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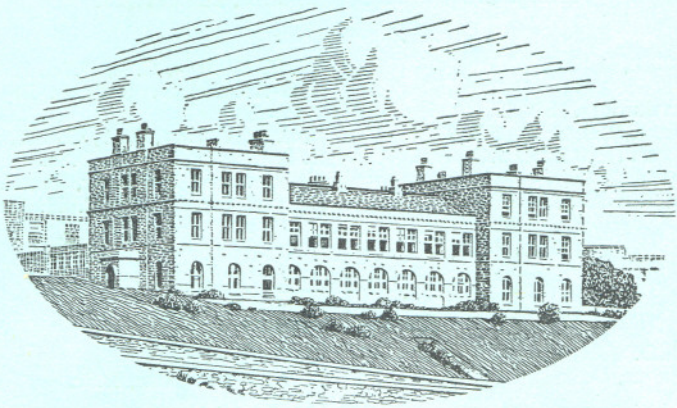

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CONTRIBUTIONS TO THE BIOLOGY OF THE MACKEREL, *SCOMBER SCOMBRUS* L.: MACKEREL MIGRATIONS IN THE ENGLISH CHANNEL AND CELTIC SEA

By G. A. Steven, B.Sc., F.R.S.E.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–6)

Introduction

The common mackerel (*Scomber scombrus* L.) is one of the important European food fishes. Forty-two species of commercial sea fishes are listed by the Conseil Permanent International pour l'Exploration de la Mer in its *Bulletin Statistique des Pêches Maritimes* as being landed in northern and western Europe. Four-fifths of these landings are made up of only twelve important food fishes, of which the mackerel is one. In 1937 (Thompson, 1939), the last year for which full normal figures are available,[1] approximately $1\frac{1}{4}$ million cwt. of mackerel were landed by all the countries of northern and western Europe (excluding Russia), having a total value, as nearly as can be ascertained, of just over £887,000. To this total Great Britain, Eire, and Northern Ireland contributed rather more than 14 % of the quantity and almost 13 % of the value. During the inter-war period, however, Britain's contribution had fallen steadily, her share in 1913 (a year that has long been used as a standard of comparison) being no less than 49 % of the total quantity and 31 % of the total value of all mackerel landings.

Of the British Islands, England is the chief mackerel-fishing country. Just prior to the outbreak of the recent war her total landings were some 140,000 cwt. valued at about £80,000. It is a noteworthy fact that rather more than one-third of this quantity was landed at the single small port of Newlyn, in Cornwall (Figs. 1 and 2). It is still more surprising to note (Fig. 1) that during the four years 1923–1926 more mackerel were landed at Newlyn than at all other ports in England and Wales put together.

There are, in normal times, two distinct mackerel fisheries worked from Newlyn. One is a long-distance, deep-sea fishery carried out by steam drifters (of the normal herring drifter type) in the Celtic Sea far to the westward of the Scilly Islands—except towards the end of the season when fishing takes place nearer land. This fishery will be called the *Newlyn Deep-Sea Fishery* for

[1] The figures for 1938, though published in 1944, are not complete.

mackerel. The other is an inshore fishery that takes place in inshore waters off the northern coasts of the Cornwall and Devon peninsula. In it, boats from other small ports take some part, but Newlyn is the chief centre. This fishery will therefore be called the *Newlyn Inshore Fishery* for mackerel.

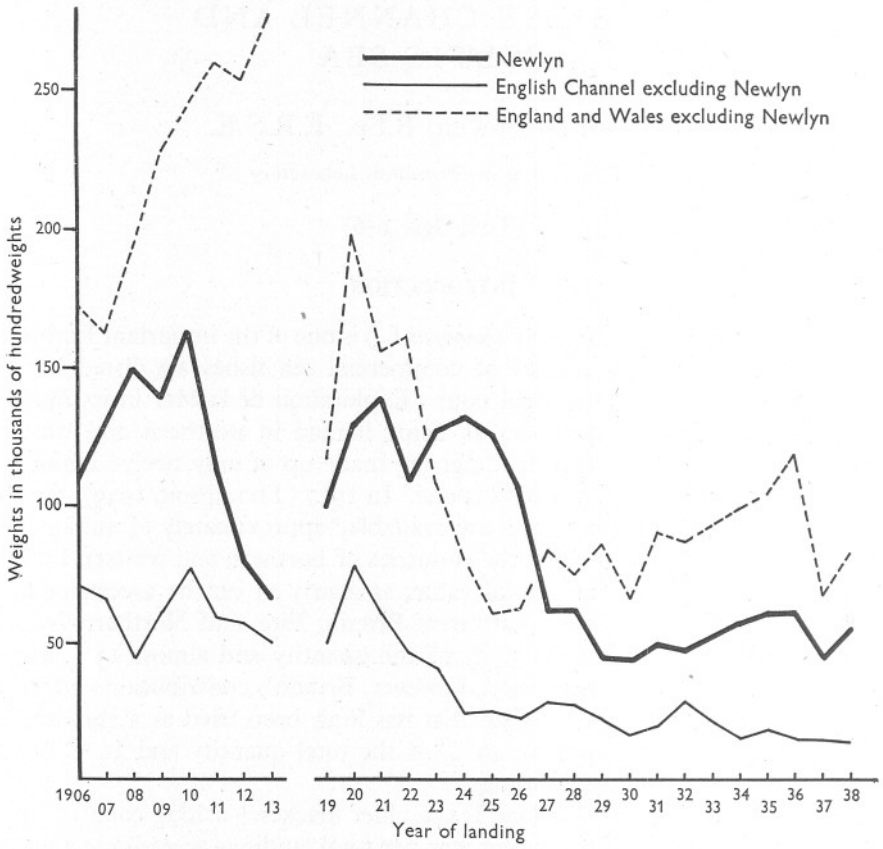

Fig. 1. Mackerel landings in thousands of hundredweights at Newlyn (——); in England and Wales excluding Newlyn (– – – –); and at English Channel ports excluding Newlyn (——). From *Sea Fisheries Statistical Tables* for the years 1906–1938 inclusive.

At Newlyn, then, in normal times, by far the most important mackerel fishery in Great Britain takes place, and it was at this port that most of the data for this investigation were collected.

The Newlyn mackerel fisheries were temporarily suspended during the 1914–18 war and again in the Second World War. Unfortunately, normal fishing has not yet been resumed after this second interruption owing to the uneconomic prices obtainable for mackerel in comparison with operating costs.

In past years there was also a flourishing mackerel fishery farther up the English Channel at Plymouth; but the Plymouth fishery, for purely economic

reasons, gradually declined and came entirely to an end about the year 1926. This fishery will be called the *Plymouth Channel Fishery* for mackerel. A brief but detailed description of all these fisheries will now be given because an adequate knowledge of them is necessary for obtaining a clear picture of the migratory movements of the mackerel upon which they all depend.

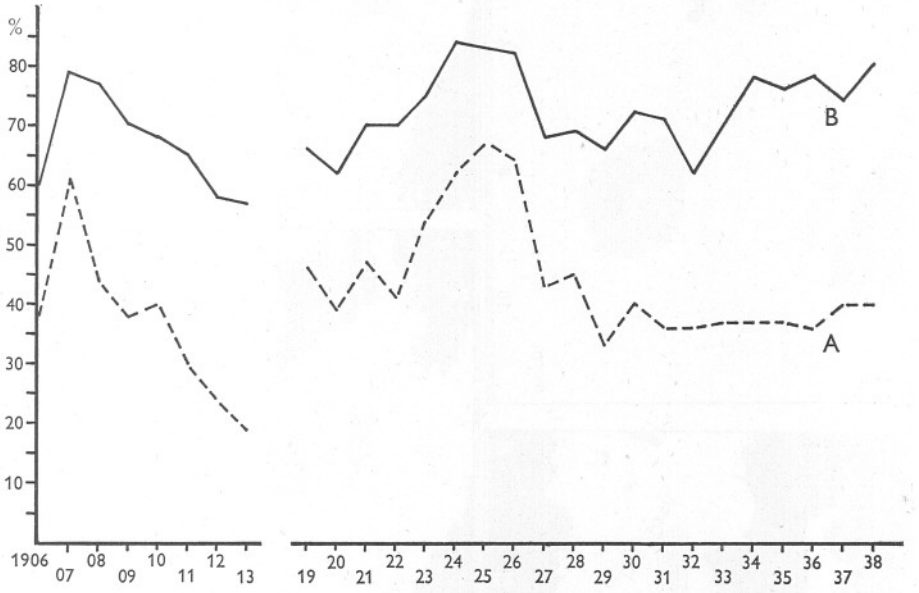

Fig. 2. Percentage contribution by Newlyn to total landings (*A*) in England and Wales; (*B*) at English Channel ports, from 1906 to 1938 inclusive.

The Plymouth Channel Fishery

Although this fishery no longer exists, it is necessary to examine its previous activities in considerable detail, for mackerel are still present on the grounds worked by it long ago and the same migrations still take place by fish that are now untouched by any catching instrument.

The mackerel season began off Plymouth towards the end of December or early in January and boats from east and west used to converge on the port in large numbers to take part in it. Ridge (1889, p. 72), reporting on the fishery of 1888, states that fishing began in that year in January and that vessels from Yarmouth, Lowestoft, Newhaven, Brighton, Eastbourne, Hastings, Porthleven, Newlyn, and Mousehole arrived to take part in it. According to Calderwood, (1892, p. 279) the Plymouth drift-net fleet alone at this season used to number between three and four hundred sail.

In a series of reports on fishing in the neighbourhood of Plymouth, in different months of each year towards the close of last century (1892 and 1893),

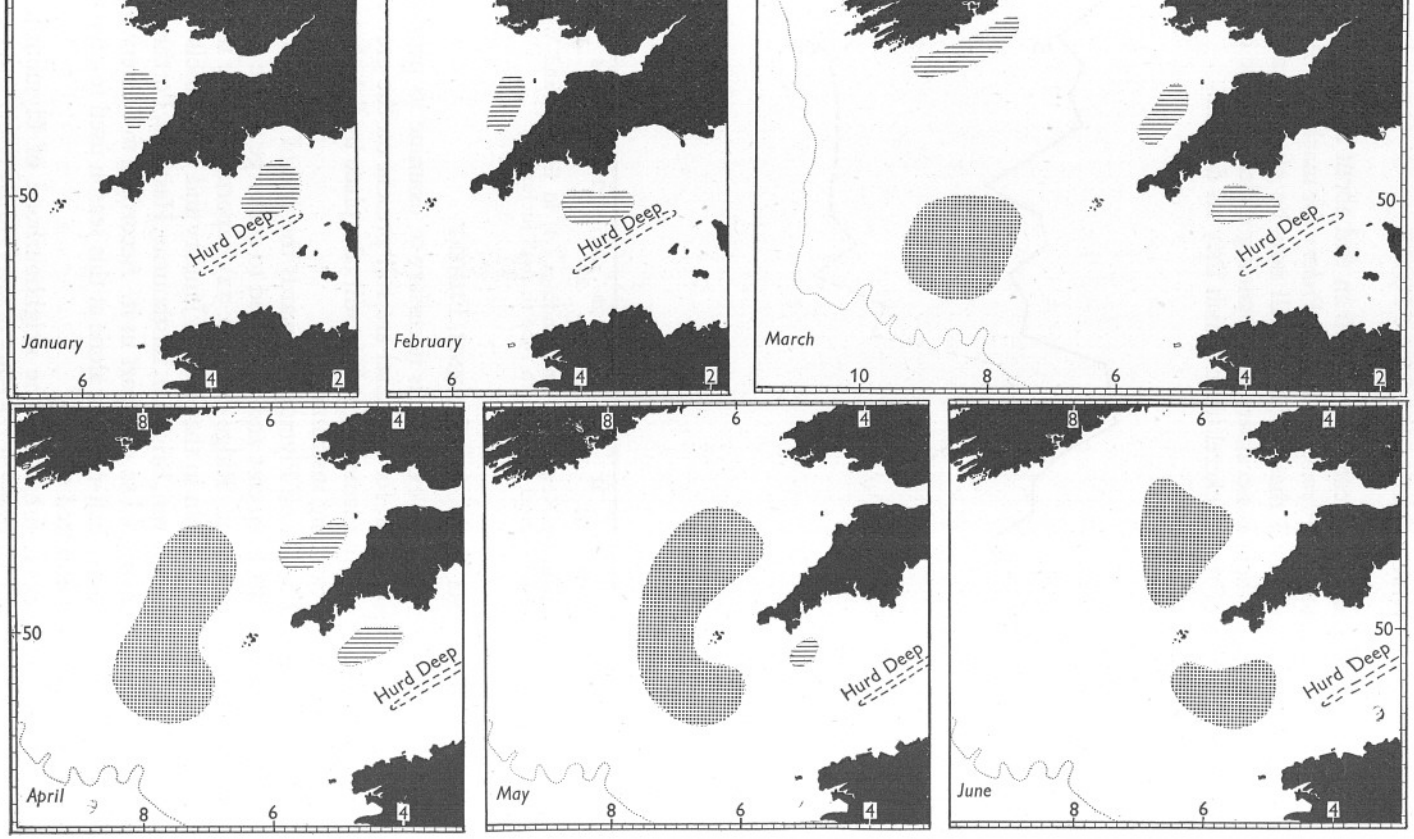

Fig. 3. Generalized charts showing times of fishing for mackerel in different parts of the English Channel and Celtic Sea.
Hatched areas, inshore fisheries; *stippled* areas, deep-sea fishery (*vide* pp. 519–24). The 100-fathom contour is indicated by a dotted line.

Calderwood constructed a series of monthly charts showing as nearly as possible the kinds of fish caught during each month and the positions of the grounds being worked. From these reports, and from conversations with some of the old fishermen who were active at that time, one finds that in January fishing for mackerel took place on grounds to the eastward of Plymouth, generally from 10 to 30 miles south to south-west of Start Point. As the season advanced the fish had to be sought progressively farther and farther to the westward. By the middle or end of March the fleet would be working from 10 to 30 miles southward from the Eddystone lighthouse (i.e. 20–40 miles to the seaward of Plymouth). By May the best catches were generally to be had on grounds still farther west, and the Plymouth fleet sometimes went as far as 40 miles south-west of Lizard Head before terminating the season's fishery. The time at which this occurred varied from year to year, but was seldom if ever later than the middle or end of May. When this happened many of the east coast boats returned to their home ports to fish no more for mackerel until another 'west-country season' came round. But some of them, together with the west-country boats, proceeded to Newlyn and other Cornish ports to carry on fishing from there on the deep-sea grounds to the westward of the Scilly Islands (*vide* p. 522). This sequence of events in the Plymouth fishery is summarized in Fig. 3 in which the hatched area in the English Channel indicates the extent of the fishing ground and the gradual shift of the fishery from its eastern end in January to its western extremity in May.

