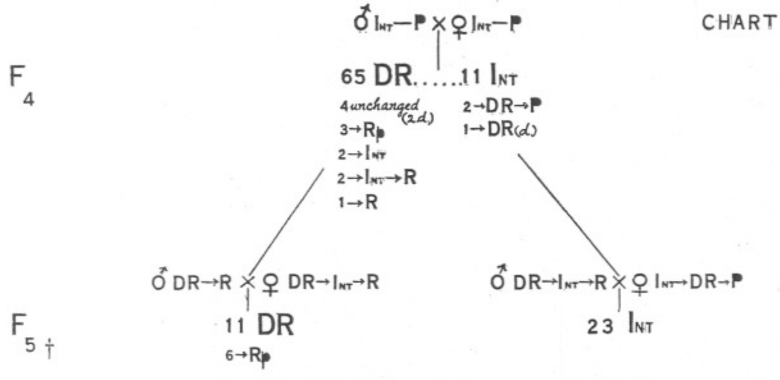
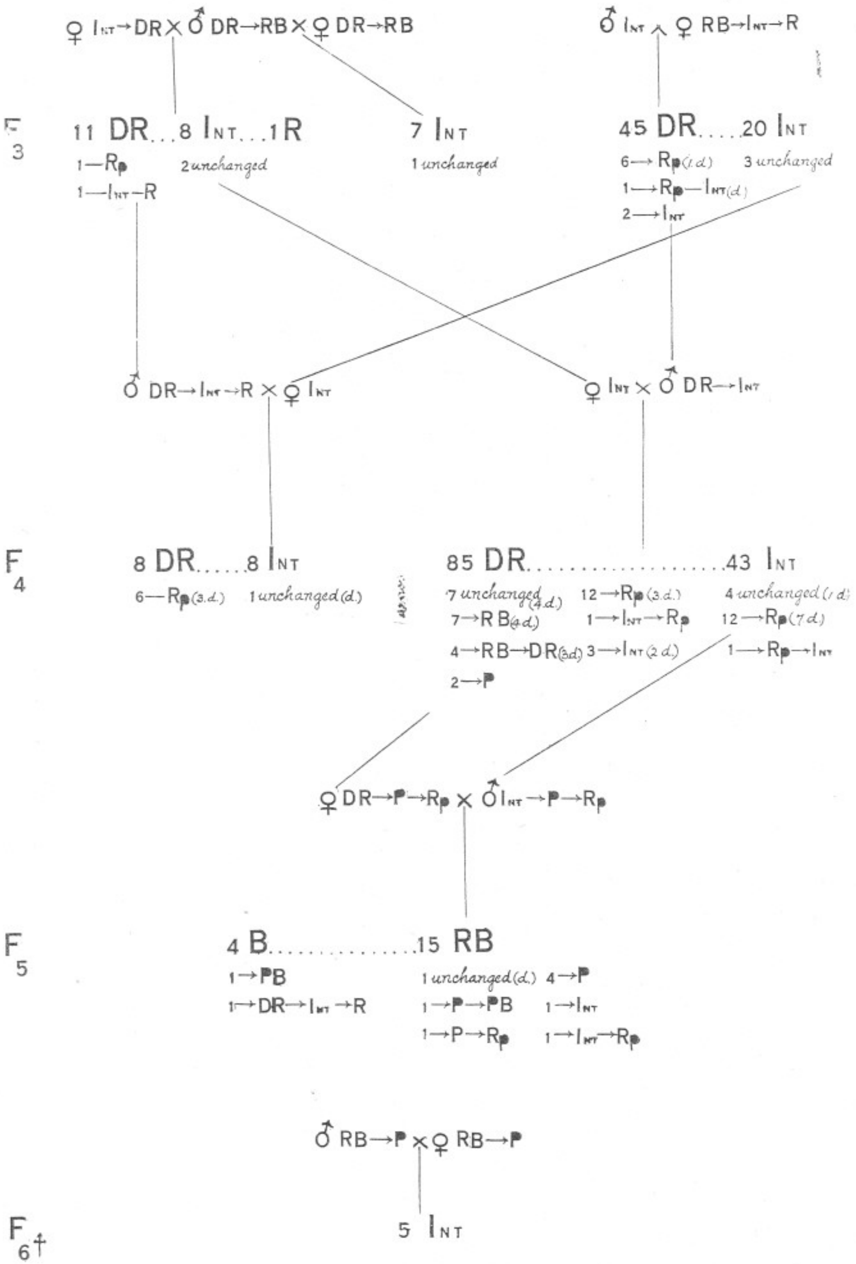


CHART 3



† Broods hatched after the heat was turned off

CHART 4



† Brood hatched after the heat was turned off.

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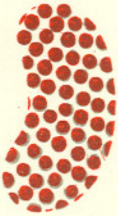
PLATE VIII.

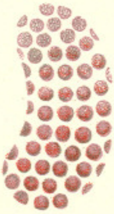
Normal Red

New Red

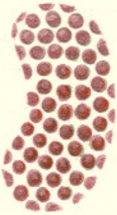
Inter. Red



Dark Red



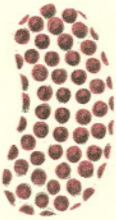
Reddish Purple



Dark Purple

Reddish Black

Black



Purplish Black

E. W. Sexton del.

CHART 4.

Here a small branch derived from the F_3 family set out in Chart 1 is shown. It starts from a mating between two IR→Purple specimens of the F_2 which might reasonably be expected to have been genetically alike. Yet the family produced by them is quite mixed—some born DR, some IR ; some turn purple, some redden. The F_5 shows one of the very frequent cases in which purple colour appeared in the progeny of non-purple parents. The other F_5 family is still going and in it so far only Intermediate Reds have appeared.

TABLE II.

All the matings up to June 1st, 1930, are contained in this table, including several not figured in the previous charts, and many derived from other matings within the F_2. It is set out in table form so as to bring together matings of a similar kind.

It will be noticed that on the whole the mean of the redness of the progeny corresponds to or varies with the mean of the redness of the parents. Thus if the matings of Blacks with various kinds of Red eyes are considered, it is seen that the proportion of Reds in the offspring on the whole increases with the redness of the Red parent. But this does not apply rigidly and scarcely holds at all as far as matings between Reds are concerned.

Again, on the whole, Black is dominant to all the forms of Red and therefore matings between Reds give only Reds. But there are a number of exceptions. For instance, Reddish Blacks not uncommonly give Black among their offspring (e.g. matings between two RB unchanged ; two RB→P's ; RB unchanged × IR→P). Other cases are : a mating between two IR→RB's which gave one Black to 13 Reddish Blacks, and a mating between an IR→RP and DR→RP, to which allusion has been made in Chart 3.

If Black were a simple dominant to all forms of Red, then there would be even chances that a mating between a Black and a Red should produce all Blacks or a mixture of Blacks and Reds. Actually only one out of 19 of such matings has given all Blacks. Even making allowance for a preponderance of heterozygotes, owing to special attention to the redder forms, a higher proportion than 1 out of 19 would be expected.

VALUE OF DATA FOR GENETICAL INTERPRETATION.

Attention has been called to the small numbers in the earlier broods. Only a few families are large enough to give adequate indications of ratios even of eye characters at birth. (The small number in the broods apparently does not always mean that numbers of eggs die off. It has been observed that many of the females giving small broods have small ovaries. There is probably not much risk of ratios being upset by a differential death-rate among the eggs.)

But more than this, since the changes undergone after birth are clearly important, it is not sufficient to know the eye-colour of the broods at birth alone. It is only from the survivors that adequate information is to be obtained. The proportion of survivors in the stock has been small, working out at 27%.* That no more than one specimen in three or four survives to maturity is a distinct handicap when so many phenotypes may occur in one family. Recently, however, the proportion has shown a marked increase.

Then there is the question, to which reference has already been made, as to how far the change of temperature has affected the phenotypes.

Finally, attention is called to a rather disturbing feature all too common in this stock, namely, disparity between the composition of and proportions within different broods of the same family. Here is a case in point :

Successive broods from an F_3 DR × B→RB mating had the following composition :

1. 15 IR (11→RB)
2. 15 RB (2→DR, 1 unchanged, 1→IR) ; 2 IR (1→PB).
3. 9 B
4. 12 RB. 10 IR
5. 7 B (2→IR) ; 16 RB (3→IR) ; 4 IR (2 unchanged).

Normally in stocks of Gammarus various phenotypes in a family are fairly evenly distributed among the broods. In this stock there is therefore clearly some irregularity which requires explanation. This at least arouses suspicion of the ratios given by families of only one or two broods.

So far, in spite of the number of families reared, the facts are still inadequate for genetical purposes. No pure lines of any sort of Red eye have yet been produced, and until this is possible there is of course little chance of testing to what extent external factors (in a wide sense) may affect a constitutional type of eye-coloration. For example, throughout the stock there is much variation in the rate of growth, and this variation may well affect the balance between the rate of growth of the ommatidia and the rate of deposition of eye-pigment. Any alteration in this balance means a change in eye-coloration.

Further discussion on the behaviour of this stock and the possibilities

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* It is incidentally of interest to note that there has been no marked variation from the 27 per cent survival when the different eye-colours (at birth) are taken separately. Black gives 25%, Reddish Black 27%, Dark Red 32%, and Intermediate Red 29½%. The lower figure for Black, whether it actually means anything or not, might be expected since Blacks occur in larger numbers and hence are kept in more crowded conditions and more at the mercy of cannibals. At any rate, the point is that there is no evidence that the bright Red individuals are less viable than the Blacks.

of genetical interpretation of the results is deferred until additional facts are available. It has been the aim of this paper to give an indication of the problems which have arisen and on which investigation is proceeding.

6. SUMMARY.

For the present, attention is called to the following points :

1. In a large number of experiments with *Gammarus chevreuxi* when the animals were kept under similar conditions at temperatures ranging from 20° to 28° C., twenty instances occurred in which red-eyed mutations appeared independently and simultaneously. The most important of these (Mutant Stock V) is described in detail in this paper.

2. The Red eyes which have arisen in this Stock V and in the four previous Stocks, I to IV, have proved to be all genetically distinct from one another.

3. There are at least two different classes of "red-eye," the one simple, the other with intermediate stages. Mutant Stock V, here described, represents the second type. Differences in the method of origin of the two classes have been pointed out.

4. The inheritance of the red-eyedness of the second class—namely, that in which intermediate stages and various colour changes occur—is of a complicated kind. For an interpretation in terms of Mendelian genes, even if allowance is made for an extent of variation in members of one particular genotype, clearly several of them are involved. Further, there must be considerable interplay of one kind or another among the different genes.

5. Although so many different colour shades have appeared in Mutant Stock V, all can be interpreted in terms of varying concentrations of two pigments—the black and the red. Dilute black pigment with little or no red gives a purple eye.

We are greatly indebted to Dr. E. J. Allen for his constant assistance and advice throughout the whole course of the work ; and our best thanks are due to Mr. E. B. Ford of Oxford for the help he has been so ready to give us.

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EXPLANATION OF PLATE VIII.

All the eyes have been figured the same size, so that the colours could be more easily compared.

The colour of each was taken from a living specimen, all the tints in the original water-colour drawings being obtained by using two shades of red with black.

Normal Red from a female of Stock I, sent by Mr. E. B. Ford. This is a pure Red, leaving no deposit of melanin when treated with alcohol, or any other preservative.

New Red from Stock V. A male, H. 814 (2), which was hatched Reddish Black and lightened through Reddish Purple to Red. All these Reds, whether born Red or lightened to Red, contain a slight deposit of melanin, as can be seen on treating them with alcohol. The red pigment, which in life obscures the melanin, dissolves out and leaves a layer of the insoluble dark.

Intermediate Red from a male, H. 813, Pair 1, hatched Reddish Black, and lightened through Reddish Purple to Intermediate Red, and afterwards to Reddish Purple again. This is an example of the fluctuation of colour shown by some specimens.

Dark Red from a young specimen, H. 859b, hatched Dark Red.

Reddish Black from a male, H. 811, hatched Black and lightened to Reddish Black.

Reddish Purple from a female, H. 844, hatched Intermediate Red, changed to Reddish Purple, then back to Int. Red, and later to Reddish Purple again, another example of the fluctuation of colour through life.

Dark Purple from an immature animal, H. 813, hatched Reddish Black.

Purplish Black, H. 835 a.a., hatched Black, lightened to Purplish Black.

Black from a female, H. 811, unchanged through life.

The Cœlenterate Plankton of the Northumbrian Coast during the Year 1924.

By

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With 1 Figure in the Text.

THE following is a report on the Cœlenterate plankton taken off the Northumbrian Coast in 1924 during cruises of the *Evadne* of the Dove Marine Laboratory, Cullercoats, Northumberland. The work has been carried out under the supervision of Professor A. D. Peacock to whom I am indebted for much helpful advice. I must thank Professor A. Meek of Armstrong College, Newcastle-upon-Tyne, for so kindly providing the material, and Miss M. Yeats for the use of her notes on the 1924 surface medusæ. Mr. P. L. Kramp of Copenhagen was so good as to check my identifications of certain specimens hitherto unnoted from Northumberland, and for this service I express my obligation. Dr. Allen, Director of the Plymouth Marine Biological Laboratory, and Capt. Totton of the British Museum, have also been kind enough to assist in questions of nomenclature. My own work consisted of the investigation of middle and bottom water samples and Miss Yeats' results on surface samples have also been incorporated here to make the yearly report complete.

Technique. This was the same as that employed by Peacock (see *Dove Marine Laboratory Report*, 1923) and need not be enlarged on here, but a short note on the method of staining may be added. A most useful stain for the medusæ as preserved in the collection* is Picro-Nigrosine, 1 part saturated alcohol solution (70%) stain to 3 parts 70% alcohol. The medusæ are immersed for a short time until they assume a pale green colour. They are then quickly transferred to a differentiating solution of 1 part formic acid and 4 parts 70% alcohol, and left for half an hour. The gelatinous umbrella takes on a bright blue colour and the gonads and manubrium a bright yellow, which colours are intensified on dehydration. This method is particularly useful in examining the oral tentacles of such small specimens as *Lizzia blondina* Forbes. Results were better when a strong solution of Picro-Nigrosine (as above) was used for a short time than when a weaker stain was used for a longer period.

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* Fixed in 5% formalin and preserved in 70% alcohol.

The count in each case was absolute for the sample received, for it was found by experiments on estimates made from only a portion of a sample that the enumeration errors were sometimes very large.

The nomenclature employed is that recommended by Mr. E. T. Browne for adoption in the proposed revised list of the Plymouth Fauna.

Notes on the Catches. The most striking feature of the catches is the very great variety of medusæ taken, 22 species in all, of which 17 are confined to middle and bottom waters. In addition to those previously listed for Northumbrian waters there are recorded 9 other species, viz. *Purena* (*Sarsia*) *gemmifera* (Forbes), *Sarsia prolifera* Forbes, *Hybocodon prolifer* L. Agassiz, *Lizzia blondina* Forbes, *Rathkea octopunctata* (M. Sars), *Leuckartiara octona* (Fleming), *Mitrocoma* (*Mitrocomella*) *fulva* (Browne), *Eutonina indicans* (Romanes), and *Æquorea forskalea* Peron et Lesueur.

The numbers of *Obelia* and *Aglantha* are rather small compared with those of former years, but on the other hand this want is balanced by the sudden invasion of the plankton by *Lizzia blondina*, which is found in large numbers at all depths during August and September. While *Hybocodon* is confined to the April catches, *Euphysa*, *Bougainvillia* and *Phialidium* are well represented throughout the whole range.

All the hauls were made in daylight.

Notes on the Species taken.

(For details regarding station, depth and numbers, reference should be made to Table I and Fig. 1. The figures in Table 1 have been arrived at by calculation and express the numbers for the whole catch.)

ANTHOMEDUSÆ.

SARSIIDÆ.

This family, contrary to previous years' experience with similar collections, is well represented. There are at least three different species and, moreover, they illustrate succession in seasonal occurrence. *S. tubulosa* has been found from April to the end of July, then its place is taken by *Purena gemmifera* and *S. prolifera* which continue to be present until the end of October when the catches ceased. The two last-named are listed in this series of Cœlenterate plankton for the first time.