It should be noted that these west-going shoaling fish never approach really close to the land, but always remain at some distance from it. This is in marked contrast to what happens when mackerel reappear in the Channel in June after the shoals have broken up (*vide* p. 524). The fish then appear hard by the beaches and in creeks and harbours all along the shoreline in the very shallowest water.

The Newlyn Inshore Fishery

This fishery is confined to inshore grounds along the north Cornwall and north Devon coast. On these grounds, extending roughly from 20 to 50 miles north-north-east of the Longships Lighthouse (Land's End), fishing in normal times begins in December or early January and continues for 3 or 4 months. At the beginning of its season the best catches are to be expected well to the northward and then progressively farther southward as the season advances. The hatched area to the north of the Cornwall-Devon peninsula in Fig. 3 indicates the extent of this fishing ground and the gradual shift of the fishery from its northern end in January to its south-western extremity by about April.

The sequence of events in this area should be carefully compared with that on the fishing grounds in the English Channel (also shown on this chart and already described) and their similarity noted.

The Newlyn Deep-Sea Fishery

The modern great spring mackerel fishery from Newlyn opens in March (Fig. 3) on grounds right out in the open Atlantic far to the westward of the Scilly Islands. It is a drift fishery carried on by steam drifters of the familiar herring-drifter type which come to this port from the east coast ports of Yarmouth and Lowestoft.

Although fishing begins in the first days of the month, it is usually somewhere about the middle of March before the fleet falls in with the main shoals. While the search for them is going on, some of the boats try their luck hard by the Irish coast to the south-west and south of Ireland. From 10 to 20 miles south to south-west of Fastnet Rock and about the same distance off Galley Head and the Old Head of Kinsale are the most favoured localities; and good catches are sometimes made there, but for only a very short time at the beginning of the season (Figs. 3 and 4 A).

The charts in Fig. 4 have been prepared to show the locus of this fishery as indicated by the activities of ten drifters out of a total fleet of twenty-four in 1938—a typical year. The information upon which the charts are based was derived from log-book records kept by each vessel. Every shot made by each of the ten drifters throughout the season is indicated by a dot in the position in which it was made. The fishing of these ten vessels is fully representative of that of the total fleet and gives a true picture of the changes in the locus of the fishery as the season advanced.

It will be seen (Fig. 4 A) that during the first fortnight of March—the opening fortnight—there was only limited fishing, concentrated chiefly near the south coast of Eire. A few exploratory tries were also made over a widely scattered area to the westward of the Scilly Islands. This 'scatter' indicates the absence of good fishing in that locality as yet. By the second half of March (Fig. 4 B) fishing is in full swing with the area of chief fishing intensity located from 70 to 100 miles west to west-south-west of the Bishop Rock, Isles of Scilly. During the first half of April (Fig. 4 C) the best fishing still persists in approximately the same place but slightly less distant. A few tries were also made on northern grounds about 70 miles north-north-west of the Longships (Land's End), but failed to find many fish. By the second half of April (Fig. 4 D) the locus of chief fishing intensity had moved to these northern grounds, all the vessels having for the time being forsaken the 'southern' grounds. During the first half of May (Fig. 4 E) good catches were being taken to the westward of Scilly, but considerably closer to land (i.e. farther to the eastward) and on a slightly more southerly bearing. After the middle of the month (Fig. 4 F) most fish were encountered still farther in towards the mouth of the English Channel, and, being productive of good catches, attracted most of the fleet to this locality. During the first half of June (Fig. 4 G) fish were being caught both to the northward of Scilly and southward from Mounts Bay, the northern

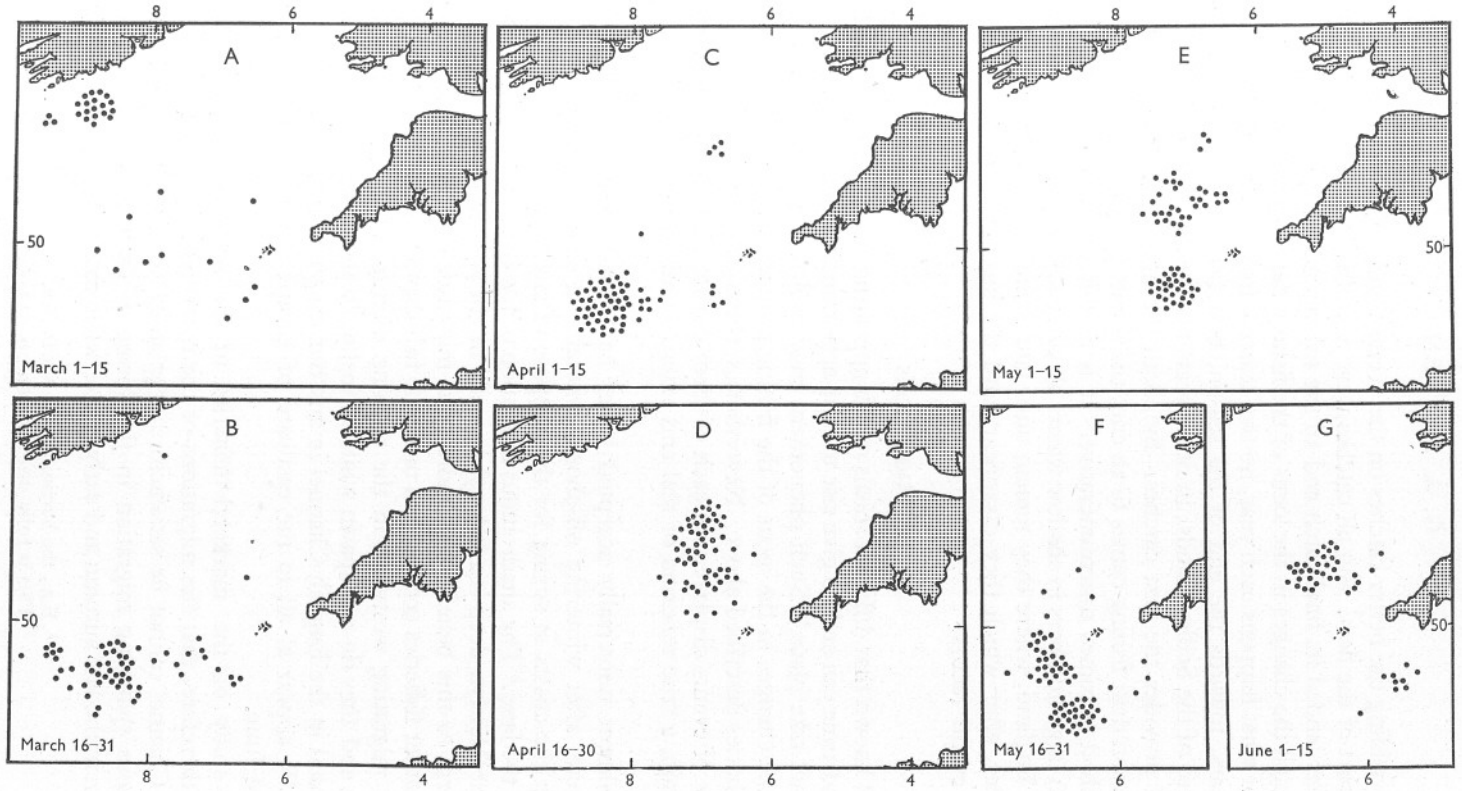

Fig. 4. Locus of mackerel fishing in 1938 by Newlyn-based steam drifters; A, in the first half of March; B, in the second half of March; C, in the first half of April; D, in the second half of April; E, in the first half of May; F, in the second half of May; G, in the first half of June. Each dot represents a 'shot' by one of ten selected drifters.

locality yielding the better catches on the average and therefore attracting the greater part of the fleet. But all catches were now dwindling; on 15 June the last drifter landed its final catch and all the fishing stopped.

Although the changes in the locus of the fishery depicted in Fig. 4 A–G are typical of what happens each year, no two seasons are ever quite the same. In some years, towards the end of the season, best fishing is obtained to the northward of the Scilly Islands; in other years the western end of the English Channel provides the best catches. By about the middle or end of June in every season drift fishing comes to an end, the shoals having so dispersed that this method becomes unremunerative. It is at this time that the mackerel appear in large numbers in shallow waters all along the shores of southern and western England, where they remain until late September, October, or even November, after which they disappear until the next year when the whole cycle of events recurs.

Migrations

It is well known that different shoals of fish appearing in orderly succession in space and time can and do give rise to false appearances of migrations that do not in fact take place.[1] Such phenomena may well underlie, to some slight extent, the changes in the locus of the fishing grounds shown by each of the three fisheries described above. Nevertheless, there can be no doubt that the sequence of events displayed by each of them during its respective season is, in the main, a true reflexion of real and extensive migrations by large bodies of fish.

The almost universally accepted belief has always been that mackerel everywhere, after wintering off-shore, generally in some unknown locality, approach the coasts in spring for the purpose of spawning in shallow water close by the land.[2] The anadromous migration of the large shoals of fish upon which the Newlyn deep-sea fishery depends might appear at first sight fully to conform to this belief; the catadromous migrations of those that support the two other fisheries certainly do not. The fish that are found in the English Channel migrating westward in the opening months of the year disappear offshore, and they do not spawn while in inshore waters. Mackerel eggs are never found in the English Channel in any but insignificantly small numbers and hardly appear at all to the eastward of Lizard Head before about the middle of June.

Close study of the mackerel fisheries in the south-west of England reveals, therefore, that the migrations of the mackerel in the Celtic Sea and English Channel cannot be satisfactorily explained simply by postulating an anadromous spawning migration in the spring of each year and a reverse migration in the late autumn and early winter when mackerel largely disappear

[1] E.g., the herring in the North Sea.

[2] This is fully discussed on pp. 532–4.

from inshore surface waters. Still less will this explanation suffice in the light of the knowledge we now possess that in all this wide region there is only one important spawning ground lying far out to the westward of the English coast. This spawning ground has been surveyed in detail and the results described elsewhere by Steven & Corbin (1939) and more fully by Corbin (1947). From the information contained in those papers a generalized diagram has been

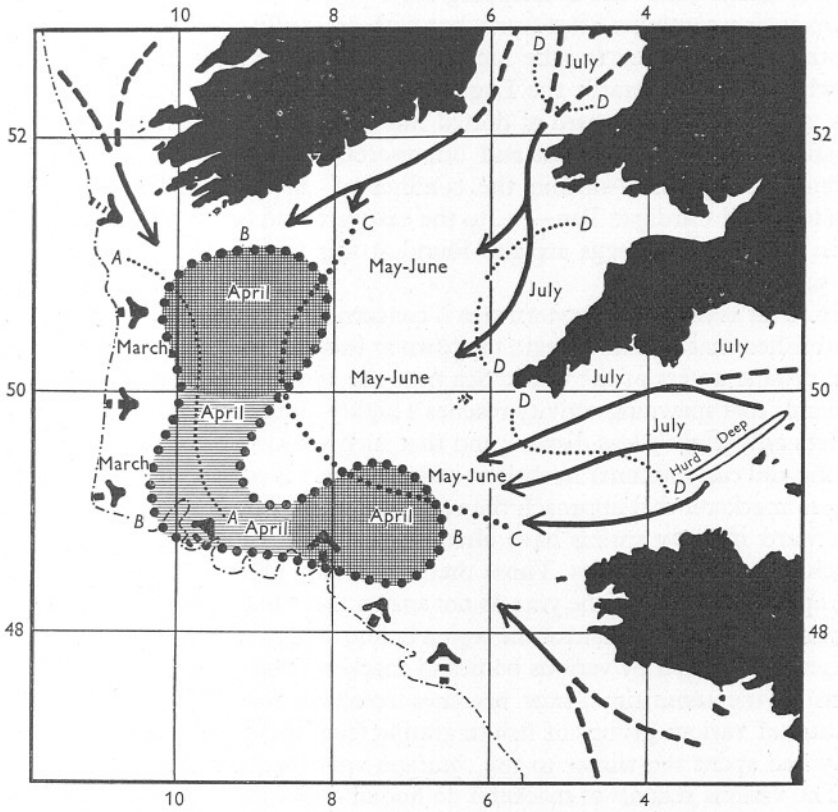

Fig. 5. Generalized diagram indicating the migrations of the mackerel in the English Channel and Celtic Sea in relation to the spawning ground. For further explanation see text, pp. 525–6. ·–·–·–· = 100-fathom contour.

prepared (Fig. 5), from which can be seen at a glance the location of this spawning ground and its relation in space to the mackerel movements revealed by the three commercial fisheries described above.

Spawning on a small scale begins as early as March to the westward of the dotted line *A* in Fig. 5—i.e. in the vicinity of the 100-fathom contour which, in that area, closely follows the outer edge of the great continental plateau lying to the south of Ireland. The greatest intensity of spawning takes place in April in the area enclosed by the dotted line *B*. Within this area there are

two sub-areas (darkly stippled in Fig. 5) of maximum egg density—one situated from 40 to 100 miles south of Fastnet, and the other from 50 to 80 miles south-west of the Scilly Islands. It will be seen that these two sub-areas are situated opposite and to seaward of the entrances to the Irish Sea and the English Channel. It may well be that they represent two distinct spawning grounds that meet and overlap, and whose boundaries cannot be distinguished where the overlapping takes place.

Spawning continues after April, but with gradually decreasing intensity, for another 3 months or so, the locus of spawning activity moving the while slowly eastwards towards the English coast. In May and June all spawning has ceased to the westward of dotted line *C*. By July such meagre spawning as still continues is residual and unimportant and is confined to the close vicinity of the land—within the confines of the English Channel, Bristol Channel and Cardigan Bay—i.e. to the eastward and landward of dotted lines *D* in Fig. 5. A few eggs are also found at this time in the Irish Sea (Scott, 1913, 1914*a*, *b*).

In so far as the south-western area is concerned, therefore, it is now definitely established that mackerel begin to spawn at least as early as March in the deep and distant waters of the Celtic Sea near the 100-fathom line to the south of Ireland; that spawning activity reaches a highly intensive maximum in April in waters only slightly less distant; and that such spawning as continues into late spring and early summer in shallow inshore waters is residual and unimportant. Those mackerel that approach the south-western shores of England from the westward in early spring have already got rid of most of their eggs before reaching inshore localities. Those that are already present in coastal waters in the opening months of the year do not spawn there but migrate offshore to the common spawning ground of the region before doing so. The apparent anomaly hitherto presented by various bodies of mackerel migrating in different directions at the same time, now becomes resolved, therefore, into the simple picture of various groups of fish migrating from the different places in which they had spent the winter to the common spawning ground of the region.

The various schools of mackerel do not all arrive in the spawning region at the same time. This gives rise to the decided 'spread' of spawning activity in both space and time. Another contributory factor is that in this species the eggs mature in successive batches that are spawned one after another during an extended spawning period. Ripe translucent ova appear in the ovary distributed widely and irregularly amongst the still unripe yellowish ova, producing a peculiar, speckled appearance that for lack of a better term has been called the 'plum pudding' stage. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, may show no trace of ripe eggs. Unless opened up such an ovary can be, and often has been, described as 'unripe'. In the mackerel, in fact, a fully ripe ovary is never present; the most that is ever found is an ovary containing some ripe eggs. Cunningham (1889,

p. 25) was therefore in error in thinking that the ovaries and testes of all adult mackerel ripen rapidly and simultaneously and that 'all the reproductive products in a given fish are matured and shed within a short space of time'.