Sarsia tubulosa (M. Sars).

The largest specimen measures about 10 mm. high in the preserved state. The basal bulbs are large and each has a prominent light brown ocellus such as is figured by Kramp (1926, Pt. 10, Pl. I, Fig. 5). The specimens from Stations 2M, 6B and 10M measure 3, 8, and 9 mm. respectively, from which we may conclude, in agreement with Kramp, that

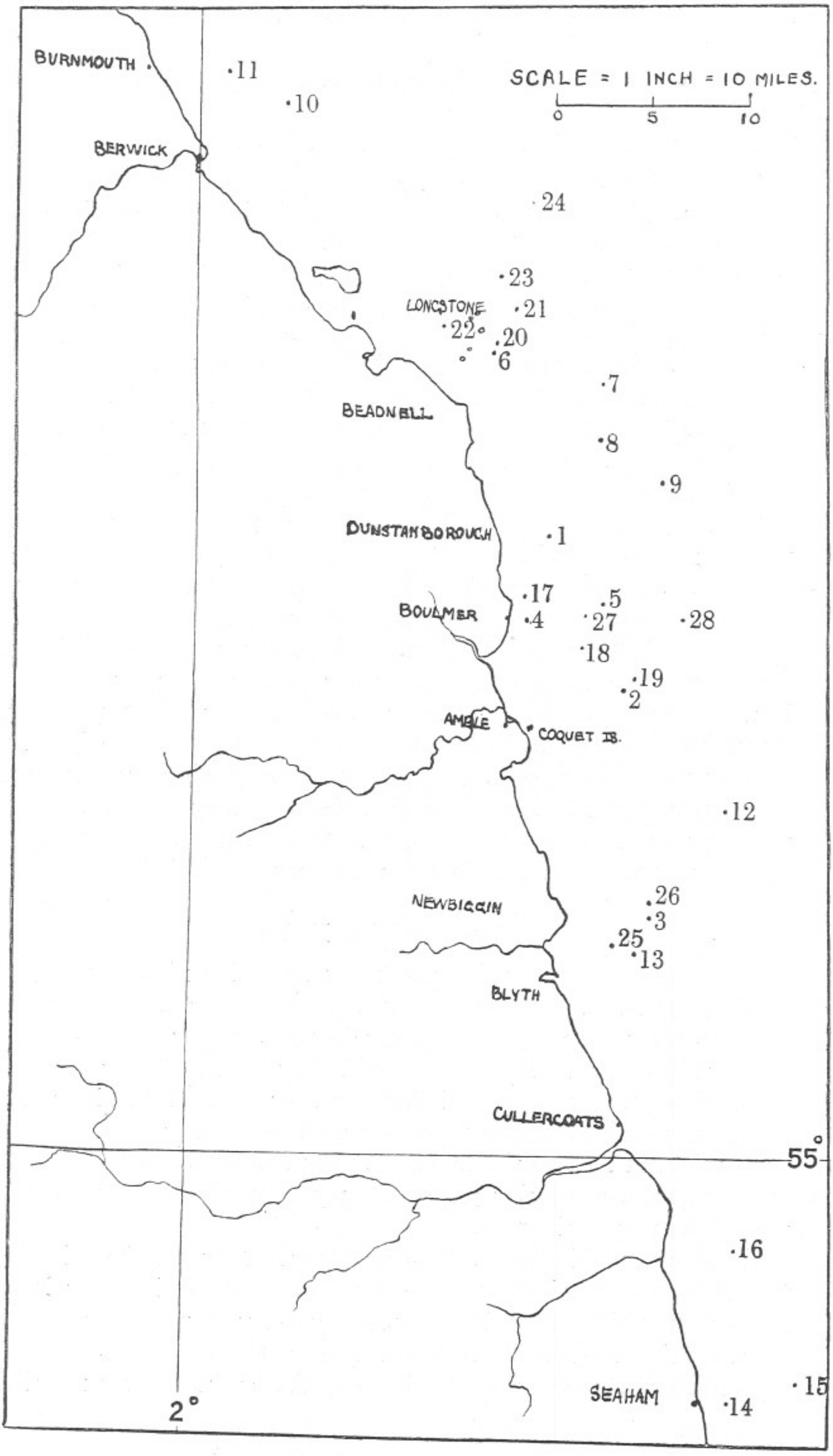
BURNMOUTH
BERWICK
SCALE = 1 INCH = 10 MILES.
0
5
10
·11
·10
·24
·23
LONGSTONE
·21
·22
·20
·6
·7
BEADNELL
·8
·9
DUNSTANBOROUGH
·1
·17
·5
BOULMER
·4
·27
·28
·18
·19
·2
AMBLE
COQUET IS.
·12
NEWBIGGIN
·26
·3
·25
·13
BLYTH
CULLERCOATS
55°
·16
SEAHAM
·14
·15
2°

FIG. 1.

specimens liberated in April do not reach their maximum size until the end of July. Both *Sarsia tubulosa* (M. Sars) and *S. tubulosa* var. *mirabilis* L. Aggassiz are listed in the 1922 plankton taken in water samples from the Coquet, but Kramp, who has made a very careful examination of the whole *tubulosa*-group (*sensa* Hartlaub), asserts that even in the living specimens he can find no specific differences distinguishing these two. Even if two distinct varieties do exist, I have been unable to determine to which our specimens would belong and have merely designated them *S. tubulosa*.

A few specimens taken are very small, about 1 mm. high, and are sexually immature. The manubrium is without an apical chamber and in some cases is short and slightly swollen above the mouth. In no specimen does the manubrium, even when fully extended, hang below the level of the bell. The tentacles are longer than the bell and are provided with incomplete nematocyst rings. Owing to the state of preservation the ocelli which would furnish a distinguishing character cannot be detected. In general appearance, however, the specimens agree very well with the *Sarsia eximia* figured by Hartlaub in *Nordisches Plankton.* On the other hand they might quite well be very young *S. tubulosa,* for in the latter the manubrium is quite undifferentiated in the young stage. If this is so, then the specimens taken in April would represent the spring brood, from which the large *S. tubulosa* recorded for July have been derived. This possibility is borne out by Kramp's assertion that this species requires 1½–2 months to develop and attain its full size. Moreover, the fact that no large *Sarsia eximia* have been taken seems further to indicate that the specimens in question are young *S. tubulosa.*

Sarsia prolifera Forbes.

In all 71 specimens of this rather rare medusa have been found in the samples examined. All were taken by middle and bottom nets in September and October, with the exception of two which were taken as early as April off Newbiggin. The largest catch was taken on 17th October but all are small, none attaining a height of more than 1·5 mm. Most of the specimens bear buds of various sizes at the bases of the tentacles, and, as those taken in April differ in no way from those taken in September and October, it seems that the species propagates by gemmation during the greater part of the year.

The species, which seems to be confined to the coast of Britain, has been taken by Garstang at Plymouth as early as March and by Mayer at Mousehole as late as November. Those found by the latter author were sexually mature, and, since none of our specimens bears gonads, it seems reasonable to conclude that sexual reproduction is confined to the winter months.

Purena (*Sarsia*) *gemmifera* (Forbes).

This species of Sarsia, which likewise has not hitherto been recorded for these waters, is rather restricted in distribution, appearing only at three stations, one off Cresswell and two in the vicinity of the Boulmer Buoy. The bell varies in height from ·4 to 1·75 mm. and the manubrium when extended may measure as much as 10 mm. The buds in the manubrium do not seem to be developed in any constant order, for in some the oldest primary bud is nearest the proximal end of the manubrium and in others it is second or third in the series. In one specimen the buds in order of size are 2nd, 3rd, 1st, and 4th from the proximal end. Chun, however, has demonstrated his law of succession of buds for this species, and the condition of the above may be explained by the fact that some of these may be secondary or tertiary buds, which first appear on the pedicels of the primary buds and continue to develop after the latter are set free. But, on the other hand, the specimens are so small that I think it unlikely that any primary buds have already been freed. Further, I have not observed any secondary bud developing on the pedicel of a primary one, and therefore I conclude that the law of succession does not hold for this species.

The larger buds also have young buds on the manubrium, but it seems that the primary buds are not set free until they have attained a height of about ·4 mm. This conclusion is based on the fact that none of the medusa buds measures more than ·4 mm. and no free medusæ have been taken in the plankton measuring less than this.

Dipurena (*Slabberia*) *halterata* (Forbes).

Only two specimens were obtained by a bottom net off the Boulmer Buoy in September, one having the manubrium missing. One specimen is about 6 mm. high and has two rings of nematocysts above the terminal bulb of the tentacles, while the other specimen is somewhat higher and the tentacles have three distinct rings of nematocysts above the terminal bulb, the proximal being the smallest and being succeeded by three or four very narrow rings which gradually give place to scattered nematocyst cells.

Euphysa aurata (Forbes).

From the tables it appears as if this medusa has its greatest distribution in bottom waters and gradually shades off in numbers to the surface layers. The largest catches were taken off Burnmouth in July and off Souter in August. The medusæ vary in size up to 2·5 mm. although some are very much shrunken and contracted. There are from 6 to 26 rings of nematocysts in the tentacles, but the majority have about 15. Mayer, in his synopsis of the characters of *Steenstrupia aurata*, states that there are no definite rings of nematocysts, but Hartlaub, 1907 (p. 83, Fig. 78), gives drawings of tentacles of what he calls *Corymorpha aurata* and *C. nutans*, in which he shows that the former has fewer but broader rings than the latter. (It should be noted that later, p. 87, Fig. 82, Hartlaub uses the name *C. sarsi* for the latter species). Moreover, the specimens, which according to Mayer would be more like *nutans* (Mayer's *Steenstrupia rubra*), from the nature of the tentacle, lack the distinct axial canal which is so characteristic of that species. In some the gelatinous apical projection is fairly well formed, but this character is very variable.

Steenstrupia (*Corymorpha*) *nutans* (M. Sars).

A single specimen, characterised by being larger than the specimens of *Euphysa aurata*, and showing an apical canal and a distinct " shoulder " in the radial canal was classified as *S. nutans*.

Hybocodon prolifer L. Agassiz.

This species has only been recorded from two stations—off Dunstanburgh and the River Coquet. All the specimens which are mentioned show marked asymmetry in the shape of the bell, which varies in height from ·5 to 1·5 mm.

Some have developed two tentacles, but none has three. The large tentacle has about 50 closely-set nematocyst rings, and the lateral tentacle, when present, has about 12. A well-formed lateral bulb may be present on either side of the main bulb, and, as all three bulbs may have secondary buds in some, the cluster is so large as to fill completely the mouth of the bell. The manubrium, which is pear-shaped, can be extended just beyond the edge of the bell, and in many of the specimens it is curved to one side. The mouth is simple and is surrounded by a fairly well-defined rim which according to Kramp bears numerous nematocysts, but these I have been unable to find.

Podocoryne areolata Alder.

This medusa has a rather restricted seasonal distribution, being found only during July and August. The specimens vary in size from ·5–5 mm. and the larger ones have 32 tentacles. Pigment is prominent in the basal bulb and also between the folds of the gonad.

Bougainvillia britannica Forbes.

This species has a regular occurrence throughout the season, but on the whole the numbers taken are fairly small. It is entirely absent from surface layers and the best catch (87) is from a bottom net. The specimens vary in height from 1–8 mm., and, although the evidence is not convincing, yet it is suggestive that the specimens attain their maximum size in July.

Lizzia blondina Forbes.

This is the first record of this species in the Plankton Reports for the North-East Coast, and it is present in such large numbers that it forms the principal part of the medusa plankton catch from August to September. A noteworthy feature is that the medusa has its greatest vertical distribution in surface waters and shows a gradual decrease in numbers towards the deeper water. Further, the hauls taken during its maximum period at stations near the coast, viz. 14, 16, 17 and 22, show a marked decrease in number. It would seem therefore that the medusæ when liberated are carried further out to sea and there find conditions more suitable for a sexual reproduction, by which large swarms can be quickly produced.

The individuals are small, less than 1 mm. in diameter. The bell in the preserved specimens is flattened on top and there are eight tentacle bulbs, the four perradial being in some cases bigger than the interradial and each bearing two tentacles. The manubrium is short and bears several buds on its sides, while the mouth has four simple oral tentacles each ending in a single knob of nematocysts. The distinct oral arms and the grouping of the tentacles show that the medusa belongs to Forbes' genus *Lizzia.* Kramp, following Haeckel, distinguishes three stages in the development of *L. blondina—Dysmorphosa minima,* with only eight tentacles, *L. claparedei* with twelve (two on each perradial bulb), and the fully developed *L. blondina* with three tentacles on the perradial and one on each interradial bulb. Our specimens would belong to the two first-named species only, for none has the full number of tentacles and none has gonads. It seems then that the medusa does not become sexually mature till after October, during which month it shows a marked decrease in numbers, possibly owing to the slowing down of the process of gemmation.

Miss Yeats found a small percentage of another medusa, *Willsia stellata* Forbes, but the numbers of these were not determined exactly.

Rathkea octopunctata (M. Sars) (=*Rathkea blumenbachii* Hartlaub).

Only two specimens have been found, one taken by a bottom net and the other by a middle net off Burnmouth in July. They are readily distinguished from *Lizzia blondina* by the light brown pigmentation of the tentacle bulb which carries three tentacles. The manubrium, moreover, has four short stout lips each of which bears two sessile knobs of nematocysts. Just above the base of the lip on either side there is, in addition, another nematocyst cluster. Although the specimens measure only 1 mm. in height, they compare very closely with Hartlaub's drawings in *Nordisches Plankton.*

Leuckartiara octona (Fleming).

This rather striking medusa has a very restricted seasonal occurrence, being found only from August till October, the largest catches being taken by middle and bottom nets. The largest specimen from the Longstone on 11th September measures 10 × 10 mm. The radial canals are broad and slightly notched and each of the 20 tentacles has an outwardly projecting spur on the adaxial side of the comparatively large basal bulb. The possession of tentacular spurs and a large prominent apical projection immediately points to the specimens belonging to *Leuckartiara octona* (Hartlaub, 1914, p. 285). Kramp has made several observations on number and order of development of tentacles in this species, and on the whole these apply fairly closely to our specimens. The smallest, taken in August off Souter, measures only 1 mm. in height, and has four well-developed tentacles and four interradial rudiments. Judging by its small size we may conclude that it cannot have been carried any great distance, and the hydroid, *Perigonimus repens*, must therefore live somewhere in the neighbourhood.

LEPTOMEDUSÆ.

Mitrocoma (*Mitrocomella*) *fulva* (Browne)
(=*Mitrocoma polydiademata* Romanes.)

This species, listed for this area for the first time, occurs in middle and bottom waters during July. The largest specimen measures 12 mm. in diameter and about 8 mm. in height, and has 42 tentacles with 3 or 4 cirri between adjacent pairs. Lithocysts are present, but I cannot be certain of the number of concretions in each. The manubrium is small and produced at the corners into a slightly recurved lip, a feature which does not seem to have been mentioned elsewhere. In the female the gonad occupies the lower three-quarters of the radial canal and ends within 1 mm. of the edge. A smaller specimen, 7 mm. by 4 mm., has 21 tentacles (5, 5, 5 and 6) and in it the gonad (male) stretches from the circular vessel to the middle of the radial canal. The gonad is relatively larger and more compact than in the female, in which the ova extend in a thin sinuous band on either side of the canal. From an examination of the specimens the males would appear to come to maturity while much smaller than the females.

One specimen, taken off the Coquet (Station 12M.), is peculiar in that two adjacent radial canals, carrying gonads, have swung round and fused about the middle of their course. The common canal formed splits again near the circular canal and gives off a short side branch.

Cosmetira pilosella (Forbes).

This species was taken in very small numbers and was restricted in distribution. The largest specimen, taken off the Longstone in September, measures 13 mm. in diameter, but is sexually spent.

Tiaropsis multicirrata (M. Sars).

In April ten small specimens were taken, the bell in each case measuring about 1·5 mm. in diameter and slightly more in height. There are 32 tentacles with smaller ones developing between them, and eight prominent adradial lithocysts. The mouth is quadrangular with four small lips. No gonads have yet developed.