The important question now arises, where do the mackerel come from to this Celtic Sea spawning ground? It seems clear that many, perhaps even the majority, must have been in offshore waters prior to March, since we now know that some of them are already spawning at that time in the vicinity of the 100-fathom line (Fig. 5). Although definite proof is at present still lacking, there is good reason to believe that these fish had come out into deep water during the autumn of the previous year, at the time when they are known to disappear from the surface waters inshore. But where did they spend the ensuing winter? Before providing an answer it is convenient to consider first those other fish which, unlike the majority, do not move outward and westward into deep water in the autumn but spend the winter months on or near the sea bottom in shallower places nearer land—e.g. along the edge of the Hurd Deep some 40 miles south-east to south-south-west of Start Point (Cligny, 1905, 1912; Bullen, 1908), along the southern side of the Vergoyer Bank near Boulogne, and around the numerous small scattered sand banks in the vicinity of Dieppe (Cligny, 1905; Le Gall, 1935). Of the northern fish, numbers sojourn during the winter months on the bottom around the Smalls and Saltees, and are fished from there, particularly by French trawlers (Le Gall, 1928, 1935). At this time these fish are truly demersal and can be caught on the sea floor by commercial trawlers specially equipped for the purpose.

It is not clear what the conditions are that attract the mackerel to certain restricted situations on the sea bed in winter. The only feature that can be detected as common to all of them is an interruption in the level of the sea bed caused by banks or gulleys. There is no uniformity of depth and none of temperature. Mackerel fished along the edge of the Hurd Deep are taken in about 40 fathoms; around the Vergoyer Bank in 12–18 fathoms; in 11–14 fathoms around the Dieppe Banks; and in 30–50 fathoms in the Smalls and Saltees areas. It seems likely that associated with these unevennesses in the sea bed there must be some condition of turbulence—slight perhaps—that is all-important for the mackerel. Although the presence of well-defined mackerel shoals (such as those of the Hurd Deep, Vergoyer Bank and the other localities mentioned) cannot be recorded with absolute precision around the many declivities and acclivities on the floor of the Celtic Sea, mackerel are regularly trawled from various parts of it.

The winter habits of the mackerel, therefore, are now seen to fall into one coherent pattern and the inconsistencies that puzzled earlier writers arose simply through inadequate knowledge. The general statement that the mackerel is a pelagic and migratory fish must be modified. The adult mackerel, at any rate in the English Channel and Celtic Sea, is pelagic and migratory only during a portion of the year. In the other part it is demersal. During the first

portion of its demersal period it packs densely in restricted areas and is non-migratory. This was first noted by Cligny (1905, p. 99), who states that these bottom shoals are so dense and so sharply delimited that of two trawlers working side by side one will have a large catch of mackerel and the other none. This is also referred to by Bullen (1908, p. 283), and has been confirmed by old fishermen who participated in some commercially unsuccessful trawling experiments for mackerel from Plymouth.

The fortunes of the fishery reveal that this strongly delimited, densely packed phase of the bottom-living period lasts only for a short time—2 or 3 months at the most. Thereafter the concentration spreads outward in one or more directions from its focal point. In so doing the fish still remain in packs, but of more normal density, the extreme compactness of the first bottom phase having been lost. The Hurd Deep fish, for example, after remaining stationary in a restricted area along its edge until about January, then spread in a north-westerly direction towards Start Point and the Eddystone, where they are caught by French trawlers until the month of March or April.

During the years 1936–39 the Plymouth Laboratory's research ship *Salpa* and a local steam trawler caught 753 mackerel in nine small lots during January–April in an ordinary otter trawl towed very fast on the bottom in the Lizard–Start Point area. The positions of capture (shown as a composite diagram in Fig. 6) of even those few catches indicate a westerly spread of the fish on the sea floor in those early months of the year.

It is during this slow dispersal phase that the change-over from demersal to pelagic habit takes place. Not all at once, but successively, shoal after shoal rises to the surface, and, after they have done so, the spring migration to the spawning ground takes place.

The presence of the Plymouth drift fishery for mackerel off Start Point and the Eddystone in the early months of the year is thus easily understood. The fish that spend the earlier winter months in the vicinity of the Hurd Deep come to the surface in that area and then make their way 'down channel' on a spawning migration to the spawning grounds in the Celtic Sea. Likewise, the fish that winter by the Smalls spread southward across the mouth of the Bristol Channel before rising and continuing their way for some distance parallel to the Cornwall coast and then turn westward to the spawning grounds. On these fish the mackerel drift fishery of the North Cornwall coast in early spring depends. The Saltees fish, and perhaps others that have wintered to the westward of the St George's Channel, spread westward parallel to the Irish coast before rising and turning southward towards the spawning grounds, thus providing the catches close to the Irish coast in the early months of the year (*vide* p. 522).

It seems unlikely that all of the vast mackerel population of the whole south-western area can find room to winter hard by the slopes of the Hurd Deep and the various banks and shoals that have been mentioned. Doubtless

some are present also in other inshore places (*vide* Green, 1894, pp. 357–8); but even so, it seems certain that the vast majority must go farther afield to find similarly suitable conditions. This involves a return to the bottom of the Celtic Sea with its numerous banks and knolls, and it is significant that mackerel are regularly caught by British steam trawlers in their vicinity. It may well be that even those slopes also are not sufficient in number and extent

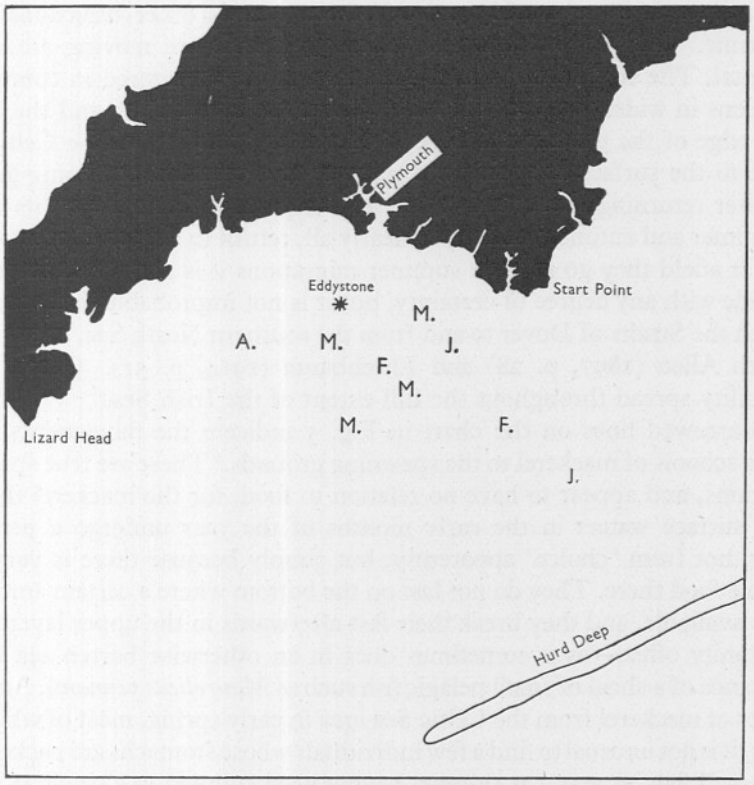

Fig. 6. Chart of area Start Point to Lizard Head. Letters indicate positions in which mackerel were captured on the bottom by two Plymouth vessels during the years 1937–39. J = January; F = February; M = March; A = April.

to accommodate the whole population and that many fish have to seek the declivity of the continental slope in order to pass the winter in the conditions they require. That mackerel should spend the winter months hard by the outer edge of the continental plateau is entirely consistent with their known habit elsewhere of concentrating where there is an interruption in the level of the sea bed.

Although absolute proof is lacking, it appears to be a fully justifiable assumption that these mackerel, acting in conformity with what is now known

of their fellows, spread inwards over the outer fringes of the continental plateau in the opening months of the year and then, rising from the sea floor, form part of the great pelagic shoals that migrate eastwards in the Celtic Sea and spawn there in the early spring before continuing their landward journey. In other words, that part of the sea floor from which they approach the spawning ground happens to be to the westward and seaward of it. Other fish, that wintered near other suitable acclivities and declivities nearer the coast-lines, approach the spawning grounds from various other directions at the same time. But the directions in which the shoals are moving are merely incidental. The significant point is that they all have wintered in comparable conditions in widely scattered localities, from the Hurd Deep and the Smalls to the edge of the continental slope at the outer boundary of the Celtic Sea; all rise to the surface in spring and migrate to a common spawning ground, thereafter returning shorewards again and dispersing along the coasts during the summer and autumn; and all, or nearly all, return to the sea floor in winter. How far afield they go in their summer migrations it is at present impossible to decide with any degree of certainty, but it is not improbable that some pass through the Straits of Dover to and from the southern North Sea, as suggested by both Allen (1897, p. 28) and Ehrenbaum (1914, p. 51). Others in all probability spread throughout the full extent of the Irish Sea.

The arrowed lines on the chart in Fig. 5 indicate the movements of the various schools of mackerel to the spawning grounds.[1] These are true spawning migrations, and appear to have no relation to food, for the mackerel that rise to the surface waters in the early months of the year undergo a period of fasting, not from 'choice' apparently, but simply because there is very little available food there. They do not fast on the bottom where a certain amount of food is available, and they break their fast afterwards in the upper layers when opportunity offers—as it sometimes does in an otherwise barren sea by the appearance of a shoal of small pelagic fish such as *Maurolicus pennanti*. Amongst samples of mackerel from the Celtic Sea area in early spring, most of which are fasting, it is not unusual to find a few individuals whose stomachs are packed with those small fish, as many as thirteen having been counted in a single stomach.

Of the 753 mackerel caught between 1936 and 1939 on the bottom between Lizard Head and Start Point (p. 528) 67 % contained considerable quantities of food consisting chiefly of small fish and Euphausiids (*Nyctiphanes couchii*).[2] On the other hand, 600 pelagic fish caught by drift net in the Celtic Sea in the months of March[3] during those years contained food in only 43 % of the stomachs and then only in very small quantities, apart from a few individuals that had gorged themselves with *Maurolicus pennanti*.

[1] Broken lines indicate movements that are as yet presumed and not proved.

[2] One stomach contained seventy-three individuals of this species plus unidentifiable crustacean remains.

[3] No drift net samples were examined in January and February.

Over the course of one full year, therefore, the life of most adult mackerel in the south-west region appears to fall into two main periods, a demersal period and a pelagic period, with a brief transition period during which the fish return to the bottom and reform shoal.[1] This can conveniently be summarized as follows:

1. DEMERSAL PERIOD

(i) *Compact phase*

Intensely dense and extremely circumscribed concentrations of fish massed on the sea floor in very localized positions distributed over wide areas.

November, December

(ii) *Deployment phase*

Concentration diminishes; still keeping to the bottom the fish spread slowly outwards over adjacent areas before ascending to the upper waters and giving rise to pelagic shoals.

December, January, February

2. PELAGIC PERIOD

(iii) *Shoaling phase*

Active migration of the shoals to the spawning grounds and return (or continuation) shorewards.

January–July

(iv) *Dispersal phase*

Shoals broken up and fish dispersed in inshore waters around all coasts.

June–October

3. TRANSITION PERIOD

(v) *Reconcentration phase*

Disappearance from surface waters and return to phase (i).

October, November

During phase (ii)—the deployment phase—the fish appear to perform small diurnal vertical movements, rising from the sea floor during the night and descending again during the day. Trawling during this phase is therefore most successful during daylight hours (Bullen, 1908, p. 283).

DISCUSSION

In the light of this new information concerning the habits and migrations of adult mackerel in the south-western region it is instructive now to examine what is known of their movements and behaviour in other places.

[1] These changes do not take place everywhere simultaneously, so there is no period of the year during which at least a few scattered schools of pelagic mackerel cannot be found.

With regard to mackerel in all the European seas Allen (1897, p. 25) makes the general and comprehensive statement that 'the first approach of the mackerel to the coast in spring or early summer is for the purpose of spawning' and adds the interesting comment that 'the advantage to the species of the young fish being hatched out near the shore where the smaller forms of pelagic organisms are present in abundance and the plankton is increased by the numerous larval forms of those species which inhabit coastal waters, is obvious'.

With special reference to the Celtic Sea and the English Channel area Allen (1897, pp. 12, 17) mentions the presence of fish 30–40 miles from land between Start Point and Plymouth in the months of January to March, at the same time giving the end of March or early April as the time of the approach of the main shoals 'towards the southwest coasts of Ireland and the west coast of France'. He makes no attempt to explain the presence of mackerel so far up channel in winter and early spring while the main shoals are still far away to the westward. Ehrenbaum (1914, p. 13) also states that the great majority of English Channel mackerel appear to arrive in early spring from the adjacent waters of the Atlantic. He attempts to explain the presence of mackerel far up the channel long before the main shoals arrive by suggesting that 'the mackerel sometimes move, in great numbers, still keeping to deep water, far eastward, into the Channel', before rising to the surface. This author, too, believed that mackerel everywhere move in towards the coasts in spring to spawn (1914, p. 17) and gives the months of May, June and July as 'the true spawning time' in both European and North American waters. Much emphasis is placed upon this uniformity of spawning in such widely distant regions. Only in the Mediterranean is the spawning time stated to be 2 months earlier. In a footnote Ehrenbaum (1914, p. 75) makes only passing reference to an important statement by Rathbun, quoting Hardin (1896, p. 81) who found in the New York market mackerel taken on the 17 April some 65 miles south-east of Cape Henry, that were already spent. This observation is possibly of much more importance than Ehrenbaum attaches to it and may indicate much earlier spawning than has been ascribed to mackerel in those waters (cf. p. 535, *infra*).

Meek (1916, p. 320), also in a general statement embracing all mackerel (*Scomber scombrus*), says that 'the spawning migration is an anadromous one', that the season is May to July, and that spawning takes place when they arrive in coastal water (*op. cit.*, p. 326).

Although, as we now know, these general statements concerning the mackerel do not hold good in the English Channel and Celtic Sea, it is significant that, in the North Sea, they are partly true. In that area by far the largest number of mackerel eggs have always been found on the Norwegian side of the Skagerrak very close to the south coast of Norway (Ehrenbaum, 1914, p. 18), and at its inner end off the Swedish coast from Väderöfjord to Hallö and Paternoster 'and thence diagonally across to the Skaw' (Ehrenbaum, 1923, p. 11). Here, without doubt, is a shoreward migration to spawn, chiefly in

the months of May, June and July. But it should be noted, by reference to a chart of the eastern North Sea, that *although the migration is shoreward from adjacent offshore waters, it is at the same time a migration from shallower water to the vicinity of the* 100*-fathom contour*.