In July twelve large specimens were taken off Seaham. These vary in diameter from 8–12 mm. and the tentacles vary in number from 176 to 236. According to Bigelow (1913), whose largest specimen measured 22 mm. in diameter, the final number is about 250. In my largest specimens (12 mm.), which are almost sexually mature, the bell margin is closely crowded with tentacles and seems to carry its maximum number, but the actual size of these specimens cannot be determined accurately owing to their preserved state. They differ from the smaller ones in having the bell relatively flatter, the manubrium much more frilled and the gonads well developed and in some cases mature. The collection shows eight females and four males. A prominent feature is the presence of granules of intense black pigment which are scattered along the dorsal wall of the ovary. This pigment is also present at the base of each tentacle, but is only seen clearly in mounted specimens with a fairly high power of the microscope, when the concretions in the marginal vesicles can also be seen to advantage. Owing to preservation these concretions are much broken up and look very like pigment granules. In the male the black pigment is not so conspicuous on the gonad.

The species has been confused with *Eutonina indicans* (Romanes) by Johansen and Levinsen (1903), and indeed the two species are very much alike in the preserved state. As both species were found in the same sample a certain amount of difficulty was experienced at first in distinguishing the two sorts. Mr. Kramp has kindly corroborated these identifications. The peduncle of *Eutonina*, however, although much contracted, is quite distinctive, as are also the black ocelli in the lithocysts of *Tiaropsis*.

Obelia sp.

This medusa occurs in very small numbers compared with those of previous records. Miss Robson has recorded five species of *Obelia* hydroids for the North-East coast (*Dove Marine Report*, 1914), and since there are five medusa-producing hydroids of this genus we should expect to find five species of medusæ. The work of Browne (1905, p. 70) in rearing different *Obelia* species shows, however, that their medusæ are practically indistinguishable so that, in view of his findings, it does not seem possible to give the specific names of the specimens handled.

Phialidium hemisphæricum (Gronovius).

The numbers of this medusa, present at all stations and at all depths, compare favourably with those of former years. The largest catch was obtained off the Longstone by a bottom net early in September. The specimens range in size up to 12 mm. in diameter and show great variation in form, especially in the number and shape of the tentacle bulbs. Although these differences may be due to the preservative, yet I believe with Kramp that possibly different varieties exist.

One freak specimen has two manubria separated by a distance equal to their own width.

Saphenia gracilis (Forbes and Goodsir).

Although by no means abundant in the collection, this rather rare medusa is present in larger numbers than in previous records. It increases both in number and size from early September to October when the mature specimens are to be found.

Eutonina indicans (Romanes) (=*Eutonina socialis*, Hartlaub).

In all, 33 specimens of this medusa were taken in middle and bottom waters in July and August. They are conspicuous on account of their large size and prominent gelatinous peduncle which bears a much-frilled manubrium. In Hartlaub's figure (1897) this frilled condition is not indicated to the extent shown in my specimens. Kramp has found this species in more northern waters and has made very careful measurements ; with his observations the Northumbrian specimens are in accord.

In the older specimens dark pigment can be detected on the tentacle bulbs, along the dorsal surface of the gonads and along the dorsal surface of the grooves in the floor of the stomach. So far I have been unable to find any reference to this in the literature dealing with this species.

Tima bairdii (Johnston).

Only four specimens were taken in July off the Longstone. All measure more than 20 mm. and one shows traces of a developing gonad.

Æquorea forskalea Péron et Lesueur.

One badly mutilated specimen was taken in July by a bottom net off Seaham. It measures about 12 mm. in diameter and has 16 radial canals. This appears to be the first record of the species for Northumbrian waters.

TRACHYMEDUSÆ.

Aglantha rosea (Forbes).

Compared with the catches of previous years, the numbers recorded for this species are very small. It was entirely absent during July, August and October, and only 25 specimens were obtained during September.

These medusæ do not belong to Kramp's larger form *A. digitale* forma *typica*, but rather to the variety *rosea* for reasons given in a previous Report (Peacock, 1923).

SCYPHOMEDUSÆ.

Aurelia sp.

A single ephyra was captured by a bottom net in April.

CTENOPHORA.

Beroe and Pleurobrachia are well represented from July to October. Beroe is the more numerous for the early part of July, then as it decreases in numbers Pleurobrachia shows a gradual increase. Both are found at all depths.

ACTINOZOA.

FAM. CEREANTHIDEA.

Arachnactis bournei Fowl. (?)

Large numbers of Arachnactis larvæ were taken in April by middle and bottom nets off the Coquet and Newbiggin. They are comparable with the figures of the species given by Carlgren (*Nordisches Plankton*, XI).

Arachnactis albida Sars.

A single specimen of *A. albida* was taken in July. It differs from the former species in the arrangement and length of the tentacles.

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TABLE I.

Species.	Month.	April.			July.											August.			September.						October.				
	Station.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
	Depth.*	13	28½	27	19	31	22	34	45	40	33	33	39	34	12	28	25	18	26	39	22	38½	11	41	35½	24	29	27½	37½
ANTHOMEDUSÆ																													
Sarsia eximia	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	2	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	B	5	–	7	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sarsia tubulosa	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	2	–	–	–	–	–	–	–	2	–	–	–	–	2	2	–	–	–	–	–	–	–	–	–	–	–	–
	B	–	–	–	–	–	4	–	–	2	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Sarsia prolifera	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	7	–	12	52	9	4
	B	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	8	43	5	2
Sarsia gemmifera	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	4
	B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	–	–	–	–	–	–	–	–	2	–	–
Dipurena halterata	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–	–
Euphysa aurata	S	–	–	–	–	–	59	–	–	–	2	–	–	–	–	–	–	–	43	–	2	9	–	2	–	65	25	–	–
	M	5	–	–	20	2	12	66	81	56	66	43	5	–	9	57	57	4	4	–	8	–	–	12	11	4	7	9	14
	B	7	2	–	7	26	40	95	221	122	499	437	55	24	46	167	549	–	10	6	4	–	–	6	35	4	2	10	27
Hybocodon prolifer	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	B	12	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Podocoryne areolata	S	–	–	–	–	3	11	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	2	4	–	2	7	7	5	10	22	–	–	70	24	–	–	–	–	–	–	–	–	–	–	–	–
	B	–	–	–	–	6	–	11	2	3	5	–	27	36	2	3	8	–	–	–	–	–	–	–	–	–	–	–	–
Bougainvillia britannica	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	5	–	–	–	7	9	14	7	–	7	–	–	9	6	–	–	4	–	–	–	2	4	–	–	–	–
	B	–	–	2	–	3	–	–	9	2	–	–	87	17	–	3	8	–	2	–	–	–	–	4	–	–	2	–	–
Lizzia blondina	S	–	–	–	–	–	–	–	–	–	–	–	8	–	–	528	5	–	23,400	9,572	8	1,092	–	68	5,152	–	–	–	–
	M	–	–	–	–	2	–	–	–	–	–	–	–	–	4	1,431	102	68	968	759	164	13	59	493	3,676	6	16	–	–
	B	–	–	–	–	–	6	–	–	–	–	–	–	–	4	235	40	18	666	1,172	73	2	36	117	376	18	6	–	–
Rathke octopunctata	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	B	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Leuckartiara octona	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	17	–	–	2	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	2	7	–	18	4	2	7	–	–
	B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	12	–	6	2	2	–	–	–

* Depth of sea bottom in fathoms.

TABLE I.—*continued.*

		Month.	April.			July.											August.				September.						October.			
		Station.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
	Species.	Depth.*	31	28½	27	19	31	22	34	45	40	33	33	39	34	12	28	25	18	26	39	22	38½	11	41	35½	24	29	27½	37½
LEPTOMEDUSÆ	Mitrocoma fulva	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	7	11	2	–	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		B	–	–	–	–	6	2	–	2	–	3	–	5	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Cosmetira pilosella	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	–	–	–	–	–	–	2	–
		B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	2	4	–	–	–	4	–	–	–	–	–
	Tiaropsis multicirrata	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		B	–	7	3	–	–	–	–	–	–	–	–	–	–	23	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Obelia sp.	S	–	–	–	–	5	–	–	2	–	17	2	22	18	–	20	–	–	–	11	2	–	–	–	–	–	–	–	–
		M	14	–	16	–	20	–	14	2	2	2	–	–	33	–	–	2	2	–	–	4	–	–	3	2	–	–	–	–
		B	–	5	2	–	6	–	–	2	6	11	–	–	12	–	3	–	–	–	–	–	–	–	4	–	2	2	4	–
	Phialidium hemisphæricum	S	–	–	–	–	5	55	–	–	–	–	2	15	2	28	4	17	–	–	4	18	–	18	–	4	–	–	–	–
		M	–	–	–	–	40	3	23	51	23	59	40	54	13	72	20	89	10	–	2	14	–	5	64	21	32	5	22	58
		B	–	3	2	7	87	4	43	155	15	35	23	33	136	119	18	38	46	16	11	5	2	4	119	469	21	30	7	46
	Saphenia gracilis	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	8	–	2	7	9	10	–	25	12
		B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	4	–	4	9	6	5	13
	Eutonina indicans	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	7	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		B	–	–	–	3	–	–	–	4	4	–	–	33	–	2	12	–	–	–	–	–	–	–	–	–	–	–	–	–
	Tima bairdii	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	4†	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TRACHY-MEDUSÆ	Aglantha rosea	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–	2	–	2	–	6	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	6	–	–	–	–
		B	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

* Depth of sea bottom in fathoms. † Absolute no.

The Cœlenterate Plankton of the Northumbrian Coast during the Year 1925.

By

Henry G. Watson, B.Sc.

With 1 Figure in the Text.

THIS is a report of the Cœlenterate plankton taken during the cruises of the *Evadne* in 1925, and investigated at the request of Professor A. D. Peacock. I am indebted to Miss Ann R. Sanderson, B.Sc., for considerable help in the identification of specimens.

The material was received from the Dove Marine Laboratory already separated from the whole catch of the plankton. In most cases only a fraction of the catch had been examined, but the numbers in the table express the total for the whole catch. Instead of hauls being taken at three depths as in previous years, hauls were taken at five depths, but the "mid-over" position was discontinued after April. All the hauls were made in daylight.

Reviewing the estimated numbers taken, it appears that on the whole the cœlenterates were not so abundant in 1925 as in previous years, *Hybocodon prolifer* L. Agassiz, and *Aglantha rosea* (Forbes) being the only species whose numbers compare at all favourably with those of former collections. Seventeen species were noted, seven occurring in middle and bottom waters only. No new species was found.

Cœlenterates were absent from several hauls taken in April, namely, off Beadnell (Sta. 1 surface, Sta. 2 surface) and off Coquet (Sta. 9 surface and mid-over).

For details regarding station, depth and numbers reference should be made to Table I and Fig. 1. The figures in Table 1 have been expressed proportionately in terms of the whole catch.

ANTHOMEDUSÆ.

Sarsia eximia Allman, and *S. tubulosa* (M. Sars).

In all only five specimens of these were found and each number in the table represents only one specimen. In the case of each *S. eximia* specimen, it was so badly mutilated as to be identifiable with difficulty.

Euphysa aurata (Forbes.)

This was common in all localities in June and July, with a tendency to be found in the lower hauls. It was notably absent in September, a similar observation being made in the Reports of 1922 and 1923. A catch far greater than any other was taken off Newbiggin (Sta. 18 Bottom) on July 11th. *Steenstrupia nutans* (M. Sars), if present, was not identified.

Hybocodon prolifer L. Agassiz.

This was far more numerous at the two stations established on June 1st, one off Newbiggin, the other off Coquet, than at any other time and in each case in the middle hauls. It was rare in April and almost absent in the catches later in the year.

Podocoryne areolata Alder.

Only isolated specimens of this medusa occur.

Bougainvillia britannica Forbes.

This was found at all depths in June and July, but was entirely absent in April and September. The best catch was taken of Dunstanborough (Sta. 16), the middle haul being the largest. It may be noted that it was absent off Boulmer (Sta. 15) on the same day. The total of all specimens of medusæ from Station 15 is remarkably small.

Lizzia blondina Forbes.

The occurrence of this species was erratic, being found only at a few stations in small numbers at all depths. Its occurrence this year bears no resemblance to that of 1924.

Rathkea octopunctata (M. Sars).

This uncommon species was a little more frequent in its appearance than in the previous year. The identification of each specimen was confirmed by the character of the oral tentacles.

LEPTOMEDUSÆ.

Mitrocoma fulva (Browne).

This occurs in middle and bottom waters in April, June and July. A single specimen was found in the fraction from a surface haul taken off Alnmouth in September (Sta. 21). Its occurrence appears unusual.

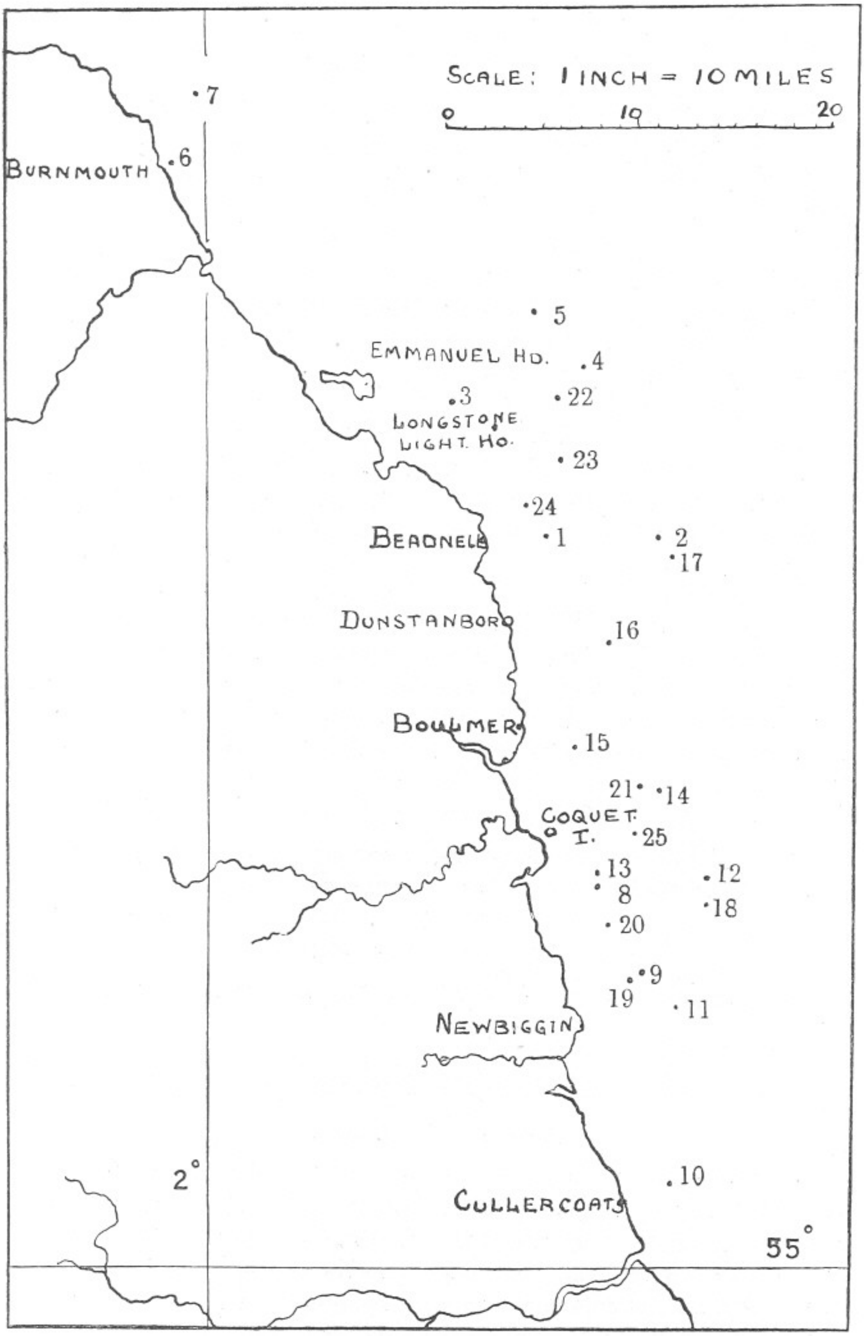
SCALE: 1 INCH = 10 MILES
0
10
20
·7
BURNMOUTH
·6
·5
EMMANUEL HD.
·4
·3
·22
LONGSTONE LIGHT HO.
·23
·24
BEADNELL
·1
·2
·17
DUNSTANBORO
·16
BOULMER
·15
21·
·14
COQUET I.
·25
·13
·12
·8
·18
·20
·9
19
·11
NEWBIGGIN
·10
CULLERCOATS
2°
55°

Fig. 1.