There is thus a very close similarity between what we now know to be the chief spawning locality of the south-western region and that of the North Sea area. Both lie close to the 100-fathom line. In both areas this contour closely follows the edge of a well-marked slope in the sea bed from shallow to deep water—i.e. to the depth of the Atlantic Ocean in the Celtic Sea; and, in the Skagerrak, to the lesser but, nevertheless, considerable depths (over 400 fathoms) that are present there and which are not found anywhere else in all the North Sea region.

There is the further similarity that mackerel eggs are found, but in much smaller numbers, widely distributed over adjacent parts of the North Sea and the Kattegat (Buchanan-Wollaston, 1911, p. 218). Ehrenbaum has shown that in the North Sea, too, during the colder season of the year, from November till about May, great numbers of mackerel are present on the bottom chiefly around the Great Fisher Bank and northwards to the Viking Bank along the edge of the Norwegian Channel (1912, p. 4; 1914, p. 36). He also points out that the trawl catches of these fish over the different months of the year 'seem to indicate that the mackerel taken in winter are for the most part identical with the shoals which in spring appear on the coasts of the North Sea and Skagerrak in order to spawn' (1914, p. 36).

What we now find, therefore, is that after spending the winter months on the sea floor in the vicinity of the slopes produced by banks and gulleys, the mackerel in both the North Sea and south-western areas migrate to certain restricted spawning grounds in the vicinity of the 100-fathom line. It so happens that in the North Sea this contour lies close to the Norwegian and Swedish shores. This brings about the anomalous result that mackerel migrating from the shallow waters of the North Sea to spawn in the deep waters of the Skagerrak, and, to a lesser extent, in other Norwegian Fjords farther north, are, nevertheless, at the same time also migrating shorewards. That is to say, that most of the mackerel in the North Sea, like their brethren in the English Channel and Celtic Sea, migrate from their winter quarters to deep water to spawn; that in the North Sea this deep water happens to lie close in by the shore whereas in the south-western region it lies far out in the Celtic Sea, a long way from the land.

It is this apparent anomaly that hitherto has led to such confusion in trying to interpret the migrations of the mackerel. The coincidence that the deep water they favour happens, in the North Sea, to lie hard by the land, and that this was the first spawning ground to be investigated has given rise to the belief that all mackerel migrate shorewards to spawn. The fact that mackerel eggs are never found except in comparatively small numbers near the shore around

the south and west coasts of England should have led to at least a suspicion that this did not hold good there. But with only one remarkable exception this suspicion seems never to have arisen in anyone's mind. The exception was a very enlightened fisherman, Matthias Dunn of Mevagissey, Cornwall, who, in 1893 (p. 3), stated quite definitely that the spawning grounds of the mackerel in the south-west region 'are in those waters covering the plateau of ground within the two-hundred-mile limit of our western and south-western shores, known to our sailors as about or within soundings'. This remarkably accurate statement is not even mentioned, so far as I can ascertain, by any subsequent investigators. Perhaps they had never come across it; or perhaps (more likely) they considered it to be too preposterous for serious consideration. Day (1880–84, p. 85), however, appears to have retained an open mind on the subject, for he says that at certain seasons mackerel approach the shores in countless multitudes 'either prior to, during, or after breeding'.

Respecting the migrations of the mackerel on the western side of the North Atlantic there existed for a long time two very well-defined schools of thought. One held that the mackerel undertook extended migrations both to and from deep water well offshore, and also along the shore, when this was reached, in a south to north direction (Brown Goode, 1879, p. 63). Other investigators and observers (quoted by Brown Goode, 1879, pp. 56 *et seq.*)[1] held that the mackerel spent the winter on the sea floor, not very far from their summer haunts, where they lay in a comatose state either on or even partly embedded in the bottom mud or sand. These apparently opposing views were, in fact, held by American and Canadian workers respectively and were fiercely debated in a controversy concerning American rights to fish in Canadian waters. The American argument was that, since the shoals moved northward from American to Canadian waters, American fishermen were entitled to follow them thither. The Canadians held that, on the contrary, such migrations did not take place and opposed the American claim to a right to fish in their waters.

Each side provided some useful evidence in support of its claim. The American view was supported by the northward movement of the fishery. Canada depended mainly on rather fanciful 'eye-witness accounts' of mackerel being seen on the bottom in a torpid state in winter months, and on the more reliable fact that mackerel occasionally could be caught by nets on the bottom near the shore in winter. Brown Goode himself (1884, p. 102) more or less admits the claim that mackerel are not infrequently found in the stomachs of cod and halibut taken on and near the bottom on George's Banks in the winter season, and Collins (1883, p. 274) reported that in late February, 1882, many mackerel were taken in the stomachs of cod that had been caught near bottom some 10 miles off Egg Harbour, N.J., in 12–15 fathoms of water. Summing

[1] The very early Canadian publications by W. F. Whitcher and Henry Youle Hind have not been available to me for direct consultation.

up, Brown Goode conceded rather grudgingly that 'it is by no means demonstrated that certain schools of mackerel do not remain throughout the year in waters adjacent to the coasts of Canada' (1884, p. 96). Nevertheless, he considered such cases to be quite exceptional and held firmly to the conviction that the weight of available evidence was overwhelmingly in favour of those who held that the mackerel make extensive migrations along the coasts, in addition to returning to deeper parts of the ocean on the approach of winter.

As more information became available, however, the views of both parties became so modified that Bigelow (1925, p. 192) was able to state that 'scientific opinion has gradually crystallized to the effect that the essential features of the seasonal migrations of the mackerel are essentially a spawning journey inshore and into shallow water in spring alternating with an offshore movement combined with a descent into deep water in autumn'. He then adds that, according to geographic conditions, these 'fundamental changes of situation' are accompanied by horizontal journeys of greater or less length and in various directions. According to this author (1925, p. 206) mackerel spawn off the North American coast from the latitude of Cape Hatteras (35° 15′ N.) to the Gulf of St Lawrence, where the heaviest spawning along the whole coastline takes place, closely followed by the Gulf of Maine, especially in the Massachusetts Bay area. In the latter region the chief spawning season is said to extend over the last half of May and the month of June; in the Gulf of St Lawrence spawning activity reaches its maximum a month later in the latter half of June and the first two weeks of July.

Although exact comparisons are impossible because of the different methods and gear used for collection, it may be significant that the records of mackerel eggs obtained in both those regions (Bigelow, 1925, p. 206; Dannevig, 1918, p. 8; Sparks, 1929, pp. 445–450) reveal widespread distribution of eggs in comparatively shallow coastwise waters in numbers that appear to be comparable with those obtained by Corbin in the Celtic Sea to landward of the main spawning centres after maximum spawning intensity had passed. If this indeed be so, much importance must be attached to Bigelow's further statement (1925, p. 207) that, in the Gulf of Maine region, egg records from offshore localities, though extremely scanty, nevertheless clearly indicate that spawning takes place in the vicinity of some or all of the many banks that lie well offshore and over deep water[1] as well as in the shallow coastwise waters of the inner parts of the Gulf.

The evidence so far available, therefore, appears to point very strongly to the probability that the habits and migrations of the mackerel on the western side of the North Atlantic will, on further investigation, be found to be very

[1] Bigelow appears here to be referring to depths of less than about 180 fathoms, the deepest soundings found in the various deeps and basins of the Gulf of Maine which is the oceanic bight between Cape Cod and Cape Sable. He adds (1925, p. 209) that 'there is no reason to suppose that they ever breed outside the continental slope', the edge of which, in that region, follows more or less closely the 200-fathom contour.

similar to those of their European kin around the south-west of England and in the North Sea. The existence of hitherto undiscovered, restricted spawning centres of high spawning intensity, probably in the vicinity of the 100-fathom line perhaps as early as April in both the Gulf of Maine and the Gulf of St Lawrence, seems highly probable; and examination of the charts of the two regions suggests that they are well suited to the needs of the mackerel as revealed by our recent researches in the English Channel and Celtic Sea.

Although the migrations of the adult mackerel in the English Channel and Celtic Sea have now become clear, the migrations of the young and immature fish are still obscure, but mention must be made of what little we do know concerning them. Corbin (1947, pp. 73–76) has shown that the larval and post-larval stages, as would be expected, are numerous on the spawning grounds for a short time after the eggs have hatched out; thereafter, they disappear from catches and little is known concerning them. During our investigations the largest post-larva captured in these waters was 21 mm. in length caught in the month of June.

But small mackerel, of from about 13 to about 17 cm. in length, appear in some years in bays, harbours, and estuaries around the south-western shores of England for a short period in early autumn. In 1926 small fish appeared in Plymouth Sound in August and several were caught in sprat nets, their size ranging from 13·0 to 17·2 cm. in length (mean length of all fish 15·3 cm.). In 1927 small mackerel again appeared in the bays and estuaries around the Devon and Cornwall coasts. Fifty of them caught in a sprat seine during August had a mean length of 13·6 cm., the total range being 12·5–15·2 cm. In 1937, 273 small mackerel caught at Newlyn on 4, 6, and 7 August had a length range of 8·0–16·4 cm. with a mean length of 12·7 cm. Those fish first appeared in the middle of July and remained inshore until nearly the end of September. They were present in very large numbers—so much so that reports of their presence in such abundance were at first disbelieved. Many Newlyn fishermen were very definite in their assertions that they had never seen mackerel of such small size before.

Their appearance, in fact, in inshore waters in this region, takes place only at long and irregular intervals. Nor are they found with any greater frequency elsewhere in British waters. The Scottish Fishery Board[1] records the capture of small mackerel on the bottom in a small-meshed covering of the cod end of an otter trawl in September and November 1929; September and October 1930; September and October 1932; August, September and October 1933; August 1935; and in September 1936.

There are no records in the Board's log-books of any catches of these small sizes in 1927, 1928, 1931, 1934 and 1937.

The capture of small mackerel is not to be expected in an uncovered trawl, but Hickling,[1] while fishing for hake off the west coast of Ireland, has come across them in the stomachs of hake and certain other fishes. Ehrenbaum

[1] Private communication.

(1923, pp. 19 *et seq.*) gives details of the capture of small mackerel in the North Sea by several workers of different nationalities in the late summer and autumn. Malm (1877, p. 409) mentions a great shoal of small mackerel that appeared in the Skagerrak, near Christenburg in the Gullmarfjord, on 27 July 1872. They were so small that they all escaped through the meshes of ordinary seines and only ten could be obtained for examination. These fish were between 67 and 100 mm. in length. To the fishermen of the district such small mackerel had until then been entirely unknown so that, as on the Channel coast of England, they must arrive only on rare occasions at long intervals.

From the information available, therefore, meagre and incomplete though it be, it is evident that juvenile mackerel, like the adults, are present at times on the sea floor and at other times in the upper layers of the sea. Their appearance in some years in huge numbers in inshore waters for a few weeks in summer and early autumn reveals that they also carry out migrations, but the fact that they do not appear around the shores every year suggests that those migrations, in the main, are less extensive and less regular than those of the adult fish.

One cannot but conclude, therefore, that the migratory behaviour of young mackerel may be very similar to that of the adults; that they seek bottom in the late autumn and winter and rise again to the upper layers in due season. As they so seldom come inshore, it would appear that their horizontal migrations are, as a rule, less extensive than those of adult fish. As they grow and approach maturity, those migrations must approximate more and more closely to those of the adults until at last, when they reach maturity, they join the spawning shoals and migrate with them.

Summary

In the English Channel and Celtic Sea mackerel spend the winter months on the sea floor densely packed in places where its level is interrupted by banks and gulleys.

In the early spring the fish rise to the surface and migrate to a common spawning ground that lies far out to the westward of the Scilly Islands in the vicinity of the 100-fathom contour.

The very localized positions in which mackerel spend the winter are widely distributed throughout the area in both deep and shallow water. Large schools of migrating fish converge upon the spawning ground from many directions, therefore, in the spring for spawning.

Fish that have wintered near the land must migrate *offshore* to reach the spawning ground; those that spend the winter on the bottom to seaward of the spawning ground must migrate *shorewards* to reach it. Off the south-west of England there is no single shoreward migration to spawn in shallow water as has previously been thought.

In the North Sea the chief spawning grounds of the mackerel are also near the 100-fathom contour which, in that region, happens to lie very close to the land

in the Skagerrak and along the Norwegian coast. The chief spawning migration of the North Sea mackerel is therefore towards the coast from offshore localities. This migration is, at the same time, chiefly from shallow to deeper water.

Existing information concerning the mackerel populations on the western side of the North Atlantic points to the probability that their spawning habits and migratory movements do not differ greatly from those of the mackerel in North European waters.

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THE LARVAL DEVELOPMENT OF *OPHELIA BICORNIS* SAVIGNY

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(Text-figs. 1, 2)

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INTRODUCTION

The development of the Opheliidae has hitherto been unknown. Eggs and sperm have previously been described, but the larvae have not. The most recent attempt to study the development was made by Brown (1938) at Millport, using the small species *Ophelia cluthensis* McGuire, which is abundant in the sand at a certain level in Kames Bay. He described the eggs and sperm, and obtained cleavage as far as the 4-cell stage. McGuire (1935) had previously also observed cell division up to the 4-cell stage in the same species. Many years previously Bullot (1904) did experiments on artificial parthenogenesis in an *Ophelia* and obtained swimming larvae, but did not figure or describe them in detail. Benham (1896), in a text-book, stated that the eggs of *Ophelia* are enclosed in a jelly, but it is not clear whence this statement derives.

The Opheliidae are a family of small worms, most of them burrowing in sand or mud. The distribution of the various species seems to be rather markedly localized and most species appear to inhabit only a fairly narrow range in grade of bottom soil. It seemed likely that the development might be of special interest, especially the settling reactions of the larvae. This has, on the whole, proved to be true. In this present paper the larvae are described; the experiments on settling reactions will be discussed separately.

I am glad to have this opportunity of thanking Mr N. A. Holme of Exmouth, who drew my attention to the possibility of collecting *O. bicornis* Savigny on the sand banks at the mouth of the Exe estuary. The species had been found there many years earlier by Allen & Todd (1902), but has not attracted particular attention in that locality since. Mr Holme on several occasions specially collected worms for me and forwarded them to Plymouth. At other times I collected them there myself.

METHOD

O. bicornis Savigny lives in the loose clean sand of the Bullhill Bank and of the Polesands at the mouth of the Exe estuary. I myself have collected them only on the Bullhill Bank, but Mr Holme has also visited the Polesands and found them there, also in lesser abundance in other parts of the estuary. He will subsequently be publishing an account of the fauna of the Exe estuary, and will deal with their recent distribution in detail. Here it is sufficient to say that they are most abundant about the half-tide level, which approximately coincides with the top of the Bullhill Bank.

The sand in which they live is thus uncovered for several hours each tide. They inhabit the top few inches and are easily turned up with a spade or a trowel, and can even be got by using the fingers alone, drawing them through the sand. The adult worms are a little over an inch long; mature males are white or pale cream, mature females a deep metallic green. Immature and spawned worms are pinkish. All have a beautiful iridescent sheen. In collecting they were put into large jars with quantities of sand, and in the laboratory were kept under sea-water circulation in bowls with plenty of their natural sand to burrow in. Some rough experiments indicated that they survive better when the water is drained away for several hours each day to simulate the tides of their normal environment. They could be kept up to a fortnight or three weeks, but the best fertilizations were made the day they were collected, or within a few days afterwards.

Artificial fertilizations were made by slitting open the worms, care being taken to avoid contamination with much blood. Several times, however, worms spawned naturally in the bowls and larvae from naturally spawned and fertilized eggs were found to be on the whole more virile than those from artificial fertilizations. Worms shedding eggs or sperm protruded the head and anterior segments from the sand; sometimes as much as half the body was exposed, particularly by the females; the males might show only the head and first few segments. The eggs and sperms issued from out of the hole from which the front end of the worm protruded; it was not possible to see them coming out of the body of the worm. The eggs and sperm were often ejected in 'puffs' caused by a sudden contraction of the worm into its hole. When worms in the act of spawning were removed in a dish to a microscope stage the spawning ceased and did not again start. After spawning, the hole of a female would often be surrounded by eggs loosely piled around its mouth; they were not adherent to one another; in nature the eggs would be swept away by the tidal current.

Developing eggs were kept in finger bowls, no more than sufficient to cover the bottom in a single layer being put into any one bowl. As soon as a goodly number of larvae had swum to the surface they were decanted off into a clean bowl and there reared. No food was needed, but the bowls were covered with

sheets of glass and tissue paper to keep out dust and excess light. Bowls placed near the sea-water circulation remained fairly cool in hot weather, with benefit to the larvae. At about the time of metamorphosis a little food in the form of small autotrophic flagellates and the diatom *Nitzschia* was provided.

Larvae were examined and drawn alive, scale being obtained by the use of a squared-net micrometer in the eyepiece, the preliminary drawing being made on squared paper. Bristles were drawn with a camera lucida.

Account of the Development

Ripe eggs are dark green or greenish brown in colour. When freshly obtained from the female by slitting the body wall they are generally oval plates (Fig. 1 *a*), about 150 μ long by 130 μ broad, with a clear germinal vesicle near the centre. When seen in side view (Fig. 1 *b*) there is a definite bulge in the region of the nucleus. Sometimes a nucleolus is present, sometimes it has already disappeared. The cytoplasm is thinned out at one end, giving a clearer region when viewed with transmitted light. The rim round this region is, however, thicker. The egg is closely invested in a well-defined membrane outside which there is a completely transparent and invisible jelly, several microns thick, which makes it impossible to push one egg into visible contact with another.

If the eggs are not fertilized, there is no change in their appearance. They can remain in this condition for many hours (overnight) and still be fertilizable, though they seem to give healthier larvae if fertilized immediately.

Eggs spawned naturally and examined at once have also been found to correspond closely with this condition. Usually, however, such eggs are fertilized at once by males shedding sperm in the same bowl, and quickly proceed to develop.

From a female which had been interrupted in her spawning I have obtained, by slitting the body wall (a few hours later), eggs which were not quite the same. They were oval disks with a germinal vesicle and a bulge (when viewed laterally) in the region of the nucleus, but there was no specially thinned-out area at one end, and one pole was flattened as though for the reception of the sperm. Some of these eggs were kept for some time, but underwent no further change; others were fertilized and proceeded to develop, but on the whole did not give such healthy larvae as eggs of the other sort.

Some other variants of egg shape have been noted, so that at the moment it is not quite certain which should be regarded as the normal recently spawned but unfertilized egg.

On fertilization the egg rounds up, becoming spherical, of smaller diameter (about 95 μ) than that of the disk-shaped unfertilized egg and more opaque. The egg-membrane rises off the surface of the egg in a crumpled manner (Fig. 1, *c*) and at the same time the invisible jelly-layer outside swells up. This is revealed by the excess sperms caught in it to form a halo around the egg,

and by the greater distance eggs are kept apart from one another when attempts are made to push them into contact. The thickness of this jelly is about equal to the diameter of the egg itself.

Whilst the eggs are rounding up, the germinal vesicle disappears and polar bodies are soon given off; they are clearly visible under the egg membranes. This is followed by the first division stages.

In 24 hours or less, according to the temperature, larvae swim actively up to the surface and gather in swarms round the side of the bowl. They are not phototropic. They are almost spherical (Fig. 1, *d*), rather opaque, and the same greenish brown colour as the eggs. Cell limits are fairly distinct, the cells being relatively large and densely granular. The central mass of the developing gut is rather more opaque and darker than the cells forming the body wall. The blastocoel is almost entirely occluded. A stomodaeal invagination is present. The whole is enclosed in the egg- or fertilization-membrane through which the cilia project. There is a long apical tuft, and a prototroch forms a complete band round the equator. The individual prototrochal cells can be traced fairly clearly—there is a double row, the cilia of the posterior row being a little shorter than those of the anterior. There is no telotroch. The larva swims forward in the direction of the apical tuft, mainly on a horizontal axis rotating as it goes.

As growth proceeds the larva elongates, the widest region of the body being at the prototroch. The apical tuft is large, the cilia varying in length, the longest in the middle. The prototroch is a broad uninterrupted band, immediately behind it ventrally is the developing stomodaeum. A telotroch of relatively short weak cilia soon appears (Fig. 1, *e*); it is interrupted ventrally and dorsally by median gaps. Some patches of neurotrochal cilia appear and there is a long very thin cilium at the extreme posterior end. Granular greenish patches (chromatophores) form on the head in a transverse row immediately behind the prototroch, and a few smaller ones just in front of the telotroch.

With further elongation the first trunk segments become discernible through the segmental arrangement of additional chromatophores on the trunk (Fig. 1, *f*). Chromatophores also appear on the pygidium. On about the third day a granular reddish brown eyespot develops on the right side. The larval cuticle thickens over the head. It can be seen that the prototroch consists of three or four moderately distinct transverse bands of cilia placed very close together. The cells of the prototroch are more opaque than are those of the rest of the body wall—a feature that persists as long as the prototroch is present. The tissues generally are very granular and rather opaque, especially gut tissues not indicated in the drawing. The neurotroch, consisting of several patches of short cilia, becomes more strongly marked; it ends posteriorly in the mid-ventral gap in the telotroch. The anus is already formed. As further structures differentiate (Fig. 1, *g*, *h*, *i*), the diameter of the prototroch shortens,

the larva acquiring a more elongate appearance without any real gain in length. Segmental grooves appear, and parapodial lobes arise as small swellings on what will be the first two setigers. The first bristles soon protrude just dorsal to these lobes. The anus opens immediately behind the dorsal gap of the telotroch, and first one and then two pairs of papillae appear at the extreme posterior end of the body. The ventral pair of these is larger than the dorsal. There are now two eyespots and sometimes a third on the right side. The eyespots are cup-shaped, the opening of the cup being directed ventrally and laterally.

The larva can now wriggle violently, indicating the development of trunk musculature. The larva is a little more transparent than previously, the prototroch being the most opaque area. It should be noted that the line drawings give but a poor representation of the texture of the tissues. The gut is probably open at both ends, but it is uncertain whether the larva is feeding or not. The gut is still fairly granular. The mouth is well ciliated and there are short cilia on each side of it. The proboscis is developing.

The trunk now slowly elongates (Fig. 1, *j*) whilst the diameter of the prototroch remains more or less the same. The parapodial lobes of the third setiger appear (Fig. 1, *j* and Fig. 2, *a*, *b*), but not for some time does this segment acquire bristles (Fig. 2, *c*). The bristles of the first two setigers grow longer and are followed by others. First each dorsal bundle acquires a second bristle (Fig. 1, *j*) and later the first setiger gets a ventral bristle on each side (Fig. 2, *a*, *b*), followed later by the second setiger. By the time the third setiger has a single dorsal bristle on each side the first had often three dorsal and two ventral (Fig. 2, *c*) to each parapodium. There is variation in the rate at which the bristles of the first and second setiger appear in relation to the time of appearance of bristles on the third setiger. For a description of the bristles see p. 548.

With further growth the apical tuft loses some of its cilia. The prototroch becomes a little narrower (Fig. 2, *a*, *b*, *c*); it can be seen to be composed of three or four rows of cells. The neurotroch consists of a series of patches of cilia, generally two per segment with considerable non-ciliated gaps between. The larvae swim steadily, sometimes swiftly, forward, rotating slowly, often in a more or less spiral path. Unless moving up or down they swim with the body horizontal, or nearly so.

When the third setiger bristles are seen the larvae are six to eight days old, though sometimes younger and sometimes older according to the temperature. It is at about this stage that metamorphosis first becomes possible, though, as will be shown later, it rarely takes place except in sand of a suitable character. At about this stage too there is a change in the behaviour of the larvae. Whereas during the first few days they had swum up towards the surface and had shown no reaction to light, they now move away from a light source and can be driven to and fro, up or down in the glass bowl by moving an electric lamp

into appropriate positions. They gather on the side of the bowl away from the window. At this same stage they are also to a large extent positively geotropic. Thus, if a bowl of larvae be stirred so that they are evenly distributed throughout, and a light-tight cover be placed over the bowl for a few minutes, it will be found that the great majority of the larvae go to the bottom. In a bowl left in darkness all night, however, the majority were at the surface in the morning, these larvae immediately moved away from the light when they were uncovered and gathered about half-way down the bowl on the side away from the window. The cover was replaced for 15 min. at the end of which period the larvae had gathered on the bottom of the bowl.

Negative phototropism and positive geotropism will in the sea lead metamorphosis-ripe larvae to the sea bottom. What happens to them there will be discussed in another paper; we are here concerned only with general details of the metamorphosis.

When ready to metamorphose *Ophelia* larvae readily cling to any solid object with which they may come into contact. The sides of a bowl, the walls of a pipette, and grains of sand are only some of the objects adhered to. They may show this habit as early as the fifth or sixth day. Attachment is effected primarily by the four anal papillae, aided often, especially in older larvae, by the parapodial lobes. Adhesion is effected by a secretion produced by glands at the bases of the papillae and of the lobes, and discharged by canals opening at pores on the tips of these protuberances. Parapodial lobes have one gland for each, but each anal papilla has several. At first, larvae can easily detach themselves and swim away, but after a few days they stick more firmly and this, combined with a loss of swimming strength due to a decrease in power of the prototroch with age, results in their being unable to get away. Thus they become stuck to the glass of a clean finger bowl, though they may be detached by squirting water from a pipette.

A larva attached by the anal papillae to the bottom of a glass dish stands upright with the prototroch beating strongly. It similarly stands upright on sand grains, unless it actually burrows into the sand and metamorphoses. This ability to cling strongly to sand grains must aid the larvae in settling on the current-swept sand banks in which they will live when adult. Such a mechanism seems to be needed in order that they may anchor themselves immediately contact is made with the bottom soil. A quick efficient attachment mechanism is a necessity for settling in regions swept by strong currents, and the anal papillae and parapodial lobes, with their associated glands, fulfil this need.

Larvae, after settling on the surface of the sand, make their way into it. If the sand be suitable, they may stay there, but they have been seen to come out and swim away. Often they remain on the surface of an unsuitable sand, attached to a grain by the anal papillae, the body upright, swaying, with the prototroch beating strongly. It has seemed as if they needed a current of water to launch them up and away from the bottom.

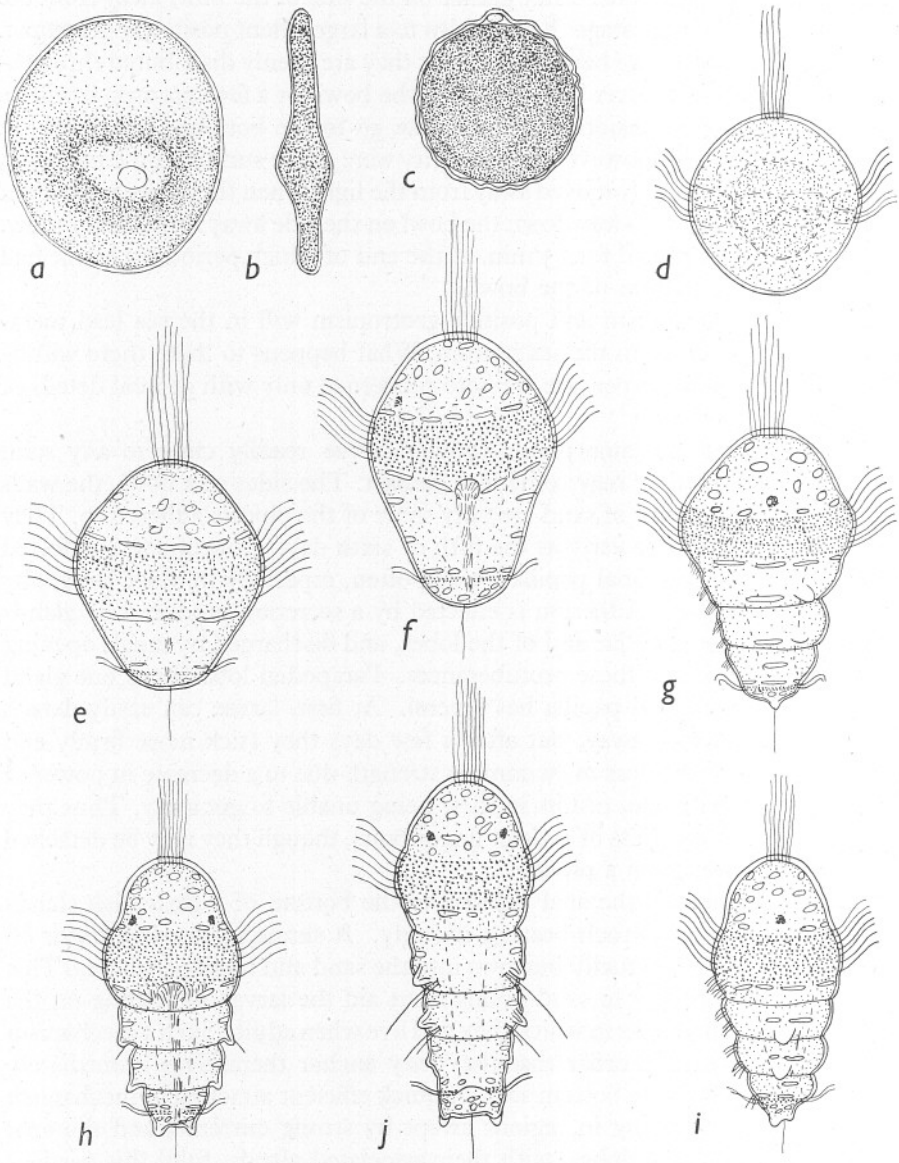

Fig. 1. Eggs and larvae of *Ophelia bicornis*, ×225. *a*, unfertilized egg; *b*, the same in side view; *c*, fertilized egg with polar body; *d*, 1-day-old larva; *e*, 2-day-old larva, ventral view; *f*, 3-day-old larva, ventral view; *g*, 4-day-old larva, view of left side; *h*, *i*, 4 to 5-day-old larva, ventral view and view of left side; *j*, 5-day-old larva, dorsal view.