Cosmetira pilosella (Forbes).

The single specimen obtained in April is doubtfully identified, being shrunken and much stained. The species occurred in small numbers in September in the lower waters only, the specimens being large if not mature.

Tiaropsis multicirrata (M. Sars).

This species occurred again this year, but in small numbers. It appeared as last year, in April and not again until the latter part of July. The specimens obtained in April were small, about 1 mm. across, while those in July were almost, if not, mature.

Obelia sp.

The difficulty of distinguishing the medusæ of the various species has caused them to be numbered together. The numbers are a slight increase on those of the previous year, except in April, and they compare favourably with those of 1923.

Phialidium hemisphæricum (Gronovius).

The numbers of this medusa are less than in any of the two previous years. It was present at all depths with a tendency to be found in the lower hauls, a similar observation being made in previous years. Specimens of all sizes occurred throughout the whole collection.

Eutonina indicans (Romanes).

A total of 8 medium-sized specimens was obtained from three stations, namely, St. Abb's Head (Sta. 7), Newbiggin (Sta. 11) and Coquet (Sta. 14).

Tima bairdii (Johnston).

One specimen only was obtained, in the middle haul off Boulmer (Sta. 15).

TRACHYMEDUSÆ.

Aglantha rosea (Forbes).

This was by far the most abundant species. Though notably absent entirely from two stations (Burnmouth, Sta. 6, and Coquet, Sta. 12) it occurred in almost every one of the other hauls at all the other stations. It was equally common at all depths. The numbers seem to reach a peak at the beginning of September, though the largest catch by far was taken at the last station. The numbers compare favourably with those of other years.

TABLE I.

	Species.	Month.	April.										June.		July.						September.						
ANTHOMEDUSÆ.		Date.	8	8	10	10	10	11	11	14	14	14	1	1	10	10	11	11	11	11	7	7	7	13	13	13	17
		Station.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
		Depth.	30	38	10	47	39½	22	37	24	32	20	27	30	25	30	21½	26	41½	25	22	30	30	32	29	24½	29
	Sarsia eximia	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	–	–	–
		M under	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Sarsia tubulosa	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M under	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	–	–	–	–	–	1·5	19	–	–	–	–	–	–	–	–	–	–	–
	Euphysa aurata	S	–	–	–	–	–	–	–	–	–	–	–	3·5	8·75	–	–	–	–	4	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	1·8	–	–	–	23	–	–	–	–	–	57	–	–	–	–	–	–	–
		M under	–	–	–	–	–	–	–	2	–	–	2	–	4	2	4	–	–	16	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	1·7	–	2·2	1·5	–	9·3	8·8	–	8·8	–	120	–	–	–	–	–	–	–
	Hybocodon prolifer	S	–	–	–	–	–	–	–	–	–	–	3·5	10·3	–	–	–	–	–	–	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	1·8	29·9	4·6	–	–	–	–	6	–	–	–	–	–	–	–	–
		M under	1	–	–	–	–	3	–	–	–	–	13	–	2	–	–	–	–	–	–	–	–	–	–	–	–
		B	–	–	–	2	–	2	5	–	–	2·2	10·8	–	–	5·5	–	–	–	–	–	–	–	–	–	–	–
	Leuckartiara octona	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7·5	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	34	11·3	–	–	–	2·1	9
		M under	–	–	–	–	–	–	–	–	–	–	2	–	–	4	–	–	–	–	135	414	46·7	–	–	–	–
		B	–	–	–		–			–	–	–	–	–	–	–	–	–	–	–	13·7	16	–	–	–	–	–

TABLE I—*continued.*

		Month.	April.										June.		July.						September.						
		Date.	8	8	10	10	10	11	11	14	14	14	1	1	10	10	11	11	11	11	7	7	7	13	13	13	17
		Station.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
	Species.	Depth.	30	38	10	47	39½	22	37	24	32	20	27	30	25	30	21½	26	41½	25	22	30	30	32	29	24½	29
	Podocoryne areolata	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2·75	–	–	–	–	–	–	–	–	–
		M under	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	1·7	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	–	–	–	–	38	–	–	–	–	–	–	–	–	–	–	–	–	–
	Bougainvillia britannica	S	–	–	–	–	–	–	–	–	–	–	–	–	–	4·8	–	16	–	8	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	6·4	–	6·2	16	–	41·3	18	–	–	–	–	–	–	–	–
		M under	–	–	–	–	–	–	–	–	–	–	8	–	2	4	–	20	5·1	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	–	–	–	7·7	76	–	–	–	13·2	12·7	–	–	–	–	–	–	–	–
	Lizzia blondina	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26·3	24	–	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–	–	–	9·5	–	–	–	–	–	–	–
		M under	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	20·6	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	19	–	–	–	–	–	–	–	–
	Rathkea octopunctata	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M over	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M under	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–
		B	–	–	–	–	–	–	–	–	–	–	6·2	–	9·3	–	–	–	–	–	–	–	–	–	–	–	–
Leptomedusæ.	Mitrocoma fulva	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–
		M over	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	8	4·3	–	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M under	–	–	–	5	–	–	15·8	1	–	–	2	–	–	2	–	2	–	–	–	–	–	–	–	–	–
		B	–	–	–	2	–	–	5	1·7	1·9	–	6·2	38	–	–	–	–	–	–	–	–	–	–	–	–	–
	Cosmetira pilosella	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
		M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7·8	–	19·1	–
		M under	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	21	8·3	6	–
		B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20·5	–	–	26	–	10	–

Tiaropsis multicirrata	S	–	–	–	–	–	1·8	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–
	M over	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9·5	–	–	–	–	–	–	–
	M under	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
	B	–	1·5	–	–	–	–	–	–	–	–	–	–	–	–	–	4·4	–	–	–	–	–	–	–	–	–
Obelia sp.	S	–	–	–	–	–	–	–	–	–	–	56	75·3	140	33·6	–	–	64	52	5	–	10	15	3·1	3·9	114
	M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	8·5	218·5	–	–	–	–	6	38	5·7	–	8·3	–	–	4·2	–
	M under	–	–	–	–	3	–	–	–	1	–	11	66	6	18	–	4	3·4	4	–	–	–	–	–	–	–
	B	–	–	–	–	–	–	–	–	–	–	10·8	–	–	23·3	–	–	19	–	–	–	–	19·5	–	–	–
Phialidium hemisphæricum	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6·8	–	–	16	5	–	–	–	3·1	–	12
	M over	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	1·8	–	–	–	2·1	–	–	–	–	–	–	19	–	–	16·7	–	–	4·2	–
	M under	–	–	–	–	–	3	4·5	1	1	–	–	–	4	20	4	2	–	4	4·5	4·6	–	–	–	–	24
	B	–	–	–	–	–	–	11·8	–	–	–	1·5	19	9·3	5·8	–	–	31·7	40	–	10·7	21·4	39	–	2	21
Eutonina indicans	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M under	–	–	–	–	–	–	4·5	–	–	–	3	–	–	4	–	–	–	–	–	–	–	–	–	–	–
	B	–	–	–	–	–	–	–	–	–	–	–	–	–	5·8	–	–	–	–	–	–	–	–	–	–	–
Tima bairdii	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M over	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5·6	–	–	–	–	–	–	–	–	–	–
	M under	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	B	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TRACHYMEDUSÆ.																										
Aglantha rosea	S	–	–	–	1·7	–	–	2	–	–	–	–	–	–	33·6	–	10·5	4	48	125	144	10	382·5	40·4	11·7	192
	M over	–	9	–	12	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	M	3·5	11	2·5	28	2	–	1·8	10·8	7·2	9	10·7	–	105·8	32	5·6	2·8	12	114	317·3	236·3	108·7	317·8	91·7	14·8	792
	M under	1	1	–	5	–	–	–	4	–	1	6	–	58	12	4	2	3·4	66	209·3	377·2	33·3	364	no catch	–	416
	B	–	4·5	–	–	–	–	1·7	–	3·8	2·2	6·2	–	28	17·5	–	–	6·3	200	416·8	346·7	92·9	318·5	60·7	10	294

Further Investigations upon the Water Movements in the English Channel.

Drift-Bottle Experiments in the Summers of 1927, 1928 and 1929, with Critical Notes on Drift-Bottle Experiments in General.

By

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With 4 Charts and 2 Figures in the Text.

As long ago as 1897 the Marine Biological Association carried out experiments with surface-floating drift bottles in the English Channel. In the course of those experiments which were described by Garstang in this Journal (**1**), 430 bottles were sent adrift in 53 batches during the year 1897. The bottles were put out chiefly in the vicinity of the Eddystone, and when Garstang reported on the results of the experiments, rather less than one-third of the bottles had been recovered. Garstang worked out a relationship between the movements of his bottles and the strength of the winds, which convinced him that "the relation between wind action and surface currents is capable of quantitative study," and declared himself encouraged to proceed further with the idea of testing the reliability of his empirical relationship between bottle travel in miles and wind *pressure*. The study of wind influence by paying attention to *pressure* constituted a step of interest, and one would like to be able to turn up the continuation of Garstang's work promised at the conclusion of his paper already quoted. We here pay more than passing attention to the attempt made by Garstang to establish a quantitative relationship which should enable one to infer surface current speed from wind, because it is our intention to examine this matter further at a later stage in this paper. For the present, one may remark that any investigator who may seek to connect wind and surface drift by means of a quantitative relationship wherein the wind factor employed is wind velocity squared, is, to all intents and purposes, expressing wind influence in terms of pressure like Garstang.* We shall refer to this worker's results again later.

In 1925 a very brief paper on the movements of surface-drift bottles put out from the Sandettie Lightship during a whole year (1920–21) was

* See page 40 of *The Observer's Handbook*—M.O. 191.

published in this Journal by the present writer (**2**). This small paper was written to throw what light could at the time be thrown upon the question of water interchange between English Channel and North Sea. Actually at the present time this is a subject upon which we have ample information from sources other than drift-bottle experiments.

In 1927 a further paper dealing with drift-bottle experiments in the English Channel appeared in this Journal (**3**), and to certain results therein set down some later reference will be made.

In view of the fact that these three papers have been published in this Journal, it is convenient that the present paper should find a place here.

It is our intention to present below the results obtained from the setting adrift of numbers of bottles (not all of the same kind) from the International Station E2, situated at 49° 27′ North—4° 42′ West. The bottles were put out from the Ministry's research vessel *George Bligh* by the writer's colleague Mr. C. F. Hickling, in early August 1927, in August 1928, and in July 1929.

The experiments of July 1924 had involved the liberation of 500 bottles—of which half were common surface-floating bottles and half bottom-trailing bottles of Bidder type; in that case liberations of 50 of each kind were made at International Station E2, at International Station E3 (48° 34′ North—5° 13′ West), and along three chosen short stretches on the steamer route between Southampton and Saint Malo. From these earlier experiments (1924) 52 per cent of the surface bottles were recovered, and much information of interest resulted.

In the case of the experiments with which we are to be concerned below, no bottom-trailing bottles call for our attention; the liberations were made only at E2, and that on one occasion only in each of the three years in question. However, the experiments were made for very definite reasons which will become apparent later. There was, of course, the obvious general wish to find out more about the surface-water movements of the English Channel in order to amplify what had already been discovered, but, since we had in 1924 been particularly fortunate in choosing what proved to be an unusually interesting time for our experiments, we now wished to repeat these to see what journeys might *again* be accomplished by ordinary surface bottles. Subsequent to the 1924 liberations, there had been an onset of S.W. wind of almost uninterrupted predominance for some 5½ months; some of the common surface bottles had travelled about 500 miles at an overall speed approaching 8 miles a day, a speed which we naturally surmised might be unusually great. This, amongst other reasons, led us to repeat the experiment. Another reason was the wish to see whether we could not obtain useful and representative data to enable us to work out on better foundations than had yet been possible, a reliable quantitative relationship between surface water movement and wind strength. On this point we have elsewhere indicated what we hold to be representative data (**3**, p. 717). The third, and chief reason, arose from our desire to try out other types of bottle, and to stage a race as it were between these latter and ordinary surface-floating bottles. Added to the foregoing reasons was the very natural wish to observe at what speed bottles travel up Channel, at a time during the whole of which we have records of the speed of water flow through Dover Straits. When the earlier drift-bottle experiments were made in the Channel we had no continuous current observations in train from the Varne Light vessel, such as are now available.

The English Channel is, of course, an ideal place for carrying out experiments with different types of floating drift bottles. Bottles may travel 1000 miles and more with very good chances of recovery when they strand ; no matter where they may go ashore short of this distance, the prospects of receiving the postcards from them are quite good.

General Remarks on Drift Bottles and their Use.

By our expression " other types of bottle " we mean various kinds of floating-bottle systems provided with sub-surface drags. The shortcomings of simple surface-floating bottles have been apparent to earlier workers, of course, and bottles fitted with suspended objects of various kinds have been used.* The writer has devised various types of fittings to enable drag bottles to be made up satisfactorily and quickly ; one of these has been described and figured already (**4**), whilst others are pictured in this present paper. Now one point concerning the employment of drag-fitted bottles is of supreme importance, but strangely enough there seems to be little indication that all earlier workers have paid proper attention to it. It is all very well to put out drag-fitted bottles, but unless one can have very definite information that the postcard bottle had actually stranded *complete with fittings exactly as when set adrift* at the place wherefrom the postcard was sent back, one surely has no option but to discard the postcard as almost worthless. This is certainly the considered opinion of the writer who has carried out various experiments to evolve a really successful drag-fitted bottle. In the course of drift-bottle experiments in the Adriatic, Italian workers did take steps to learn whether the entire floating system stranded at the place from which the postcard was returned.

A few general considerations will repay attention at this point. If ordinary surface-drift bottles move (as they have been known to do) up the English Channel into the North Sea at an average speed exceeding 6 miles a day (**3**), we may not assume that there has been any commensurate translocation of water unless we have special evidence of this.

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* References are given later.

Such evidence might be available from the study of changing salinity distribution. As Harvey (**5**, p. 103) so rightly remarks, "it appears probable that the wind-blown surface particles, after travelling a short distance, sink, to be replaced by particles from below, and in this way translocation of water masses with particular characteristics, containing characteristic organisms, does not take place at anything approaching the speed of a floating object."

It is surely high time that the implications of these considerations should be fully weighed. All the passively conveyed organisms whose movements in the sea interest us fishery researchers, are so nearly of the same specific gravity as the water itself, that we cannot refuse to entertain the possibility that they may undergo passive vertical movements in the upper water layers of equal magnitude with their passive horizontal movements. An object like a simple floating bottle (even when perfectly properly ballasted to float correctly) escapes the vertical movements referred to, and will move along at a rate approaching the onward movement of individual water particles as impelled by the wind during their brief sojourn at the surface. Now without going too fully into the matter, it is at any rate clear that a system comprising a buoyant bottle from which a drag is suspended, will move forwards at a rate much more nearly approximating to that of planktonic organisms in the same milieu ; *in cases where the water movements can be regarded as wind-impelled*—an important reservation. Just how badly out (if errant at all) are the results obtained with simple surface bottles in an area like the southern North Sea, where wind plays a potent rôle in influencing waters constantly moved to and fro in immense masses by the swing of the tides, the writer is not prepared even to attempt to indicate here. Of course, the remarks just quoted from Harvey demand fuller attention in some cases than in others. Imagine a large still lake having no outlets and no noticeable currents. Let us put out in such a lake a number of simple surface-drift bottles and await the onset of strong persistent winds. We shall evince no surprise if the bottles (though properly adjusted to float only just awash) move away down wind at a speed very much greater than does, say, the centre of mass of a population of plankton which we may earlier have discovered to be distributed throughout the upper layers where we put out the bottles. This is a simple case. In a sea affected by strong tidal streams the question is very much less simple. It may be that on days without wind the sub-surface tidal streams are, at places, faster than are the surface streams. In the case of the English Channel at times of strong southwesterly winds, rapid North Sea-going travel of simple surface bottles may be attributable to the wind hindering the bottles moving back again on the southwest-going streams. Thus all sorts of complications arise ; a certain strength of wind in one direction may be much more potent than the same strength of wind in the opposite direction in influencing the travel of surface bottles, due to unequal speed of the streams opposed. To what degree the ideas so clearly applicable to waters free of tidal streams apply, is a matter for experimental elucidation.