In a suitable sand the larvae metamorphose. The apical cilia are lost, the prototroch, telotroch and neurotroch disappear and all power of swimming is

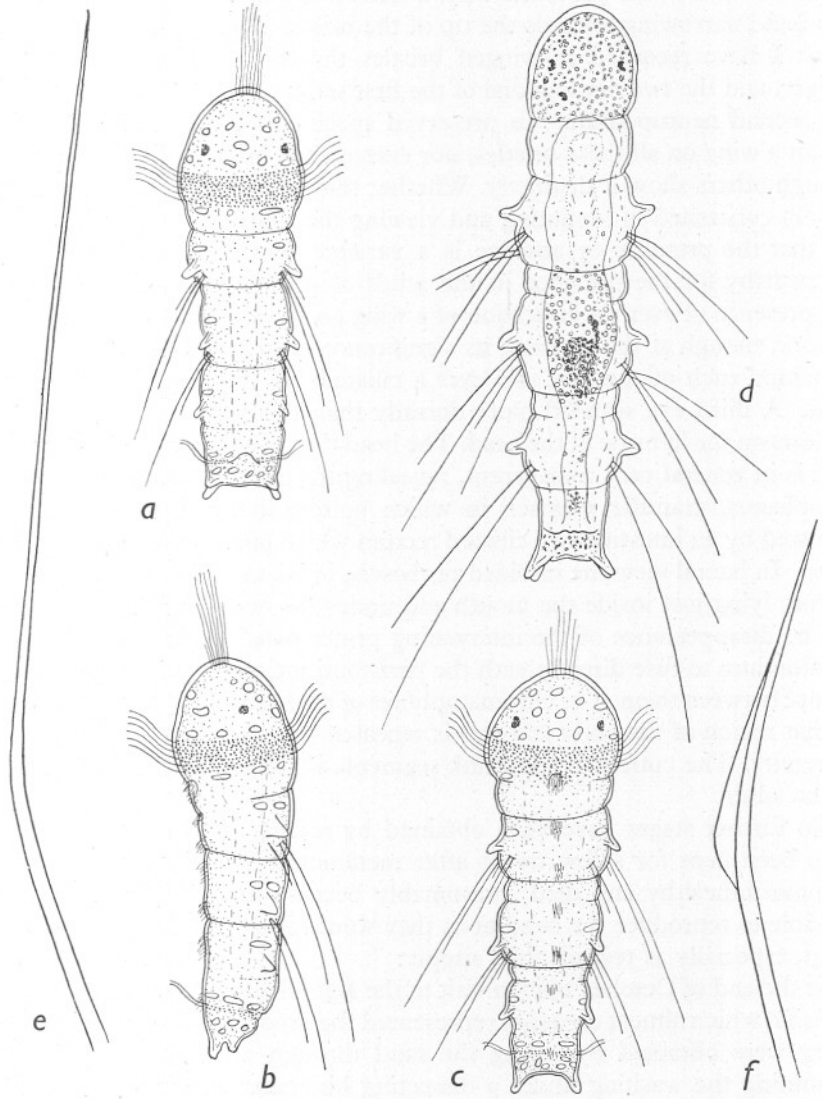

Fig. 2. Larvae of *Ophelia bicornis*, ×225; bristles, ×1600. *a*, *b*, 7-day-old larva, ventral view and view of left side; *c*, 11-day-old larva, ventral view; *d*, young worm, after metamorphosis and 19 days old, dorsal view; *e*, capillary bristle; *f*, winged bristle.

lost. The body elongates and the worm (Fig. 2, *d*) crawls among the sand grains to which it can adhere strongly. The bristles grow rapidly, especially those of the third setiger which soon exceed in length the anterior ones.

The bristles appear at first sight to be all fine smooth capillaries, often bent at a slight angle near the base (Fig. 2, *e*); more careful observations, however, show that a few are provided with a narrow bordering wing, widest at the bend and narrowing towards the tip of the bristle (Fig. 2, *f*). In living specimens I have recorded as winged bristles the third notopodial in the first setiger, and the two neuropodial of the first setiger, also the shorter ventral of the second neuropodium. In preserved specimens I have not been able to detect a wing on all these bristles, nor even on any bristles of some specimens, though others show it distinctly. Whether this is due to preservation and the factors concerned in mounting and viewing the specimen is not clear, it may be that the presence or absence is a variable feature. The Opheliidae are noteworthy for the presence in the adult of capillary bristles only, so that the presence of even an indication of a wing on larval bristles is an interesting feature, though at the moment its significance is far from clear.

Behind each of the first two eyes a ciliated pit, the nuchal organ, can be seen. A third eye situated more dorsally than the others and behind them, appears on the left side of the head. The head tissues are granular, but the body wall is in general very transparent, revealing the gut. The latter has a ciliated oesophagus, granular stomach in which bottom-living diatoms are visible, followed by an intestine and ciliated rectum which opens at a dorsally situated anus. In lateral view the infolded proboscis, or buccal mass, is a conspicuous feature lying just inside the mouth and under the oesophagus.

The disappearance of the intervening prototrochal tissues has allowed the prostomium to fuse directly with the peristomium, there being a well-marked groove between them. The chromatophores of the head give a darker appearance to that region of the body and this is repeated to some extent at the posterior extremity. The cuticle of the trunk segments is transversely wrinkled as it is in the adult.

No further stages have been obtained by rearing, although young worms have been kept for a few weeks after metamorphosis. They have gradually become unhealthy and died, presumably because in dishes it has not been possible to reproduce the conditions they would find in their natural environment, especially as regards food supply.

At the end of October 1947, a visit to the Bullhill Bank produced two young *Ophelia*, which almost certainly represented the brood of the previous summer. They were obtained by sifting the sand through a fine meshed sieve and examining the washing under a dissecting binocular in the laboratory. The smaller specimen was about 5 mm. long (fixed) and had twenty-five setigers; the gut contained about ten relatively large sand grains. The larger specimen was about 7 mm. long (fixed) and had twenty-eight setigers; there were a few small sand grains in the gut. The general appearance of these specimens resembled fairly closely that of the adult, but there were differences due to incomplete development. Thus the smaller specimen had only two pairs of

branchiae, definitely recognizable as such, though the larger had fifteen, the adult number. The first and last branchiae in both specimens were very small. An interesting feature was that whilst in the adult the anterior pair of branchiae occur on the eleventh setiger the anterior pair in the smaller specimen was on the twelfth setiger and was smaller than the succeeding pair. However, there was some slight indication of the presence of branchial rudiments on the eleventh setiger suggesting that these grow at a later stage. This is in agreement with the condition of the larger specimen which bore small but distinct branchial rudiments on the eleventh setiger, whilst the second pair on the twelfth setiger were considerably smaller than on the thirteenth and immediately succeeding setigers. In the adult the first few pairs of branchiae are rather smaller than those succeeding them, but it is, nevertheless, evident that the order of appearance of the branchiae in *Ophelia* is worthy of some attention when more material is available.

Discussion

Slowly the gaps in our knowledge of polychaete development are being filled, but the work that remains to be done before anything like a reasonably complete picture of polychaete embryology can be attained is very great indeed. There are still whole families for which data are either non-existent or of the most fragmentary kind. The position has changed little since my assessment of it twelve years ago (Wilson, 1936), and one has only to read Thorson's recent (1946) magnificent and painstaking compilation of old and new notes on the planktonic larvae of Danish polychaetes to be forcibly reminded of this unsatisfactory state of affairs. Thorson adds much that is new and he brilliantly summarizes many aspects, not least that of the confusion which still remains to be cleared up. 'In spite of the rather copious literature the larval Polychaetes are still poorly known' (p. 34). As he points out, the development of several common species is quite unknown.

That this should be so is not always the result of lack of effort directed to their elucidation. Several families have defied long-sustained efforts to penetrate their secrets, not least among them being the important Maldanidae and Ampharetidae, and to only a slightly lesser extent the Nephthydidae and Glyceridae. More than one worker has spent much time attempting to investigate the embryology of species belonging to these groups, with very little to show for it. From time to time, however, a species of polychaete is reared for the first time and should it happen to belong, as in the present instance, to a family whose development was previously not known, its development, even though it be of a simple straightforward type, cannot fail to be a valued addition to previous knowledge.

The development of *Ophelia* is of this simple straightforward type; its larva differs only in relatively minor details from that common to several other families of polychaetes (Syllidae, Eunicidae, Cirratulidae, Capitellidae, Areni-

colidae, Terebellidae, Sabellidae). The common type is of moderate size, often rather yolky though not exceedingly so and, apart from the usual ciliated girdles (prototroch and telotroch) and ciliary tufts (apical and anal), shows no great structural specializations for swimming. Relatively few segments have been formed by the time the prototroch and telotroch are lost, that is, when metamorphosis can be said to have taken place. These segments, if setigerous, bear, as a rule, developing parapodia each with a few bristles of no great length. Slight variations of this pattern occur from family to family; sometimes a whole organ, such as the telotroch, may be reduced or absent. Some families have more yolk than others and, naturally enough, there is variation within the family, though often the development of so very few species within a family is known that on this latter point the statement rests on a little more than conjecture. The pelagic life of this typical simple form of larva is frequently, though not always, relatively short; that is, it does not extend over more than a few days (except when the post-larva is also pelagic, as in some terebellids). Food is often not taken until settlement has been effected.

In rather marked contrast to the foregoing are the larvae of some of the other polychaete families, larvae which show pronounced structural features which appear to be adaptations to a prolonged and active existence in the plankton. There may, for instance, be supernumerary rings of strong cilia (as in Spionidae and Chaetopteridae), sometimes on many segments, and there are frequently very long provisional bristles (especially well seen in Spionidae, Magelonidae, Oweniidae and Sabellariidae) which, in addition to their protective, and possibly suspensory functions, may with the aid of specialized cilia give rigidity to the body when swimming (in some, at any rate, of the Spionidae and Sabellariidae). The prototroch may be enlarged as it is in the Amphictenidae, Sabellariidae, Magelonidae and, above all, in the Oweniidae where it is sometimes looped and twisted in the manner of an echinoderm larva. A relatively spacious blastocoel is sometimes associated with an enlarged prototroch; this is especially well seen in the Oweniidae and it is a feature of the large trochosphere of *Polygordius*, and to a lesser extent of the smaller trochospheres of the Serpulidae, and perhaps one or two other families as well.

The larvae of the Aphroditidae, Phyllodocidae, Nereidae, Nephthydidae and maybe others, fall somewhere between these extremes. Thus the larvae of the polynoids have for the first part of their pelagic life a fairly well pronounced prototroch and long and numerous bristles, but their development is in many ways specialized along lines peculiar to the family. In the Nereidae there is much variation but the larvae of the family are at best feeble swimmers; some do not swim at all. Apart from their rather long bristles they resemble more nearly the simple type of larva than does the larva of the polynoids. The mode of their development fits them for early crawling rather than for prolonged swimming. The Nephthydidae and Phyllodocidae, however, contain a number

of species with long planktonic lives, their larvae reaching a considerable size with numerous segments before settling. They do not possess specially long bristles and their prototrochs and telotrochs are not unduly large, though it is possible that they are specially strongly ciliated. More information is needed on these points before any definite conclusions as to the manner of their adaptation can be reached.

The development of *Ophelia* and other families with a simple larva is less specialized than the developments of the more spectacular types. Whether this is primitive or is a secondary simplification is not clear; the polychaetes are a very old group in geological time and many changes must have taken place in their ontogeny during the long period of their evolution; such points therefore are not easy to decide. It does, however, seem reasonable to suppose that long provisional bristles, enlarged prototrochs, swollen blastocoels and the other features of the more structurally complex pelagic types are adaptations which have been evolved over a very long period of time. In each family possessing one or more such structural features a somewhat standard pattern has been followed, common to the family but differing from that of other families. It is possible, in theory, to imagine that all these modifications have been produced by the exaggeration or suppression of the structures present in an ancestral simple type of larva not greatly different from that of *Ophelia*. This latter type of larva should be regarded as the typical polychaete larva and it is unfortunate that in the text-books the rather specialized *Polygordius* larva and the trochosphere of the serpulids should, apparently largely by the accident of having been among the first to be described in detail, have been taken as standard types. As long ago as 1911 Shearer pointed out the unsuitability of the serpulid larva for a text-book type and more recently Segrove (1941), working on the same family, has concurred in this. A larva such as that of *Ophelia* or of *Notomastus* has far more claim for consideration for this purpose, though there may be others, as yet undescribed, that would be even more suitable.

The projection of the posterior bristles well behind the anal extremity in the newly metamorphosed young *Ophelia* is a feature of the young of the allied *Polyophthalmus* and of mature sexual individuals of the latter also. Good figures of this are given by Stolte (1937). In adult *Ophelia* the bristles of the posterior setigers are not so pronounced, though they are moderately long and numerous, they barely pass behind the extremities of the anal papillae. In *Armandia* the last setigers bear very long capillary bristles, although it appears that the anal tube is produced beyond their backward reach. The posterior bristles of *Travisia* and *Ammotrypane* are short and rather inconspicuous. If now the grade of the bottom soil in which these various genera be considered, there becomes apparent some slight correlation with grade, for, on the whole, the finer the soil the shorter the posterior bristles. Thus *Ammotrypane* and *Travisia* inhabit fine sand and mud, *Ophelia* sands of varying grade according

to the species. *Armandia* is found in coarse loose sand (Fauvel, 1925, 1927), *Polyophthalmus* among rocks and weeds (Southern, 1914; Fauvel, 1925). In the latter the bristles are specially well developed at the time of sexual maturity when the worm becomes pelagic at night. It may, therefore, be that the function of these bristles is in some way connected with the kind of bottom inhabited by the adult. What this function is can as yet scarcely be guessed, but if it be true that the length of the posterior bristles is functionally related to the grade of the soil then the relatively long bristles of the very young *Ophelia* are probably an expression of this relationship. For to the newly metamorphosed worm the sand in which it has settled is comparatively coarse, but with increasing stature becomes relatively finer. In the young, therefore, the bristles are longer in relation to the body size than they are in the adult.

Summary

Fertilizations of *Ophelia bicornis* Savigny were made and the larvae reared. This is the first time the larval development of any member of the family Opheliidae has been described.

The trochosphere is small and somewhat yolky; it has a broad prototroch, a narrow telotroch, a strong apical tuft and a long anal cilium.

Annulation is accompanied by the appearance of parapodial lobes and bristles. When the first pair of bristles of the third setiger protrude the larva is ready to metamorphose. It has two, sometimes three eyes.