Granted that it is desirable to employ drag-fitted bottles, how best may we construct such bottles ? It is obviously desirable that the drag unit should hang as vertically as possible below the buoyant floating unit. This implies that as much weight as possible should reside in the drag to prevent it from riding up, for, in a sea where the water movements are wind impelled, we desire by the very nature of things that the drag should always hang as deep as possible. This desideratum requires that the upper floating bottle shall be as buoyant as possible so that it shall be able to support a drag of maximum weight. In turn this demands that the suspending line or wire shall be good and strong, and that its attachments to the two constituent units shall be above suspicion. All these features go to make a satisfactory system, but, as an offset, they impose a need for great caution in making safe deductions from the use of floats embodying them. It is clear that such a bottle system as meets all the requirements outlined above might float in good style from E2, say, as far as the Straits of Dover, whereupon it may elect to strand. It will become moored in a fathom of water perhaps, and the constant moving about and battering it may be subjected to there can very easily be expected to cause a breakage adrift as between bottle and drag. What happens now ? The buoyant bottle receives a new lease of life as it were, and may easily move offshore again for any one of a variety of reasons. It is now almost completely useless as an indicator of surface-water movements, for it will be blown about by the wind from place to place, being entirely unballasted. It may ultimately strand and be found, say, in Jutland, in which case its travel might be taken without comment as in no way amiss. It might on the other hand strand on the Yorkshire coast, when one would be presented with the choice between inferring an interesting because unusual drift, and the possibility of something being very much amiss. A period of southeasterly winds could (and has been known to) cause the upper unit of a drag-bottle system to travel to the Yorkshire coast after having come from E2 to the North Sea with nothing wrong with the system. All these considerations imply that we must have a good drag-bottle system so designed that we shall know whether *all* was present when the questionnaire bottle stranded. We shall feel inclined to appraise earlier work involving the use of drag-fitted bottles in the light of the foregoing considerations.

RELEVANT COMMENTS ON THE VIEWS HELD BY, AND THE APPARATUS EMPLOYED BY EARLIER WORKERS WITH DIFFERENT KINDS OF DRIFT BOTTLES.

The literature concerning drift-bottle experiments is already very considerable, and it can be no aim of a paper such as this to attempt to give an adequate account of the actual apparatus employed by different workers except in such cases as have a particularly close bearing on matters here dealt with. The first point of interest, of course, is the importance attached by earlier workers to the necessity of using bottles very carefully ballasted to escape windage effect. Let us see what degree of reliance investigators have found it possible to place on the travels of simple surface bottles regarded as true indicators of surface currents. Thereafter will come the wish to learn what views have been held by earlier workers regarding the desirability of employing bottles fitted with sub-surface drags.

It is definitely a fact that there exists a cleavage of opinion. Krümmel (**8**) discusses the earliest-known drift-bottle experiments and weighs the opinions as to their usefulness held by various authorities. He declares his own opinion (**8**, p. 437) thus : " Wir wissen jetzt, dass die Flaschen auch ohne einen besonderen kleinen Ballast von Sand tief genug eintauchen (sie werden meist mit der Zeit immer schwerer durch Bewachsung), um überwiegend dem Strom, nicht einfach dem Winde zu folgen : ganz abgesehen davon, dass in der offenen See die Richtung der herrschenden Luft-und Meeresströmungen nicht eben sehr verschieden zu sein pflegt."

That drift bottles may move against the prevailing wind even when the current is weak and whether they are ballasted or not has been proved by Schott especially (**9**). Ryder (**10**) was content to use ordinary champaign [*sic*] bottles without ballast ; these we are told floated horizontally in the water but with only a very small part of their side above water, " so that they were practically inexposed to the action of the wind." Nielsen (**11**) attached great importance to using bottles carefully adjusted to approach very nearly the specific gravity of the water. Schmidt (**9**) apparently used ordinary champagne bottles, some ballasted to float with only a very little surface exposed, and some unballasted. He intended, however, to ascertain whether the two types performed journeys significantly different, and promised a discussion in the second report on the drift-bottle experiments, but in this report written by Giovanni Platania (**12**) no such discussion appears. Gilson (**13**) in his very fine and detailed report discusses in detail the advantages of using bottles other than simple surface floaters. Incidentally we learn (**14**) that his report only presents a quarter of the material at his disposal for publication. The surface-drift bottles used by the English Ministry of Fisheries (**7**) were all of a type carefully shingle ballasted to float vertically with the tips of their necks only just awash (**15**). In these experiments the bottles certainly did not experience a direct wind pressure, but their travels were conspicuously in accord with the direction of the prevailing winds, a fact which makes one wish very strongly that contemporaneous liberations of drag-fitted bottles had been possible, for it is fair to suppose that such a large-scale bottle experiment will never be repeated—indeed, two of the lightvessels from which the bottles were then set adrift are no longer in existence.

The foregoing remarks serve to show that various opinions have been held as to the necessity of carefully weighting simple surface bottles, but it is surely a very elementary precaution to take, and the present writer (who gives experimental findings bearing on this matter below) certainly holds the view that it is a necessary step to take, being convinced that the strictures made by Sir John Ross so long ago (see **8**, p. 437), when he spoke of the "bottle fallacy," could be levelled with good reason against results obtained from the use of bottles not weighted to ride with practically all their surface submerged.

There can be little doubt that it is much better to use bottles fitted with suspended sub-surface objects; though they are less easy to make up and use in large numbers, their superior usefulness can hardly be challenged. That many workers have held this view is quite clear, and it certainly represents the majority opinion of most marine researchers with whom the writer has spoken. A well-ballasted simple surface floater may certainly be taken along by the current in spite of the prevalence of a strong opposing wind, but it is a matter of experience that if one chooses an occasion when a pronounced surface stream is opposed by a strong wind to put out bottles of both kinds, one will soon see that the bottles separate considerably. This is a fact not to be neglected, and it can with reason be urged that the travels of a bottle system fitted with a drag of adequate surface hung, say, a fathom deep, are likely to give to the marine fishery researcher indications of superior value to the travels of simple surface-floating bottles.

Admittedly a most obvious advantage of the simple surface floater resides in the fact that with it, we are free from the risk that a large proportion of our returned postcards may be useless as a result of ignorance as to whether the bottles when they stranded were exactly as when set adrift. Drag-fitted bottles have been used by various earlier investigators, though reference can here be made only to such experiments as are of special interest to us. Garstang realised the desirability of experiments to determine the depth of the currents induced by wind action (**1**, p. 225) and envisaged a comparison of results obtained by bottles floating at the surface, and by other objects designed to come under the influence of lower strata of water. He appears, however, to have reported upon no experiments to the end outlined. Cunningham in a paper rarely quoted (**6**), in the third year of his drift-bottle experiments in the Irish Sea, continued his liberations of simple surface-floating bottles, " but side by side with it other schemes were tried with a view to ascertain the movements of the deep water. ' Vehicles ' of various form were designed, bamboo and wood being used in their construction ; some were weighted with lead to make them sink, and others left without any ballast to float lightly on the water."* It is not possible to learn all one would like from Cunningham's paper, and he gives no wind data.

References to work with drag-fitted bottles are given by the writer elsewhere (**7**, p. 7). In Gilson's well-known experiments (**13**, p. 7) coupled bottles were used. He deals fully with the reasons for using coupled bottles, describes his apparatus in detail, and gives an account of instances when he has noticed a marked difference in rate of travel in the southern North Sea as between simple surface-floating bottles and his drag-bottle systems, consisting of pairs of bottles linked together by cords 3 metres long. When wind and current are in the same sense the simple floater quickly races the other ; where opposed the reverse is the case. Gilson was aware when his postcards came back whether his coupled bottles had been found still fastened together, and realised that the upper buoyant members of his systems, in cases where the suspending cords had broken, were " beaucoup plus aptes à être emportés par le vent." He cites cases where simple bottles had travelled at 13½ miles a day, whereas their fellow coupled bottles had, under the same favourable wind conditions, travelled at only 6 miles a day. Again, he gives instances where simple floating bottles and coupled bottles put out at the same time have performed significantly different journeys in point of direction. We read of cases where simple bottles at times of strong on-shore winds have been cast on the beach, whereas their fellow coupled bottles escaped such a fate. Still, Gilson gives no account of just how his simple surface bottles floated, and there is a special point of interest which occurs to the present writer in connection with his experiments.

If the floating buoyant upper members of his coupled systems were found stranded *minus* their drag members, it can hardly have been possible for Gilson to know whether these bottles had finished their journeys whilst still properly linked. This is a point which has greatly exercised the writer in his experiments, because it is so clearly possible to receive many records which may or may not be above suspicion. Many drag bottles may become moored close inshore whilst complete, and though the severance of the links may take place at some distance from

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* In this present paper experiments with bottles entirely unballasted are described—see below, page 267.

the beach, yet the upper bottles containing the postcards may go ashore in the immediate vicinity and be perfectly reliable witnesses to acceptable travels. An attempt to get over this difficulty has been made, as will be seen later. No doubt many of Gilson's coupled systems, from the upper bottles of which he received postcards indicating that the bottle systems had become "decoupled" before discovery of the questionnaire units, were found at places to which the complete system *had* travelled, but the element of doubt cannot but have existed.

In the case of the very fine Italian experiments (**16**), the postcards definitely asked whether when the postcard bottle was found it was alone or fastened to another. Of great interest in connection with these experiments are the entries in the tabulations of returns showing that many coupled systems were recovered still coupled long before stranding, and of particular interest is it to note that some such systems were retrieved complete at distances from the beach, which can mean only that they were moored there by reason of the suspended bottles having grounded. In our rougher northern waters we are much less likely to be so favoured, but it nevertheless remains our chief aim to have drag bottles retrieved whilst still complete—before their suspension cords or wires have become broken. An additional point of interest in these Italian researches lies in the fact that they evidently employed an upper questionnaire bottle almost identical with that since devised and thought novel by the present writer (see **4**, Fig. 2). This bottle was made in quantity for the writer by a commercial firm of bottle manufacturers* to permit drag bottles to be made up easily, but the Italian experimenters have the credit of having had this idea first carried into practical effect. The bottle in question has a pierced bulge at its base to permit the easy attachment of a cord or a wire.

Before passing on to consider the experiments which are the major concern of this paper one may note (**8**, p. 438) that coupled bottles were used a considerable time ago by Hautreux in the Bay of Biscay.

THE DRIFT-BOTTLE EXPERIMENTS OF AUGUST 1927, AUGUST 1928, AND JULY 1929 IN THE ENGLISH CHANNEL.

We may recall the fact that we desired to ascertain whether there would be any significant differences in the journeys performed by bottles of different types put out at such an ideal place for the purpose as E2. A very important secondary consideration was our desire to become possessed of ample good material upon which to base attempts to work out quantitative relationships between wind and bottle travel. The

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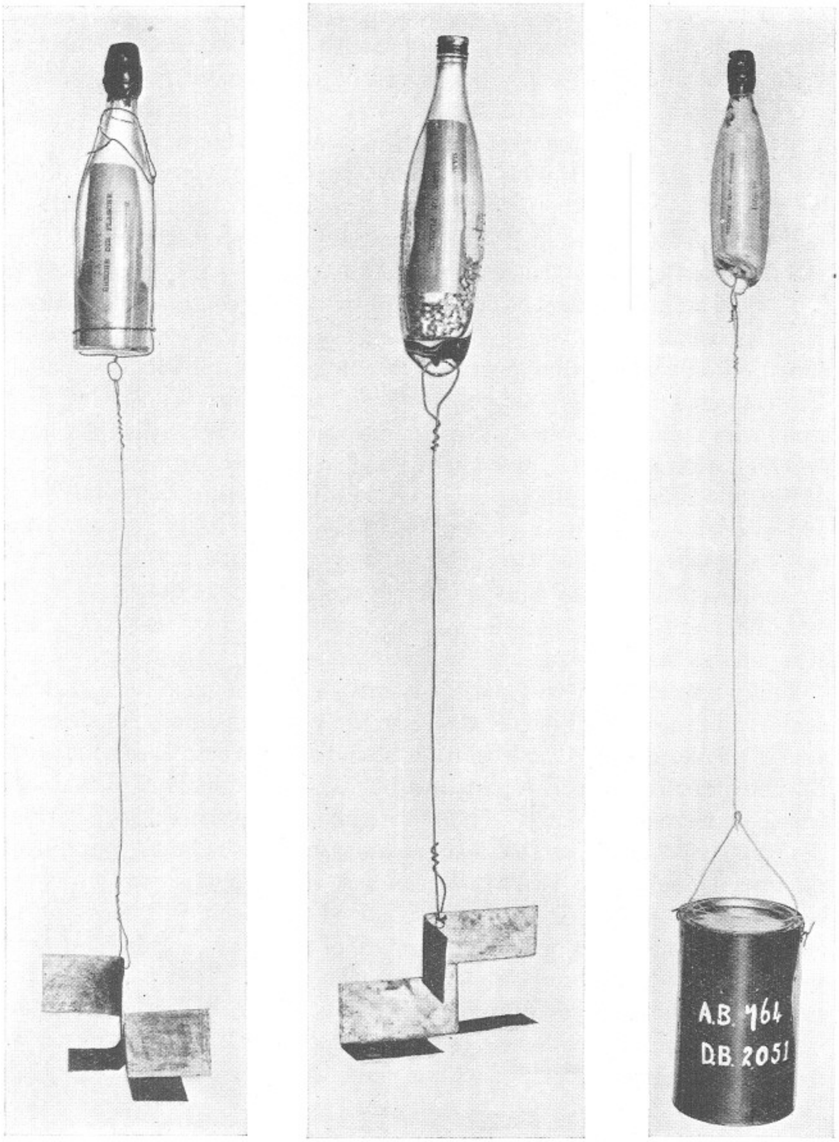
* By Messrs. Redfearn Bros. of Barnsley.

bottles were of three kinds, (1) ordinary simple surface floaters properly ballasted to float just awash, (2) bottles entirely unballasted so that wind could be expected to play its maximal rôle in influencing their movements, and (3) bottles fitted with sub-surface drags and expected to perform journeys as little affected by direct wind influence as possible.

THE BOTTLES.

The simple surface floaters used in all three years need no comment; they are figured in (**7**). The completely unballasted bottles used in 1928 were what are known in the trade as "oval twelves," and they contained nothing save the questionnaire card and papers. The other bottles are figured opposite.

The drag bottles put out in August 1927 were of the type shown in Fig. 1 (a). The wire suspension was half a fathom long and the drag was that previously described (**7**, p. 7). The wire used had to be thinner than desirable in order that it might be manipulated satisfactorily in making the attachment. Actually, these floats closely resemble those which were used by the American investigators in their researches in the Bay of Fundy. Our bottles were of 20-oz. capacity. No means save correspondence with the finders was available to enable us to learn whether the drag was still attached when a bottle was found. These bottles were far from satisfactory, and unless we have known that the drags were still attached when found, the records have been regarded as unreliable. The drag-fitted bottles set adrift at E2 in August 1928 were of two kinds, as pictured in Fig. 1 (types b and c). Those with the metal drag were made up by using bottles of the special type already mentioned and whose unusual features can be seen in the illustration. In this case stronger wire was used, the bottles were sealed by means of screw-on copper caps, the suspension wire was 3 ft. long, and, in general, the systems were much better than those used in the previous year. The questionnaire postcards in this case definitely asked whether the drags were attached when the bottles were found. It may be seen that these bottles are easy to make up, since, when the drags are attached to the empty bottles, several dozen can be floated in a tank and sand poured in from a jug until ballasted satisfactorily. The second type used were designed to serve as drag systems, having specially large drags, the idea being to learn whether these would travel significantly differently from the bottles carrying the smaller metal drags. A number of large cylindrical brightly coloured toffee tins were obtained new (the one figured was painted for photography purposes) from the makers. These tins were nine inches high and of six inches diameter. It was thought inadvisable to ballast the tins and rely upon their proving watertight; holes were



a. b. c.