The larva in its later stages can adhere strongly to solid objects, such as sand grains, by a secretion from the four anal papillae and the parapodial lobes. This is interpreted as an adaptive aid to settlement on sand banks swept by strong currents.

At metamorphosis the larval external cilia are lost and the bristles rapidly elongate, especially those of the third setiger.

Some of the larval bristles are slightly winged. So far only capillary bristles have been known in the Opheliidae.

It is pointed out that a development such as that of *Ophelia* is more typical of polychaetes as a whole than are the developments of certain species commonly used as text-book types.

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ADDENDUM

Just before going to press a paper[1] has been received from Shiro Okuda giving for the first time an account of the development of an ampharetid worm. The development is of the simple straightforward type, the larva being of moderate size, somewhat yolky, and not differing greatly from that of *Ophelia* and similar types, especially in the earlier stages.

[1] Okuda, S., 1947. On an ampharetid worm, *Schistocomus sovjecticus* Annenkova, with some notes on its larval development. *Journ. Faculty Sci. Hokkaido Imp. Univ.*, Ser. VI, Vol. IX, pp. 321–9.

A CONTRIBUTION TO OUR KNOWLEDGE OF THE LIFE HISTORY OF *ARENICOLA MARINA* L.

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(Text-figs. 1–12)

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Introduction

A survey of the literature reveals the rather surprising fact that the breeding habits and spawning of the common British lugworm, *Arenicola marina* L., which is such a frequent and conspicuous member of the polychaete fauna of our intertidal zone, are by no means fully known.

Most of the available accounts deal with lugworms on various continental shores and there are also good descriptions of spawning and early development of the Pacific lugworm, *A. cristata*. There seem to be no recent references to the breeding of lugworms off British coastlines. Such accounts as exist are by no means in complete agreement, even on such important points as the time of the breeding season, its duration, or on the possibility of the seasonal occurrence of a pelagic spawning phase, whilst descriptions of the early development are almost completely lacking.

Thamdrup (1935), one of the more recent workers on the breeding season of European lugworms, was led, as a result of his own observations on the mud-dwelling fauna of Skalling and from results of previous authors, to put forward a 'working hypothesis', as he terms it, in order to link up the known facts. Thamdrup believed that the worms spawn in a period restricted to a few days and probably related to definite phases of the moon, in the late summer. The resulting larvae, he thought, live pelagically throughout the winter (a suggestion due to Blegvad, 1923) and then take to the bottom some time in April and June. Here they grow through the summer and winter to a size

which then lies within the adult size-group range. The young worms may spawn during the second summer after they have hatched from the egg. These conclusions of Thamdrup are to a large extent based on those of Blegvad (1923) and of Pirlot (1933). Pirlot studied the lugworms of the Belgian coast, particularly at Blankenburghe. Here he noted that in September and the early part of October all the worms except the very small ones had gametes filling the coelom, but that after 15 October and throughout the winter no gametes were to be found in the body cavity. Spawning was restricted to a 2-day crisis at either the full or new moon, and in 1928 was on the 13–14 October, in 1932 on 14–15 October and in 1933 on 6–7 October. The weather had, apparently, no effect on spawning, which is probably governed by a lunar effect acting indirectly through the tides. Pirlot states that both sperms and eggs remain immature until they pass out of the body via the nephridia, and he was unable to obtain a successful artificial insemination from coelomic gametes. For this reason he remained unacquainted with the early larva. He found, however, larvae with one pair of chaetigerous segments in the sand about 14 days after the spawning crisis. In fact, with the doubtful exception of Child (1898), who merely describes fertilization and maturation (but no later stages) of the eggs of the American *A. marina*, Pirlot's failure with artificial means is typical of all other results. Naturally fertilized eggs have been recorded on two occasions. The first is that of Blegvad (1923), who was fortunate enough to find some eggs laid by worms in the aquarium at the Nyborg Biological Station. These were deposited loosely on the sand and conformed closely to the description given by Ashworth (1904). They were laid on 6 August 1923 and hatched into trochophores 4 days later. These and larvae with three chaetigerous segments were briefly described and figured. After reaching this stage of development the brood of larvae died. However, in successive Septembers Blegvad obtained larvae with five chaetigerous segments, but no stages between this and the 'post-larval' stages of Benham (1893) were seen. Post-larval stages occur in numbers in the early spring from April to June, and Blegvad believed that the pelagic larval stage must extend over the whole winter.

The second record of early larvae is that quoted by Thorson (1946), who mentions that Erik Smidt (unpublished) found newly hatched larvae crawling among the sand grains of the tidal zone at Esbjerg, but these are not described in Thorson's paper. Pelagic larvae were never found by Thorson, despite very extensive plankton hauls, and he believes that such a stage is omitted from the life cycle, the larva from the beginning being a bottom-dweller. The breeding season of lugworms in Danish waters takes place in the autumn, as is shown by the presence of coelomic gametes in August onwards for some time and by their absence in the spring. Post-larval stages as described by Benham were also not found, and it is suggested that when they occur they may be bottom stages that have been stirred up accidentally, or else they are abnormalities

due to larvae metamorphosing in mid-water. The fact that young bottom-dwelling, metamorphosed worms are first met with in the summer may be explained by assuming that the young larvae settle in the autumn soon after hatching, and then stagnate until the rise in temperature of the following spring, when growth is resumed.

It will be seen from these summaries that whilst the accounts of Blegvad and Pirlot are substantially in agreement they differ in many important respects from that of Thorson and, as will be mentioned below, all three differ from those of British workers.

The possible occurrence of a pelagic stage or swarming of breeding adults has been discussed by several workers, notably by Fage & Legendre (1927), who give a useful review of what was known of the breeding habits of lugworms up to that date. It appears that the evidence for a swimming phase rests on a few but perfectly definite observations, some of which are by British observers, and on reports by fishermen. Meek & Storrow (1924), for example, noticed lugworms swimming at the surface of the sea in Northumberland for 2 days, 21 and 22 March, at the time of the full moon. The worms were enclosed in a gelatinous capsule which, it is suggested, may act as a float. All the worms were spent as if breeding had just taken place. This conclusion is, however, open to criticism, for it may well have happened that the gametes had not yet begun to develop for that season. In fact, Storrow himself (1925) noticed *Arenicola* sperms in the sand on 23–24 September 1924, which suggests an autumn breeding season. Fage & Legendre and also Pirlot (who was unable to find pelagic adults) take the view that if a pelagic phase does occur it is not directly related to the emission of the gametes.

From these various sources it would seem fair to summarize our knowledge of the breeding habits of lugworms on the shores of Europe as follows:

(i) Breeding is restricted to a period of a few days in the autumn and is probably related to spring tides. (ii) Gametes pass out through the nephridia and are fertilized in the sea. Before discharge, coelomic gametes are not fully mature. (iii) It is uncertain if the larva is a free-swimming trochophore with a lengthy pelagic life extending until the spring following hatching, or if the pelagic phase is omitted or curtailed. Recent evidence (Thorson) suggests that the latter alternative is more likely. (iv) There are almost certainly occasions on which the worms forsake their burrows and swim actively in the surface waters, but this burst of activity may, or may not, be related to spawning. The evidence here is very fragmentary. (v) All the accounts so far cited agree that the eggs are not enclosed in any sort of gelatinous capsule after they have been laid. This is an important point of difference between *A. marina* and certain other species, e.g. *A. cristata*, a Pacific lugworm common in Japan and America. The eggs of *A. cristata* and their capsules have recently been redescribed by Okada (1941), who also showed that spawning takes place at 4-day intervals from July to September during which period eggs and sperms

are discharged synchronously throughout the whole habitat. Fertilization is aided by the close proximity of male and female burrows which connect one with the other so that the eggs are fertilized in them.

With regard to the breeding of lugworms in British waters it appears from the fragmentary and conflicting accounts that very little is known with certainty. Thus, Cunningham & Ramage (1888) state that in the Firth of Forth the gametes are shed in August and September. Kyle (1896), on the other hand, believed that the breeding season extends from January to September though with a cessation during April, May and early June. Gamble & Ashworth (1900) stated that the ordinary littoral forms of *A. marina* of the Lancashire coasts are not mature in the spring, but breed throughout the summer when the deeper water variety has ceased to do so. In a later publication (1904) Ashworth, who again worked at stations on the Lancashire coast and also on the Firth of Forth, states that two varieties of *A. marina* are to be found in these districts. One, smaller and abundant in the littoral zone, appears to be the form most usually met with in the British Isles and on the Continent. The other, large and having slight morphological differences from the littoral form, is restricted to the laminarian zone. Using as his criterion the presence of ripe eggs or sperms in the coelom, Ashworth concluded that the smaller, littoral variety breeds in the spring, usually from the end of February onwards for about a month or more, but he found specimens containing ripe 'ova' up to the end of April or even later. Unfortunately, Ashworth does not give any exact description of what he means by 'ripe gametes' and, as will be mentioned later, a superficial examination of the stage of maturity of the coelomic gametes gives only a rather vague indication of the time of the breeding season. The larger laminarian variety of lugworm breeds in March and onwards, but Ashworth is inclined to believe that both varieties may have a second spawning season in the late summer. This double-breeding season is certainly true for *A. ecaudata*, as mentioned by Hentschel (1930). The actual release of the gametes into the sea was not observed by Ashworth, but he believed that they pass out through the last five pairs of nephridia. He, then, like later workers, disagrees with Bohn (1903) who thought that the germ cells passed out through temporary perforations in the body wall. Full descriptions of the eggs and sperms are given in Ashworth's monograph and also an account of cleavage and early larva of *A. claparedii*, but it is stated that nothing is known of stages intermediate between the egg and the post-larval stages of Benham for *A. marina*. For British lugworms his statement would seem to be substantially correct up to the present day. Reference must, however, be made to a paper by Williamson (1916). His observations were made on the worms of the Bay of Nigg, but the species, although probably *A. marina*, was not determined in all instances. Williamson noted that ripe sperms were discharged on 2 October from worms kept in an aquarium and also believed that egg masses discharged at intervals from May to June also belonged to *Arenicola*. These

egg masses were gelatinous, green in colour and contained numerous green eggs. A few days later they contained greenish embryos with two eye spots. They closely resembled egg masses found on the beaches where they were anchored by strands to the substratum or to sea weeds. Each egg mass was apparently composed of a ball of fibres loosely invested in a thin outer skin which it was believed was the cast cuticle of the female worms. In view of the wide differences between this description and those of other authors, and because other polychaetes such as *Capitella* and *Polydora* were also present in Williamson's aquarium, some doubt must attach to the view that the greenish egg masses were really spawned by *Arenicola*.

The embryology of lugworms has been fully dealt with up to the formation of the young larva by Child (1900) and by Okada (1941). Both of these authors worked on *A. cristata*. Ashworth (1904) gives a somewhat briefer description of the development of *A. claparedii*. All the descriptions are substantially in agreement, and the cell lineage seems to follow the usual polychaete plan. Descriptions of the free-living larvae of *A. cristata* are given by Lillie (1905) which agree with those of earlier workers, e.g. Child (1897).

This review serves to show that whilst a good deal is known of the breeding and embryology of foreign lugworms of various species, yet a re-examination of the life histories of British lugworms is needed to fill in gaps in our knowledge. Points which seem of particular interest are the duration and season of the year at which breeding takes place; the correlation between spawning and the tides; the method of egg-laying and fertilization; the nature and duration of larval life and a description of later stages.

This paper deals exclusively with the lugworms of the Whitstable Flats and the results may well not apply to other districts.

Acknowledgements

It is with pleasure that I tender my thanks to Mr G. P. Wells for his suggestion that I should investigate the breeding habits of the common lugworm. Not only has he given me much help and encouragement but has also very kindly read through the manuscript. Mr D. P. Wilson was kind enough to give me considerable help with the literature. The work has proved a good deal more arduous than I expected and the records I have kept could not have been so complete were it not for the very considerable help I have received from my small children who throughout the severe winter of 1946–47 helped me collect my specimens. Mr Cullen of Queen Mary College took the photographs of the developing eggs and to him I am extremely grateful.

The Breeding Season

As already mentioned, there is considerable disagreement in the literature as to the time and duration of the breeding season of *A. marina*, some sources stating that it occurs in the spring, others in the autumn. All accounts dealing

with British lugworms, with the possible exception of Meek & Storrow (1924), indicate a protracted period in contrast to a concerted spawning, or crisis, as described by some continental workers for the same species. Over a period of many years it has been noticed that the lugworms of the Whitstable Flats have their body cavities full of germ cells throughout the late summer and early autumn and that by the end of October all the worms are 'spent'. This clearly points to a breeding season in early autumn. A further point noticed in a purely qualitative way is that the worms are very much scarcer in the

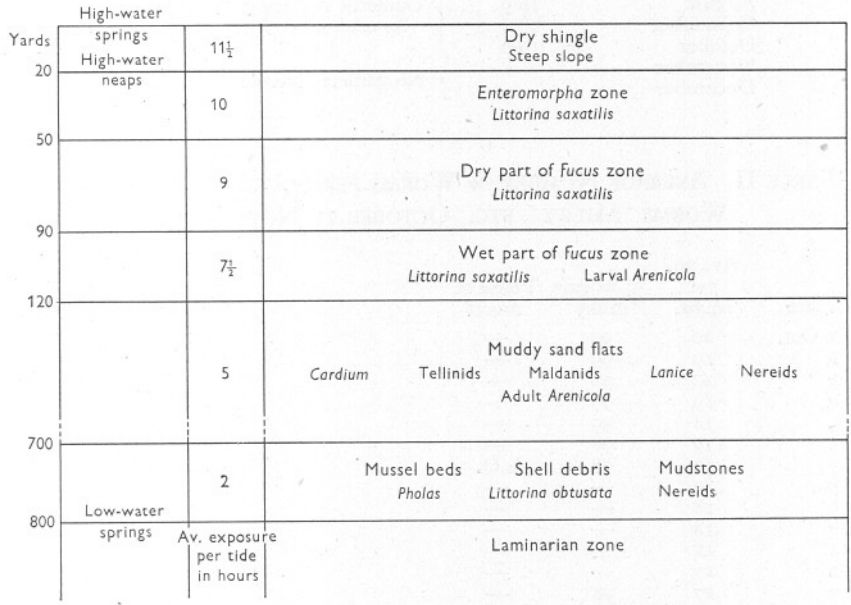

Fig. 1. Diagram to show the approximate zonation and some of the commoner animals of the intertidal zones.

winter than in the summer and the impression was gained that the drop in numbers occurred rather suddenly at about the middle or end of October. If this is, in fact, true then it indicates a mortality among the spawning adults or else a migration related to spawning. It seemed that a record of the density of the worm population over a whole year, in conjunction with observations on the state of sexual maturity, would throw a good deal of light on both these points. Accordingly, with a few exceptions due to adverse weather or tides, worms were dug at weekly intervals, or even more frequently, throughout the period November 1946 to November 1947. Each sample was collected from the same general area of the Flats about 50 yards seaward of the pebble and *Fucus* zone (Fig. 1). Each sample was usually in excess of forty worms and sampling was carried out in each instance by digging up areas measuring 6 ft. × 1 ft. 6 in., giving areas of 1 sq. yd., so that the density of the worm