FIG. 1.—Illustrating various types of drag-fitted drift bottles.

punched in them and an unweighted bottle containing a postcard was suitably "imprisoned" in each of them before hanging the tins from the upper bottles. The underlying idea here was, of course, the thought that we might in some cases receive both postcards back from the same stranding place, which would be a very welcome experience indeed. Again, the lower buoyant bottle contained in the tin made it possible to have a larger drag than would otherwise have been practicable. The suspension wires were of good quality and were 3 feet long.

The drag bottles used in 1929 (not figured here) were better altogether, and consisted of two equal bottles linked together by means of a length (3 feet) of stout sashcord. Only the upper bottles contained postcards, and the bottom ones were so ballasted that the whole systems when afloat left only the smallest portion of the upper buoyant bottles exposed. The attachment of the cords was effected by means of loops of very stout wire fastened to the bottles by means of a device which we have found exceedingly useful, and whose nature can be seen from the pictures of Fig. 2. A monel metal cap pressed specially by the makers to bell out at the open end is screwed home on to the bottle neck to bear down upon a monel metal disc previously placed in position. The "disc" is an annulus; the central hole is just big enough to take the bottle neck, and there are holes punched in it to accommodate wires. Thus the attachments are easily made.

Being unwilling to rest satisfied until sufficient success had been achieved in these experiments as measured by the attainment of the aims stated above, one further liberation of bottles has since been made at E2 just prior to the time of writing. This time we have used material which we have good reason to hope will prove quite successful. Besides the customary simple surface floaters we have put out bottle systems of the type figured below (Fig. 2). In this case the bottle systems are much less likely to "come adrift," and it is hoped that some will be retrieved entire. It is hoped to present the results of this latest experiment next year in the form of a brief supplement to this paper. Then we shall have surface drift-bottle records from experiments in five separate years, and will find ourselves, it is hoped, in a position to speak with confidence as to the correspondence between wind and surface current in the English Channel.

The coupled bottle systems put out in July 1930, and which are much superior in strength and promise to others used earlier, are shown in Figure 2.

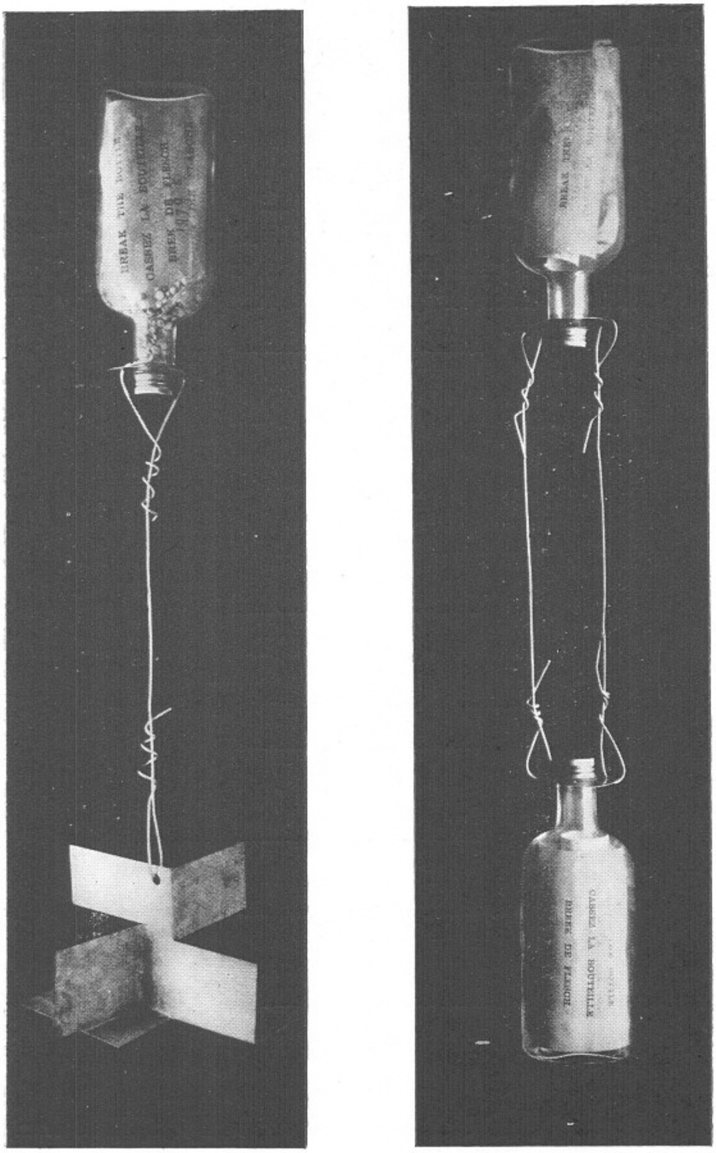


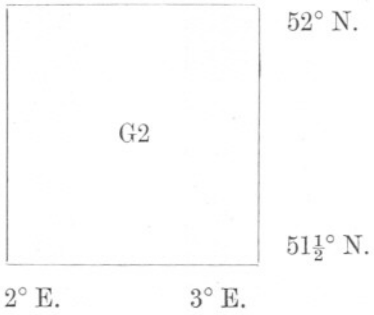
Fig. 2.—Illustrating improved types of drag-fitted drift bottles.

The Recoveries from the Experiments under Review.

The following procedure has again been adopted in reporting :—

A chart of sufficient geographical range was prepared embracing the whole of the English Channel, the North Sea as far north as the Shetlands, and the Cattegat—with the Belts. On this chart were superscribed the ordinary statistical rectangles, each rectangle being delimited by one degree of longitude and one-half a degree of latitude. The positions of recovery of the bottles were (as the records were received) referred to and tabulated in terms of these statistical rectangles. For greater precision in the statement of results, the rectangles were visually divided up into sub-rectangles after the manner of Army cartography practice, thus :—

the rectangle



can be considered to be subdivided thus :—

a	b	c
d	e	f
g	h	j

so that the position of recovery of a bottle might be tabulated as :—

G2 g,

and the latter can be much more quickly referred to a chart than could the usual co-ordinates of latitude and longitude. Chart 1 shows the position at which bottles were put out ; it is also divided up in the manner described to serve reference requirements for the recovery positions of the bottles. Remembering that all the bottles here dealt with were put out at E2, we may proceed to tabulate the details of recovery.

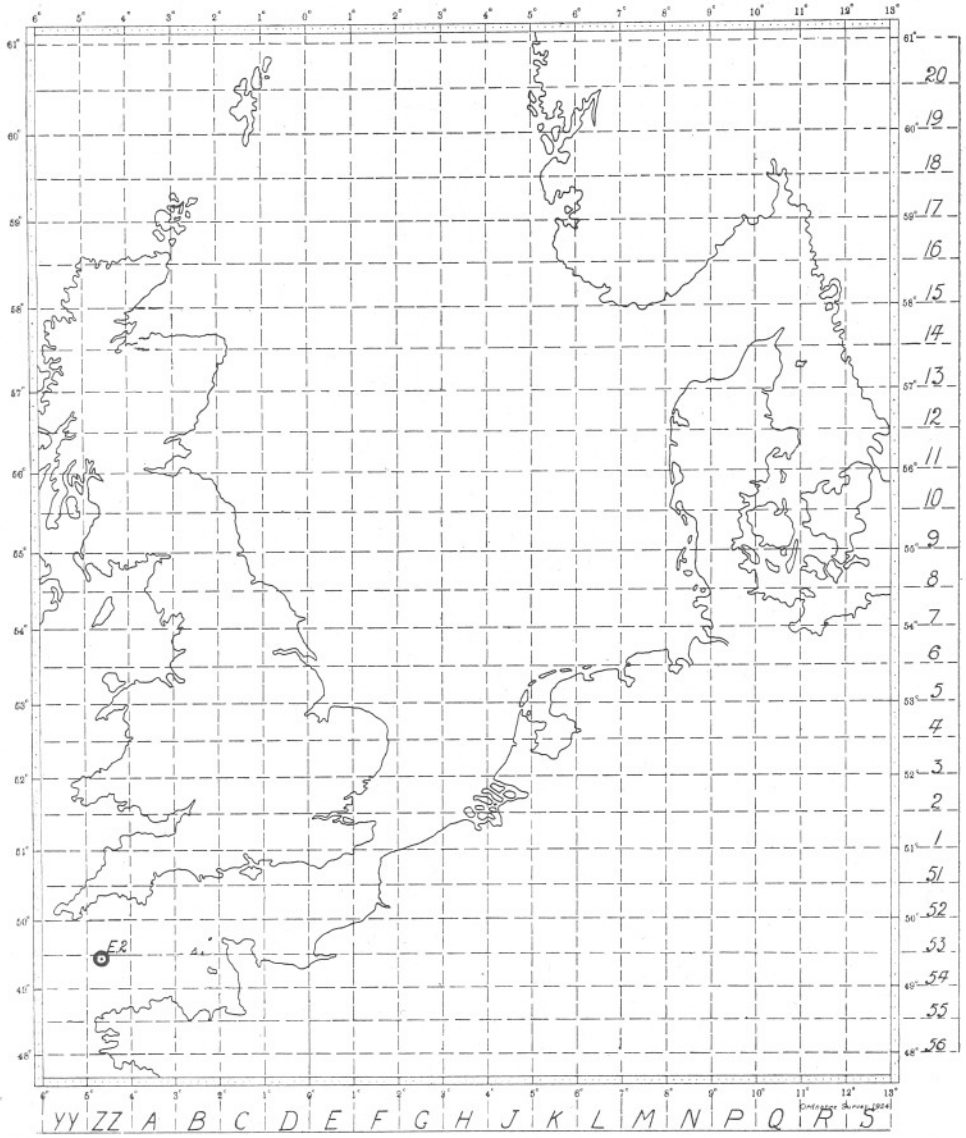


CHART 1.

Key Chart to which tabulated recovery positions of bottles may be referred.

TABLE I.

Experiment of 1927. (1) **Drag Bottles** (Fig. 1, a).

Liberation date : 2.8.27.

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.*
12	H 2 h	79	328
14	J 5 f	97	440
14	J 4 b	97	410
14	J 4 c	97	410
21	C 9 b	146	552
22	D 6 f	148	456
22	C 8 j	149	515
27	K 16 e	189	730

Number put out	30
Number recovered	8
Percentage	26·7

TABLE II.

(2) **Simple Surface Bottles.**

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
10	J 3 g	65	378	5·8
10	,,	66	372	5·6
13	J 4 c	86	420	4·9
13	,,	86	410	4·8
13	J 5 j	86	418	4·9
13	J 4 c	86	410	4·8
13	J 5 j	89	420	4·7
13	,,	86	420	4·9
13	J 4 c	86	410	4·8
[illegible]	K 5 a	96	450	4·7
14	N 8 a	97	585	6·0
31	K 16 e	201	730	3·6
37	N 26 g	257	1290	5·0
51	S 31 j	353	1250	3·5

Number put out	25
Number recovered	14
Percentage	56·0

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* Lengths of the shortest tracks which can be drawn on the chart without crossing land. These distances are in many cases certainly much too small—particularly where bottles recovered beyond the Skaggerak are concerned.

TABLE III.

Experiment of 1928. (1) Completely Unballasted Bottles.

Liberation date : 10.8.28.

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
4	D 51 d	27	167	6·2
4	C 51 h	28	147	5·3
4	C 51 j	28	153	5·5
4	,,	28	153	5·5
4	,,	28	155	5·5
4	,,	28	155	5·5
4	,,	28	153	5·5
4	,,	28	153	5·5
4	C 51 e	28	146	5·2
5	C 51 f	29	158	5·5
5	,,	31	162	5·2
5	,,	34	159	4·7
5	,,	34	161	4·7
5	C 51 j	34	155	4·6
7	C 53 f	45	134	3·0
7	C 54 c	48	155	3·2
7	C 53 j	48	145	3·0
11	E 51 c	71	230	3·2
12	E 51 d	78	202	2·6

Number put out	25
Number recovered	19
Percentage	76·0

TABLE IV.

(2) Simple Surface Bottles.

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
11	D 51 d	71	167	2·4
11	C 51 g	72	130	1·8
11	C 51 h	72	147	2·0
11	,,	73	146	2·0
11	,,	74	147	2·0
11	D 51 c	75	192	2·6
11	C 51 j	75	153	2·0
11	D 51 c	77	192	2·5

TABLE IV—*continued.*

Weeks from liberation.	Position of recovery (refer to Chart I).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
11	D 51 d	77	173	2·3
11	,,	77	172	2·2
12	C 51 b	78	155	2·0
12	E 51 b	78	220	2·8
12	D 51 e	78	177	2·3
12	,,	78	177	2·3
12	,,	78	187	2·4

Number put out	75
Number recovered	15
Percentage	20·0

TABLE V.

(3) **Drag Bottles.** (Fig 1 b.)

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
12	D 51 c	78	192	2·5
12	E 51 d	78	198	2·5
15	,,	102	200	2·0
16	C 54 a	108	116	1·1
16	H 2 h	111	338	3·0
16	L 6 j	111	505	4·5
23	H 1 d	161	310	1·9
37	J 5 j	259	420	1·6
38	J 4 c	260	418	1·6
46	L 6 j	322	510	1·6
47	N 10 a	325	625	1·9
47	M 6 d	325	540	1·7
48	N 6 b	333	577	1·7
48	N 7 j	333	586	1·8
48	,,	334	586	1·8
48	N 7 e	336	582	1·7
49	P 6 a	342	600	1·8
51	N 7 j	351	685	2·0
51	N 9 f	351	618	1·8
71	N 6 c	491	575	1·2

Number put out	50
Number recovered	20
Percentage	40

TABLE VI.

(4) **"Toffee-Tin" Drag Bottles.** (Fig. 1, c.)

(SYSTEMS BOTH OF WHOSE BOTTLES WERE RECOVERED).

Bottle concerned.	Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
Upper	11	ZZ 2 e	71	170	2·4*
Lower	11	D 51 c	76	192	2·5
Upper	11	B 51 h	74	110	1·5*
Lower	11	C 51 e	71	143	2·0
Upper	11	D 51 d	76	168	2·2*
Lower	11	D 51 e	74	180	2·4
Upper	11	D 51 c	77	186	2·4
Lower	16	F 51 e	107	256	2·4

NOTE.—The "lower" bottles, i.e. those initially fastened in the tins, could only themselves perform journeys on escaping from their tins; in this eventuality the upper bottles would sink so long as wire and tin remained hanging from them.

(SINGLE RECOVERIES).

Member.	Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days "out."	Distance travelled in miles.	Corresponding speed in miles per day.
Lower	11	D 51 e	76	180	2·4
Upper	11	D 51 c	76	196	2·6*
Upper	11	C 51 h	72	147	2·0
Upper	11	D 51 e	74	182	2·5*
Lower	11	D 51 c	74	186	2·5
Upper	15	E 51 d	105	200	1·9
Lower	11	E 51 b	75	220	2·9
Upper	11	B5 1 j	71	102	1·4*
Lower	10	C 51 g	64	130	2·0
Upper	11	D 51 c	75	190	2·5*

Number of pairs put out—25.
Number of pairs recovered intact—Nil.
Number of pairs both of whose bottles were recovered—4.
Number of single bottles recovered—10.
Number of bottles recovered in all—18.

* Denotes stated absence of attachment when found.

TABLE VII.

Experiment of 1929. (1) Sashcord Linked Coupled Bottles.

Liberation date : 30.7.29.

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days " out."	Distance travelled in miles.	Corresponding speed in miles per day.
11	C 54 a	72	115	1·6
37	F 52 a	253	228	0·9

Number put out 47
Number recovered 2

NOTE.—In this case there was only one postcard, which was in the lower non-buoyant suspended bottle. Thus any recovery is witness of a journey performed with the system intact. The fewness of the returns may be due to breakage of the suspension cords ; if so (1) we are well rid of the useless postcards which we should have recovered had we put cards also in the upper bottles, and (2) we may perhaps later receive some postcards from bottles retrieved by trawl.

TABLE VIII.

(2) Simple Surface Bottles.

Weeks from liberation.	Position of recovery (refer to Chart 1).	No. of days " out."	Distance travelled in miles.	Corresponding speed in miles per day.
6	B 55 g	38	102	2·7
6	B 55 d	40	82	2·1
7	B 55 h	46	102	2·2
7	B 55 j	48	114	2·4
8	B 55 j	50	108	2·2
8	B 55 d	50	88	1·8
9	,,	60	82	1·4
10	E 51 c	70	220	3·1
11	C 54 a	71	114	1·6
11	,,	71	114	1·6
11	F 51 e	73	252	3·5
11	C 54 a	74	115	1·6
11	C 54 h	77	126	1·6
12	C 54 d	82	118	1·4
13	C 54 a	91	114	1·3
14	F 51 c	93	259	2·8
20	N 10 g	138	620	4·5
20	P 14 j	139	740	5·3
22	N 10 a	148	625	4·2
24	Q 17 e	166	850	5·1

Number put out 39
Number recovered 20
Percentage 51·3

GENERAL COMMENTS.

The extent to which the records from the various types of drag bottles used in the three experiments are to be regarded as reliable will be indicated in the discussion which follows. It is clear that we must set down some account of the relevant wind conditions, and it would be a great convenience if some of the more interesting bottle journeys were represented pictorially, as was done by means of charts in the earlier paper in this Journal (**3**). However, it is not possible here to present charts except for the more interesting records.

To present for each year detailed wind data from various suitable observing stations would occupy too much space. Such data as do demand inclusion must yield the following: (1) Information as to wind at some place not too far from E2, at least for a period just after the bottle liberation in that year which saw the putting out of the completely unballasted bottles, and (2) the most acceptable information for each year concerning what may be regarded as the average wind conditions applicable to the entire journeys of those simple surface bottles which moved right up-Channel into the North Sea. In this latter connection it might readily be agreed that suitable continuous wind records made at some place well up-Channel from E2 would best serve; in the considered opinion of the writer the most useful data for the purposes in view are the autographic wind data from the Eastbourne Observing Authority. We mean that these data are considered likely to reflect the mean wind conditions over the track of the far-travelled bottles as well as any we could turn to, and they have the merit of being very convenient.

It is deemed very desirable to seek some quantitative relationship between surface current and wind, a problem which can only be viewed as a series of steps. The fullest and most reliable bottle-travel data at present available are the travels of the simple surface floaters, since with these one pays attention to the travels of the fastest long-distance individuals—a convenience not possible in the case of the drag bottles for obvious reasons. It seems perfectly reasonable, therefore, to attempt first to associate wind and *surface* bottle journeys, hoping later to deduce some amending factor from results obtained with drag-fitted bottles, and to apply this amending factor later to whatever inter-relationship we may have been able to establish between wind and surface-bottle travel. This would be a step nearer to satisfaction, considering that surface current is what we ultimately wish to deal with.

As regards wind in this connection, it seems clear that we can best concern ourselves with data setting forth the daily mileage run of the wind up-Channel (as deduced from Eastbourne autographic records) for periods of time covering the journeys of the long-distance bottles. This means that, if we regard the trend of the Channel as S.W. to N.E., we must learn what run of N.E. going wind has been associated with the bottle journeys. In obtaining our wind data we should in this case simply regard S.W. going wind as of negative sign, knowing that over several months it cannot predominate. One feels that the numerical association of long period means of up-Channel winds with long bottle travels, is the only possible procedure in attempting to work out any useful quantitative relationship between bottle travel and wind, when dealing with an area like the Channel whose waters are always in tidal motion. The phrasing here intentionally avoids the implication that bottle travel and surface current are one and the same thing. With the remark that the wind data applicable to the 1924 bottle experiments from E2 were very simply handled, since the wind was uninterruptedly "up-Channel," we may pass on to set down such data as suit our present study.

TABLE IX.

RELEVANT WIND DATA FROM EASTBOURNE AUTOGRAPHIC RECORDS.

[Extracted from the appropriate yearly Meteorological Reports of the Eastbourne County Borough and thrown into a form suited to the present study. By "Up-Channel winds" we mean SW.+W.+NW. and by "Down-Channel winds" NE.+E.+SE.]

Period.	Total miles run by wind.	Daily mean mileage run of wind.	Corresponding hourly mean.	Derived multiplying factor to obtain up-Channel wind.	Derived multiplying factor to obtain down-Channel wind.
Aug. 1927	6076·00	196·00	8·17	0·69	0·20
Sept. ,,	6420·60	214·02	8·92	0·77	0·10
Oct. ,,	5567·12	179·58	7·48	0·62	0·15
Above Period	18063·72	196·35	8·18	0·69	0·15
Aug. 1928	5811·04	187·45	7·81	0·69	0·15
Sept. ,,	4450·48	148·30	6·18	0·38	0·33
Above Period	10261·52	168·22	7·01	0·53	0·24
Aug. 1929	5178·40	167·05	6·96	0·72	0·17
Sept. ,,	4088·90	136·30	5·68	0·49	0·36
Oct. ,,	6845·40	220·82	9·20	0·77	0·06
Nov. ,,	6998·28	233·28	9·72	0·64	0·06
Above Period	23110·98	189·43	7·89	0·67	0·16

DAILY MILEAGE RUN OF "UP-CHANNEL" AND "DOWN-CHANNEL" WIND AS DERIVED FROM THE FOREGOING TABLE.

Period.	up-Channel.	down-Channel.	Balance up-Channel.
Aug. 1927	135·24	39·20	96·04
Sept. ,,	164·80	21·40	143·40
Oct. ,,	111·34	26·94	84·40
Foregoing Three Months	135·48	29·45	106·03
Aug. 1928	129·34	28·12	101·22
Sept. ,,	56·35	48·94	7·41
Foregoing Two Months	89·16	40·37	48·79
Aug. 1929	120·28	28·40	91·88
Sept. ,,	66·79	49·07	17·72
Oct. ,,	170·03	13·25	156·78
Nov. ,,	149·30	14·00	135·30
Foregoing Four Months	126·92	30·31	96·61

[On treating the corresponding wind data for the three months July, August, and September of 1924 by this procedure, we obtain the figure 131·06 as the residual "up Channel" daily run of the wind in miles.]

Additional information which may be set down as likely to be definitely illuminating, concerns the known flow of water through Dover Straits at times germane to our present study. Long-period averages only are what we want in this connection, and such Dover Straits records are in the writer's hands in the form necessary.*

As a glance at the charts (Charts 2, 3 and 4) or at the tabulations of bottle recoveries shows, there must have been considerable differences between the three experiments as regards the paths of the bottles in the earlier stages of their wanderings. It is readily surmised that this may have been due to differing wind conditions in the western Channel, and it is necessary to see if such differences did characterise the months concerned in each case. If one can establish such an explanation something of importance will have been accomplished, for we know far too little of the influence of wind on water movement in the area concerned. One experiment would be of little avail in this connection, but we have four experiments (counting that of 1924 already published) in four different summers, and since, as is clear, the bottles moved off differently

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* We refer to the continuous current measurements in train at the Varne Lightvessel.

our data can be regarded as being of special promise. We can get the requisite information respecting appropriate wind conditions from the relevant annual " Meteorological Notes " of Falmouth Observatory. Suitable treatment of the published data yields the following information :—

TABLE X.

WIND DATA FROM FALMOUTH

Period.	Direction and duration of residual wind.
Aug. 1927	360 hours from S. 59° W. true.
Sept. ,,	420 ,, N. 70° W. ,,
Aug. 1928	370 ,, S. 57° W. ,,
Sept. ,,	86 ,, due E. ,,
Aug. 1929	425 ,, S. 86° W. ,,
Sept. ,,	145 ,, N. 12° W. ,,

Before proceeding to discuss the bottle experiments we will present that remaining set of data which might be expected to bear upon our study—the available information as to the contemporaneous flow of water through Dover Straits.

TABLE XI.

THE FLOW OF WATER THROUGH DOVER STRAITS AT TIMES CONCERNED

Period.	Mean daily flow in miles per lunar day.
Aug. 1927	3·21 towards N. 25° E. true.
Sept. ,,	3·47 ,, N. 32° E. ,,
Oct. ,,	3·34 ,, N. 40° E. ,,
Aug. 1928	3·20 ,, N. 36° E. ,,
Sept. ,,	1·30 ,, N. 7° E. ,,
Oct. ,,	5·80 ,, N. 17° E. ,,
Aug. 1929	3·80 ,, N. 22° E. ,,
Sept. ,,	1·80 ,, N. 12° W. ,,
Oct. ,,	4·10 ,, N. 25° E. ,,
Nov. ,,	7·10 ,, N. 46° E. ,,
Dec. ,,	11·40 ,, N. 49° E. ,,

DISCUSSION OF THE EXPERIMENTS.

It will be convenient first to comment upon the individual experiments in turn, and later to make comparisons and draw contrasts between them.

Experiment of 2nd August, 1927.

In Table I have been set down the histories of the drag bottles put out. These bottles (see Fig. 1, a) were, as experience has shown, far from good enough. The wire was, of necessity, much thinner than desirable, and it is a safe inference to make that many of the suspension wires must have broken. It is fruitless to discuss these drag bottles in any detail, and one is not prepared to place any real reliance upon the apparent speeds attained by those individuals which stranded on the continental coast after 12 to 14 weeks. There is ample reason for this reluctance. Although the bottles which did so strand exhibit no excessive speed as compared with their fellow simple surface floaters, yet a consideration does arise which makes them suspect. One bottle was found on the Yorkshire coast, another near the Tyne, and one further north. This is indeed surprising, and can only mean that these bottles lost their drags, became much under wind influence, and were literally blown across the North Sea by the strong S.E. winds of December 1927.* It may be that some of the bottles which stranded earlier on the continental coasts had also lost their drags but had gone ashore before the onset of the December easterly winds, which caught the others still afloat. However that may be, here we have strong evidence of the potent influence of winds in influencing the travel of partially submerged bottles, and in causing them to perform journeys which properly ballasted bottles were not constrained to do.

As regards the simple surface floaters (see Table II), none stranded short of the North Sea which, in view of the winds tabulated above, is not surprising. The tracks can be seen in Chart 2, and that journey of 585 miles in 97 days will be referred to again. We may assume a speed of travel up-Channel on the part of these bottles of quite 6 miles a day.

Experiment of 10th August, 1928.

In this case no simple surface floater (see Table IV) was recovered beyond Kent ; all the recoveries were made on the south coast of England along a stretch between St. Alban's Head and Pevensey. Probably the overall rate of travel of the fastest was about 3 miles a day (see Chart 3). The easterly winds of September 1928 are to be held accountable for these facts.

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* The residual wind for Gorleston over the period of 5 weeks commencing 20th November, 1927, was : 4·6 m.p.h. from S. 70° E. true.

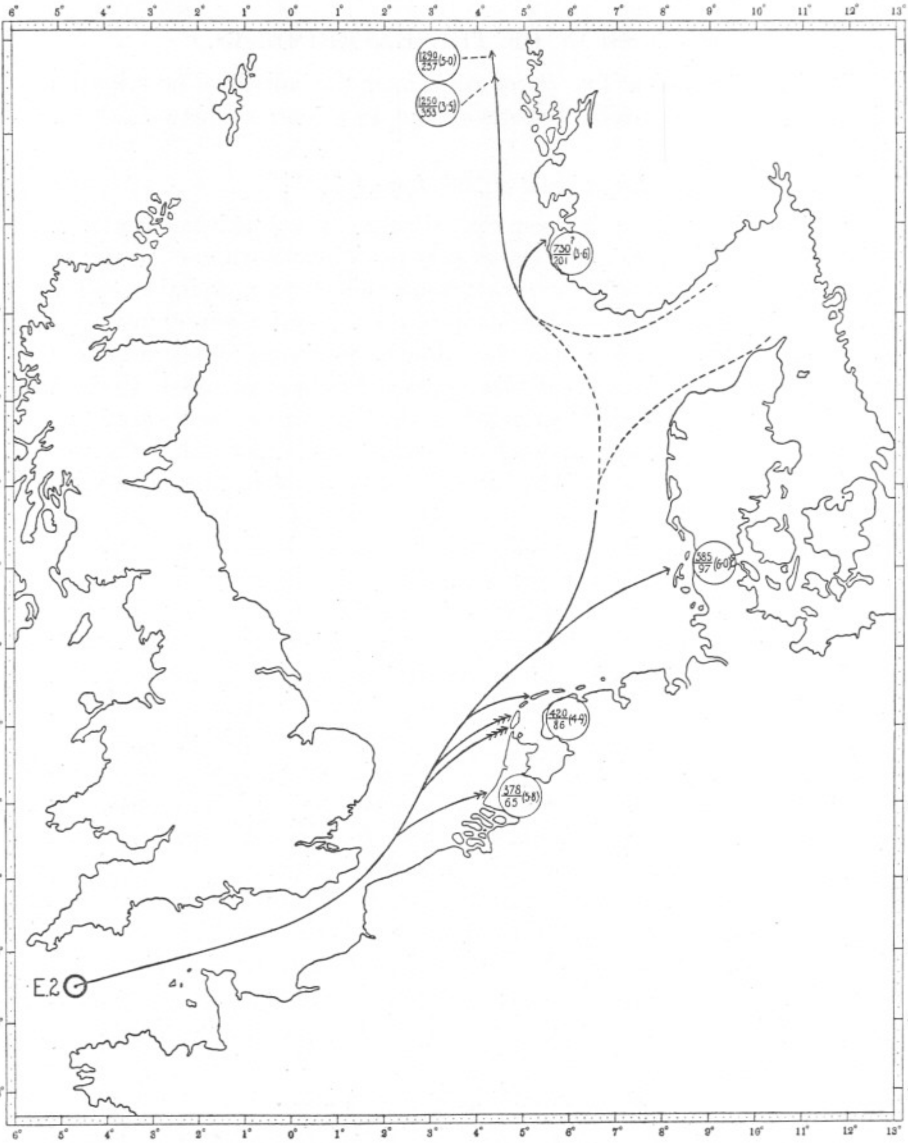

CHART 2.

Illustrating the journeys accomplished by simple surface floating bottles put out at International Station E2 on 2nd August, 1927. Where the arrows are multi-barbed, the number of barbs denotes the number of bottles recovered at the place indicated. The figures in the circles refer to the stranding places near by, and have the following signification :—

The numerator indicates chordal distance travelled in miles.
The denominator gives the time " out " (in days) of the fastest bottle.
The bracketed figures denote the corresponding speed in miles per day.

The completely unballasted bottles (see Table III) were most obviously at the mercy of the strong south-westerly winds which carried them on to the English coast around the Isle of Wight. They covered the short distance of some 150 miles at a speed of about 6 miles a day. Three individuals evidently came offshore again to strand later on the east coast of the Manche département—a fact which a study of the winds already presented can elucidate. It is of very great interest indeed to note that none of the properly ballasted surface floaters accompanied them to the Manche coast. Here then is an answer to those workers who have not thought it essential to ballast their drift bottles with great care.

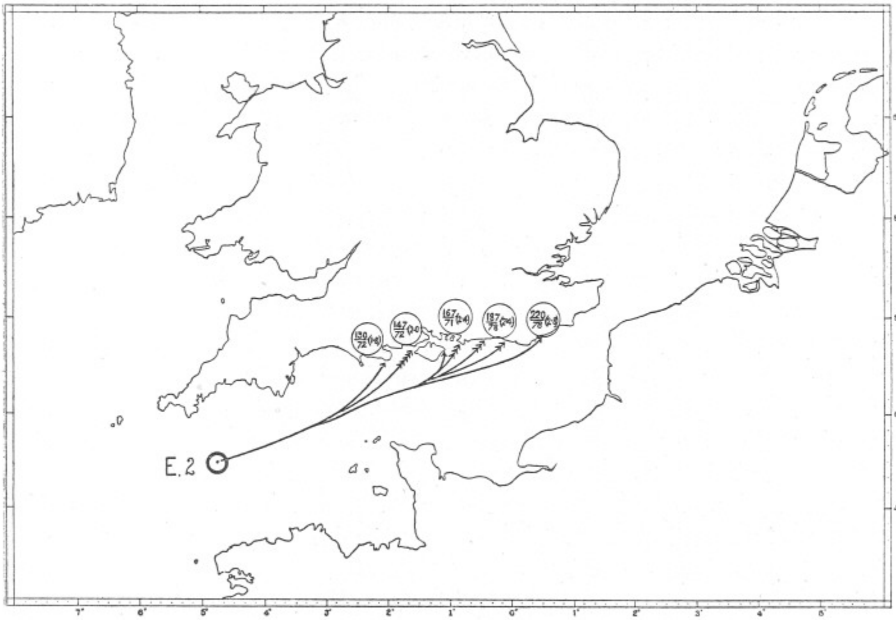

CHART 3.

Illustrating the journeys accomplished by simple surface floating bottles set adrift at International Station E2 on 10th August, 1928.

The figures in circles refer to the strandings near by, and have the same signification as on Chart 2—as also have the arrows.

The drag bottles put out (see Fig. 1, b) were of a type in which considerable reliance could be placed. A glance at Table V reveals much of interest. The journeys accomplished were very significantly different from those performed by both simple surface floaters and completely unballasted bottles. Recoveries were made all along the continental coasts from Belgium to north Jutland (several being recovered right in the German Bight), whereas no simple surface floater was recovered clear of the English

Channel. Why was this ? Only four of these drag bottle returns came from the English Channel, and it cannot be denied that these strandings may have been consequent upon loss of the drag. The balance of probability is that such was the case.

Here surely is indisputable evidence that the travels performed by drag-fitted bottles may be markedly different from those of simple surface floaters put out at the same time and place. We see clearly that the wind was unable to influence the movements of these drag-fitted bottles to nearly the same degree as those of their fellow simple floaters. We could not have wished wind conditions to have been other than what they were, seeing what striking results we have obtained, but at least they have deprived us of one piece of information which would have been very welcome. We had hoped from this experiment, to have learnt by what amount (if any) the speed of drag-fitted bottles falls in defect of that of simple surface floaters put out at the same time and place, for, as has been said earlier, we had wished to be able to apply an "amending factor" to the quantitative relationship to be presented connecting wind with travel of simple surface floaters. The idea here was, of course, to get information more acceptable as representing surface drift, than does perhaps the travel of simple surface bottles. Such information as was wished for, cannot be gleaned from the experiments in 1928, since the two types of bottle did not perform comparable journeys. One may note in passing, that the predominant speed of these drag bottles was round about $1\frac{1}{2}$ to 2 miles a day.

It remains to comment on our experiences with the bottles like that shown above (see Fig. 1, c). These "toffee-tin" bottles, as we may conveniently call them, cannot be considered to have proved much of a success. Not one system was recovered intact (see Table VI), but there emerge a few facts of interest. It is highly probable that the two bottles (both members of the same pair) which had stranded in the rectangle D51 did journey, there in concert, and we note that the speed was about 2·4 miles a day. Those bottles which were originally "imprisoned" in the tins, must, for some reason, have got free, perhaps owing to the tins perishing. Only by getting free could they avoid being carried to the bottom on the rupture of the suspending wires. One upper bottle on losing its large drag, journeyed to South Wales. It is to be noted that not one bottle (neither upper nor lower member) got free of the English Channel, the majority stranding on the south coast of England east of 3° W. longitude. This is very illuminating in view of what has gone before. Had they proceeded on and on as perfect drag bottles, we should (on the analogy of the results from the other drag bottles put out with them) have expected them to have got clear into the North Sea. Obviously they have proved to be "neither fish, fowl nor good red herring," though they have not been entirely without interest. It is probable that these " toffee tin " systems broke up just as the easterly winds which so affected the movements of the simple surface floaters, commenced.

Experiment of 30*th July*, 1929.

Much was hoped for from the coupled-bottle systems put out, but as yet (see Table VII) only two returns are to hand. This leaves us completely unable to assess speed satisfactorily ; for this purpose we require a number of returns to get rid of the difficulties arising out of the possibility that the bottles may have lain undiscovered for a considerable time. As regards direction of travel, the meagre records are quite good, for the postcard bottles can only have performed journeys at all so long as they hung from their buoyant partners. One suspects that many of these postcard bottles are lying at the bottom of the sea somewhere in very shallow waters just off-shore. The upper bottles were purposely devoid of postcards. Actually the further travelled bottle was recovered by trawl 29 miles north of Dieppe. The stranding place of the less travelled of the two bottles recovered is of interest in the light of the frequent northerly winds of September. As will be noted later, the simple surface-floating bottles were carried into the Bay of Saint Malo, and this drag bottle must also have been urged thither by the wind, for it failed to round Cap de la Hague. This fact speaks much for the influence of the wind on this occasion.

The journeys performed by the simple surface floaters put out on 30th July, 1929, are very striking (see Chart 4 and Table VIII). They were carried first into the Bay of Saint Malo and stranded round its shores after travelling at a speed low enough to make one surmise that they had been, as it were, hovering about in the open sea for some time under wind conditions not making for quick travel. With the onset of the frequent northerly winds of September they were evidently urged ashore. Such individuals as succeeded in rounding Cap de la Hague went on up-Channel, and some of them reached the Skagerrak.

BRIEF REVIEW OF THE MAIN RESULTS OF THE THREE EXPERIMENTS.

Common surface-floating bottles put out at the same place (E2) in the same part of the year in 1927, 1928 and 1929 have exhibited very marked differences in their travels ; these differences have been seen to reflect the wind conditions which characterised the three occasions.

In one of the experiments (liberation of 10.viii.1928) completely unballasted bottles, common surface-floating bottles properly ballasted, and drag-fitted bottles of two kinds were put out at the same time and

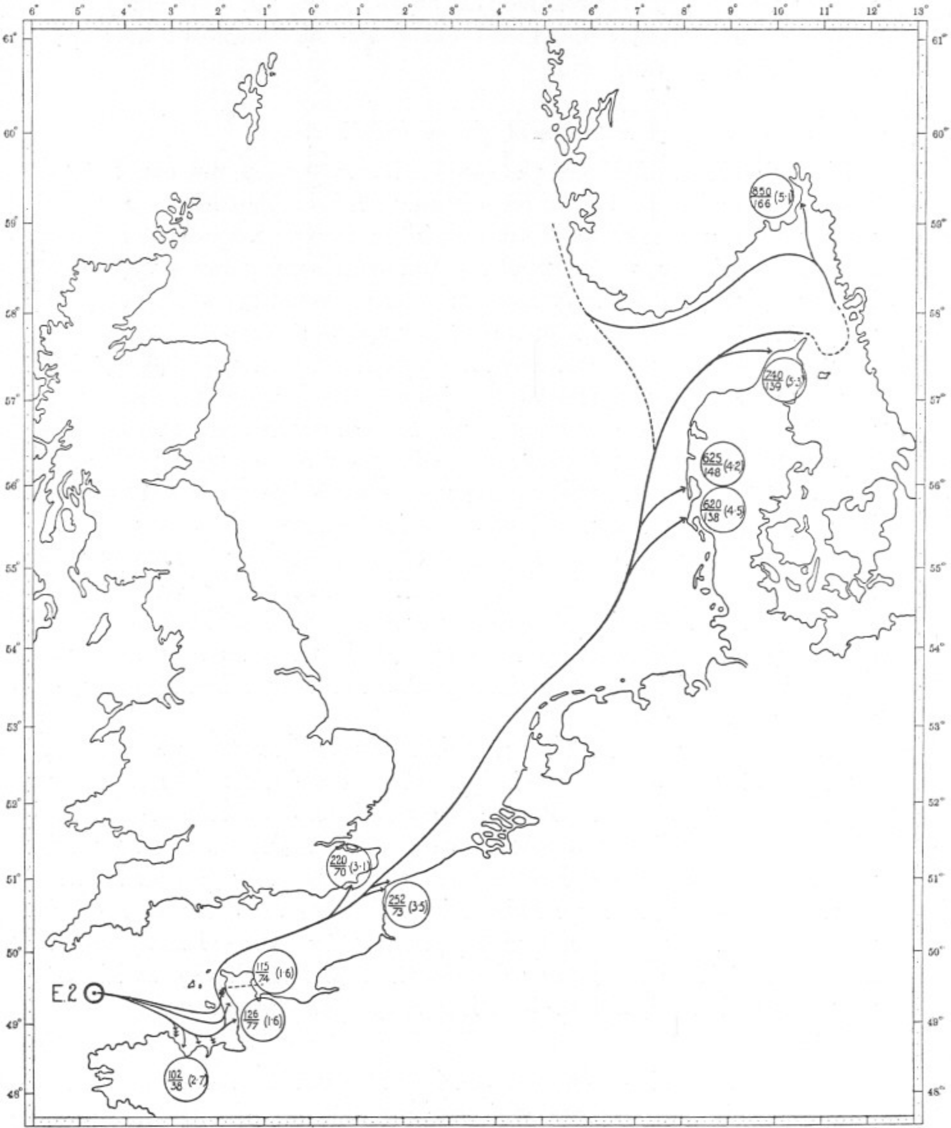

CHART 4.

Illustrating the journeys accomplished by simple surface floating bottles set adrift at International Station E2 on 30th July, 1929.

The figures in circles refer to the strandings near by, and have the same signification as on Chart 2—as also have the arrows.

place. The travels of the different types have been seen to have differed very significantly. The associated wind conditions were, of course, the same for all four kinds of bottle, but the influence which the wind-urged surface water had on the different types in determining their travels has proved strikingly variant.

In the case of the 1927 experiment, when the bottles were carried straight up-Channel without any stranding short of the Dutch islands, there was a continuous flow of water through the Straits of Dover of about $3\frac{1}{3}$ miles a day (see Table XI) during each of the three ensuing months.

Whilst August 1928 differed hardly at all from August 1927 in point of water flow through Dover Straits, yet September 1928 was a month characterised by strong reversals of the usual E.N.E. going flow from English Channel to North Sea. This fact throws much light on the travels of the 1928 simple surface-floating bottles. August 1928 must have been a month of good travel up-Channel, but in September 1928 the bottles were constrained to strand on the south coast of England. The extra brisk flow of water through the Straits in October 1928 was too late to give rise to subsequent strandings on the North Sea shores.

August 1929 was, so far as the Dover Straits current is concerned, little different from the same month in the two previous years, but September 1929 was quite remarkable. In this month the flow of water from English Channel to North Sea was completely held up ; the resulting condition in the Channel must have been that no pronounced drift of water existed. Thus local winds could play a specially strong rôle, and we have seen how the 1929 surface bottles, after drifting about the Bay of Saint Malo for some time, made progress up-Channel, and how three individuals stranded on the coasts bordering Dover Straits. The latter fact is of special interest in view of the contemporaneous hold-up of the water flow through the Straits.

Thereafter, in 1929, the Dover Straits flow of water waxed so very greatly in strength that bottles which had escaped stranding were able to accomplish such rapid journeys across the North Sea that their overall speed for their complete journey touches the high figure of at least 5 miles a day.

We have now one remaining task—to see if we can find any relationship of a numerical kind between the two quantities :—

(1) Speed of Surface-Bottle Travel, and
(2) Speed of Wind at the time.

It is necessary to emphasise here that one must just apply ordinary common sense to the problem. We are not dealing with quantities of a rigid character ; what we must use if we can get them are values for bottle travel and wind, which are acceptable as being the most comparable we could arrive at. The waters of the English Channel being continually in movement as a result of the tidal streams, we have no simple case of wind action on a placid body of water to tackle. It is necessary to proceed as follows :—

Suppose that bottles have moved up-Channel from E2 and have accomplished journeys of several hundred miles. We must, for our purpose, get ample wind data (preferably autographic) from some place situated, say, half-way along the bottle tracks, and work out the appropriate residual wind over the period of time occupied by the bottles' journeys.

It is difficult to see how one can allow sufficiently for the tidal streams if one seeks to establish the desired relationship any other way. Even if we do arrive at an acceptable result, we may not necessarily assume it to be applicable to other waters than those with which we are here concerned.

Over a period of time exceeding a few months, the balance of wind direction will always be up-Channel. We have earlier set down the requisite wind data for our present purpose (see Table IX), and they, together with the bottle-travel data with which we may associate them, will here be given. It is to be noted that the bottle data refer to the simple surface bottles for each year, and attention is drawn to the fact that we are not begging the question by tacitly assuming that bottle travel and surface current are the same thing. They may be so within a little, but we must wait until we have ample satisfactory contemporaneous data from drag bottles and simple surface bottles to work out what we have earlier called an " amending factor." In a previous paper (**3**) the writer was merely able to *fit* a constant to a type of wind-bottle equation. We are now able to go much further and to establish an equation for our area. We have re-cast the relevant data from our 1924 experiments for inclusion here, and in all have data from four different experiments at our disposal. Here are the quantities which call for our attention :—

Experiment.	Mean daily travel of fastest long-distance bottle* (miles per day).	Mileage run of " up-Channel " wind per day during relevant period.
July, 1924	8	130
August, 1927	6	105
August, 1928	2·8	50
July, 1929	5·3	95

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* Having regard only to bottles which did not go beyond the Skagerrak ; beyond this the distances actually covered can only be very roughly assessed.

It would indeed be foolish, considering the kind of data with which we are dealing, to seek to deduce any equation other than a simple one. The inter-relationship between the quantities just set down can be expressed by the following simple equation as satisfactorily as by any other :—

$$S = \tfrac{1}{18} W.$$

where S is bottle travel in miles per day and W the wind speed in the same units—both being worked out over considerable periods as herein done.

ADDENDUM.

Since this paper was written, it has been felt that fuller wind data from the western English Channel could, with advantage, have been included. Accordingly, additional suitable records have since been worked up into the form of residual winds—this being a conveniently brief way of presenting much information in a small space. It was thought that by far the best thing to do would be to extract from the relevant daily weather reports, the records published for Scilly and Guernsey (four observations daily in each case) and to add these together so as to obtain results particularly representative of the average wind conditions over the western Channel. The following table presents the resulting information :—

Residual Wind Data relating to Scilly and Guernsey considered as one Observing Station.

1927	August	9·3	m.p.h.	from	S.67° W.	true.
	September	9·1	,,	,,	N.88° W.	,,
1928	August	7·0	m.p.h.	from	S.63° W.	true.
	September	3·7	,,	,,	N.75° E.	,,
1929	August	7·1	m.p.h.	from	due W.	true.
	September	2·0	,,	,,	N.19° E.	,,

The fact that the simple surface bottles of 1927 travelled rapidly up-Channel and into the North Sea, is not surprising in view of the wind data just set down. In that year, the winds were overwhelmingly more favourable to the accomplishment of up-Channel travel than they proved to be in 1928, and much more favourable than those which prevailed in 1929.

All the bottles put out in 1928 must have set off up-Channel at a good speed aided by the favouring winds of August. The unballasted bottles reached the longitude of the Isle of Wight very quickly, being blown ashore near there within the month. The ordinary surface bottles escaped being blown ashore with their unballasted fellows, and went on up-Channel, until, before they reached the North Sea, easterly winds held up the Dover Straits current and caused them to strand on our south coast. It is to be noted that these surface bottles were not constrained to strand down wind at the time, as were the few unballasted bottles then afloat.

The extra "west in the wind" in August 1929 as compared with August 1928, made itself strongly felt. The surface bottles were carried into the Bay of Saint Malo, from which area the subsequent N.N.E.'ly winds prevented them easily escaping to travel on up-Channel.

ACKNOWLEDGMENT.

I am indebted to my colleague Mr. H. Stokes for preparing the fair copies of the charts from my rough drafts. The paper has been checked by the Statistical Branch of the Fisheries Department.

Many of the views elaborated in this paper have been previously dealt with in considerable detail by Professor Gilson in the course of his reviews of earlier papers by the present writer (see *Journal du Conseil*, February 1926, March 1927, and September 1928).

SUMMARY.

In July–August of three different years common surface-floating bottles were set adrift at International Station E2 (49° 27′ N.—4° 42′ W.). With them, various types of drag-fitted bottles were also put out. The journeys accomplished are discussed, and the striking differences as between year and year in the case of the common surface floaters, and as between the different types in the same year, are commented upon in the light of the prevailing winds. An inter-relationship of great simplicity is deduced between wind speed and the rate of travel of simple surface floating bottles up-Channel and across the North Sea from the results of experiments carried out in four different summers.

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