Table I. Average Number of Worms per Square Yard, November 1946 to November 1947

Month	Average number per sq. yd.	Coelomic gametes
1946: November	8·4	—
December	10·0	No gametes in coelom
1947: January	10·1	No gametes in coelom
February	10·0	No gametes in coelom
March	12·0	No gametes in coelom
April	14·2	No gametes in coelom
May	19·0	No gametes in coelom
June	17·0	Gametes maturing in coelom: 10 % adults 'milky'
July	16·5	Gametes maturing in coelom: 80 % adults 'milky'
August	16·9	Gametes maturing in coelom: 95–98 % adults 'milky'
September	18·5	Gametes maturing in coelom: 98 % adults 'milky'
October	19·0	Gametes maturing in coelom: 98 % adults 'milky'
November	—	No gametes in coelom
December	—	No gametes in coelom

Table II. Average Number of Worms per Square Yard, Percentage Worms 'Milky', etc. October to November 1947

Date	Av. no. per sq.yd.	% worms 'milky'	Phase of moon		Remarks
1 Oct.	20	99	—		—
2	19	99	—		—
3	20	98	—		—
4	19	97	—		—
5	18	99	—		—
6	19	98	—		—
7	20	98	L.Q.		—
8	19	—	—		—
9	18	—	—		—
10	18	—	—		—
11	18	—	—		—
12	17	—	—		—
13	17	98	—		—
14	18	—	N.M.		—
15	18	—	—		—
16	18	98	—	Spawning period	Puddles of sperm observed at low tide. Spring tides
17	17	98	—	Spawning period	—
18	19	—	—	Spawning period	—
19	18	—	—	Spawning period	—
20	20	—	—	Spawning period	—
21	20	—	—	Spawning period	—
22	19	—	F.Q.	Spawning period	Max. number of puddles of sperms
23	18	—	—	Spawning period	—
24	20	—	—	Spawning period	Neap tides
25	20	60	—	Spawning period	—
26	19	—	—	Spawning period	—
27	—	—	—	Spawning period	
28	—	—	—	Spawning period	
29	18	8	F.M.	Spawning period	
30	15	5	—	Spawning period	Approx. 40 % mortality of spawning adults.
31	—	0	—	Spawning period	No spawning seen. Spring tides
1 Nov.	12	0	—		
2	—	0	—		
8	8	0	—		

population could easily be expressed in numbers per square yard. This rather tedious method of sampling was found to be essential, since counting the number of casts per square yard is a most unreliable index of the number of worms, varying as it does with, among other conditions, the state of the tide. For most of the year there was little variation in the numbers of worms per square yard from week to week, and for simplicity the results have been consolidated and given as monthly results. For September and October, however, more frequent results are given. The results are given, together with remarks on the state of sexual maturity and phases of the moon, in Tables I and II and Figs. 2 and 3.

Discussion of Results

It will be noticed from Table I and Fig. 2 that the average number of worms per square yard rises throughout November and December, remains at about 10 per square yard during January and February and then reaches the high figure of 19 per square yard in May. From this point onwards, until the end of October, it is fairly constant at between 17 and 21 per square yard. There is a very marked sudden decrease in numbers on or about 31 October.

The soil from which the worms were dug is a favourite area for bait diggers and minor fluctuations in the numbers of the worms may probably be attributed to their activities. The digging of lugworms for bait, cannot, however, account for any substantial decreases in the worm population, for more bait is dug throughout August and early September than at any other period of the year and yet the density of worms remains high. Furthermore, there is practically no bait dug in the middle of the winter when the worm population is at its lowest (November to February), and the numbers continue to increase from February to May during the later part of which period bait diggers resume their activities. It can be assumed, therefore, that the density of the worm population is virtually unaltered by the interference of man, and some other explanation must be sought for any striking variation in the number of worms per square yard of the soil.

An observation made in October 1946 gave a clue to the cause of the sparcity of worms in the late autumn and winter of that year, for on 26 and 27 October, on which there were neap tides, large numbers of spent worms were found cast up dead on the shore. Previous to these dates worms were plentiful, but afterwards were scarce. Unfortunately, quantitative observations had not then begun, so that no figures can be given for this period. Before the end of September 1946 the overwhelming majority of the worms were of a milky appearance owing to germ cells packing their body cavities, but of the worms remaining in the Flats after this date few only were milky, although about 75 % retained a few germ cells until the end of October. By the beginning of November all were completely spent.

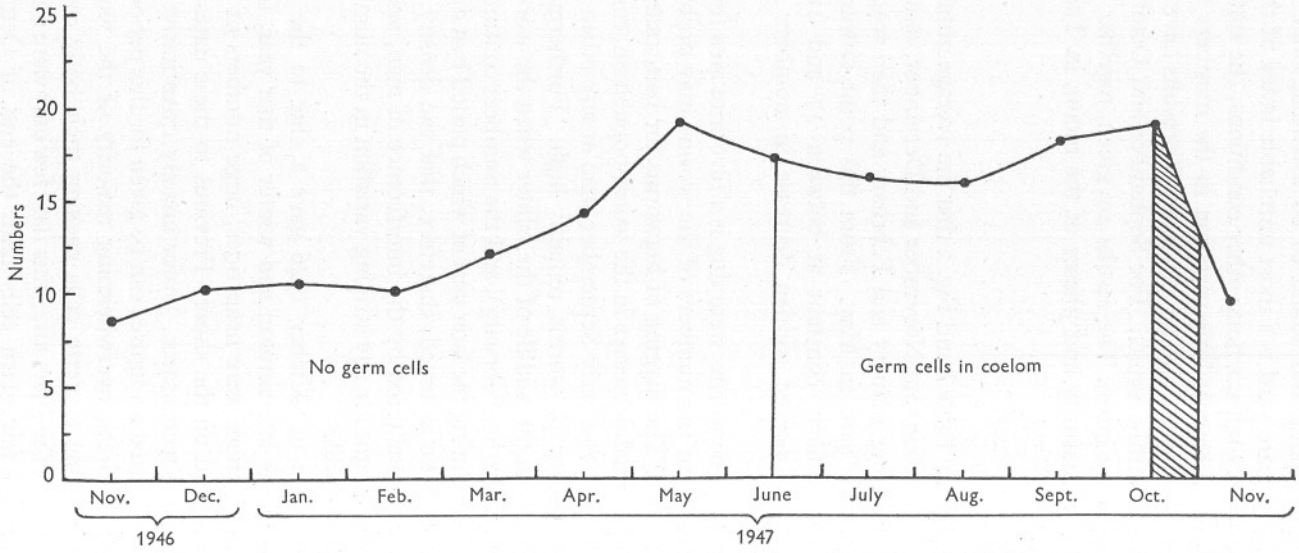

Fig. 2. Monthly variation in numbers of worms per square yard of soil dug. Shaded portion indicates spawning period.

The upshot of these preliminary observations is that the breeding season of the lugworms of the Whitstable Flats is during a period in the autumn which agrees with statements of Blegvad (1923), Pirlot (1933), Thamdrup (1935) and Thorson (1946), whereas Kyle (1896), Ashworth (1904) and others believed the breeding season to extend through the spring and early summer. The drop in numbers noted would seem in some way to be related to spawning.

As has been seen, the general conclusions are borne out and amplified by the records kept during the period November 1946 to November 1947. From Table I it will be seen that germ cells in any quantity first make their appearance in the coelom in June when about 10 % of the worms appear milky. From June to the middle of October the germ cells multiply and mature, and from August onwards, until the end of October, 98 % or more of the worms are 'milky'. After 31 October all the worms are spent, although it is true that in

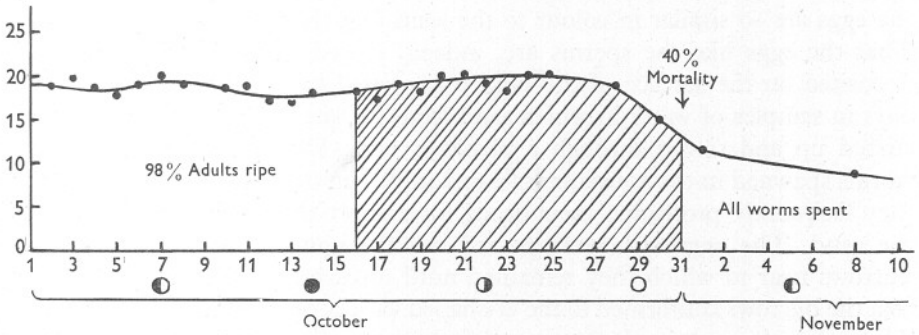

Fig. 3. Average numbers of worms per square yard of soil dug in October and November 1947 Shaded portion indicates spawning period.

about 5 % of the worms a few ripe eggs and sperms could be detected, but then only in specimens dissected under a binocular microscope. They are so few in number that they can play no significant part in the main spawning process. Tables I and II clearly indicate that spawning ends on, or near to, 31 October, but they give no exact information as to when it begins. Fortunately, other evidence is available. On 16 October and onwards, until 31 October, small puddles of white fluid were noticed on the wet sand of the Flats. These proved to consist of lugworm seminal fluid containing active sperms. None was seen before dead low tide and it was later observed that the discharge of seminal fluid takes place all over the area within about half an hour. On several occasions sperms were seen being pumped out of the exit from the tail shafts of the worm burrows. Observations over the spawning period showed that spawning, as indicated by the number of sperm puddles, began slowly, reached a maximum intensity on 25 and 26 October and then decreased to finish on 31 October. Examination of the worms at intervals also suggests very strongly that each worm can spawn several times in the fortnight,

for there is an obvious decrease in the number of germ cells in the body cavity, although this is difficult to assess quantitatively. Not all the worms, however, become exhausted of germ cells at the same time, as is shown in Table II. Here also is indicated the relation of spawning to the phases of the moon and to spring and neap tides. It will be seen that spawning begins and ends on a spring tide, but is most intense at the intervening neap tides. The dates, but not the tidal relations, are similar to those noted by Pirlot (1933) for the lugworms of the Belgian coast. How strictly spawning is related each year to a particular moon is not known, but there is some evidence that spawning in 1946 was about a fortnight earlier than in 1947 and would then have been related to the period between the spring tides following the new moon of 25 September and those following the full moon of 10 October.

During the period 16–31 October close watch was kept for eggs on the surface of the sand, but none were seen. It was assumed that this was because the eggs are so similar in colour to the sand that they are virtually invisible. That the eggs like the sperms are, indeed, passed out of the burrows and deposited on the surface of the sand was proved by finding eggs on several days in samples of water in which sand from the surface of the flats had been stirred up and sieved through a plankton net. Also, on 29 October some worms spawned in the aquarium in London. When the females were spawning they frequently protruded their heads for a short time above the surface of the sand. The eggs also were passed out through the head shafts of the burrows near to which they remained until disturbed, so that it seems clear that the burrows conformed to the U-shaped variety described by Wells (1945). These females spawned on several successive days, thus confirming the conclusion reached from a study of the worms in their natural surroundings. The eggs laid in the aquarium proved to be fertilized and a brief account of their development is given below (pp. 568–70).

To sum up, it may be stated that lugworms of Whitstable, and almost certainly of neighbouring districts, spawn during 2 weeks in early autumn in the period between two spring tides. The spawning period, although sharply defined, is not a 2-day crisis as described by Pirlot, nor is it an extended one as was believed by Ashworth and others. There is only one spawning period in each year and the actual dates vary with phases of the moon. A decrease in the lugworm population takes place rather suddenly towards the end of, and immediately after, the spawning period. It is almost certainly due to death of about 40 % of the adults (probably those which have spawned) and accounts for the smaller numbers of worms present during the winter (see also pp. 575–7). Some of these dead worms were found in their burrows on 8 November 1947, but in this year none was seen floating in the sea.

Maturation and Structure of the Germ Cells

As is well known from the descriptions of Ashworth and others, the gonads are situated immediately behind the coelomic funnel of each nephridium. They remain minute in size, and for some considerable time before the breeding season immature oocytes and spermatogonia are shed from the gonads into the coelom, where they accumulate and give to the worms a milky appearance. The germ cells grow and mature in the coelom, but the oocytes, although gaining their full size, remain as primary oocytes until after they are fertilized.

It can be stated quite definitely that the lugworms of the Whitstable district for the greater part of the year, namely from the end of October until June, have no appreciable quantities of germ cells maturing in the body cavity. In 1947 the first time that germ cells were noticed was in June, when about 10 % of the adult worms had small numbers of oocytes or spermatogonia floating in the coelomic fluid. This conflicts with the findings of Ashworth (1904) for the lugworms of the Lancashire coast, for he states that 'the body cavity of large worms is filled with them almost to bursting by about the end of February' and that 'specimens containing ripe ova may be occasionally met with up to the end of April'.

Ashworth's description of the maturation of the germ cells agrees in essentials with what has been found for the Whitstable lugworms, and a redescription in detail seems, therefore, not to be called for. However, the results of the present investigation, together with any divergences from previous accounts, are summarized below. In mid-June maturing coelomic germ cells could be detected with the aid of a hand-lens in about 10 % of the specimens dissected and it is probable that a higher percentage of worms had germ cells already liberated into the coelom, but that these escaped detection by the rough and ready methods which were employed on the shore. Previous to this date, by the same standards, no worms had any coelomic germ cells. More detailed examination revealed that the oocytes were practically spherical cells, only slightly flattened in the plane at right angles to the main egg axis. They had a largest diameter which varied from 0·07 to 0·08 mm., whilst the nucleus had a diameter of about two-thirds that of the cell. The developing male germ cells were in the form of thick disk-like masses of spermatogonia of varying size.

By the middle of July, 80 % of the adult worms were full of germ cells, even down to the end of the tail, but these seemed not to have advanced appreciably towards maturity. At the end of August 98 % of the worms were 'milky'. Throughout the month of September 90 % or more worms were 'milky' and coelomic germ cells were examined at fairly frequent intervals. By 8 September all the oocytes were much alike in size, being discoidal cells, usually with a circular outline but sometimes slightly oval, and having a diameter of 0·17 mm. and a depth of 0·08 mm. The main egg axis was at right angles to

the plane of flattening. The cytoplasm is orange in colour and very opaque, whilst the nucleus appears in the living oocytes as a clear vesicle with a diameter of 0·06 mm. The egg cytoplasm is full of yolk granules and has a great affinity for most stains, including haematoxylin, but permanent preparations are extremely difficult to make successfully. The vast majority of the male germ cells were spermatids, still united into flattened masses by residual cytoplasm. A few (about 10 %), however, had metamorphosed into spermatozoa, although the tails showed no signs of motility. The heads of the spermatozoa remained

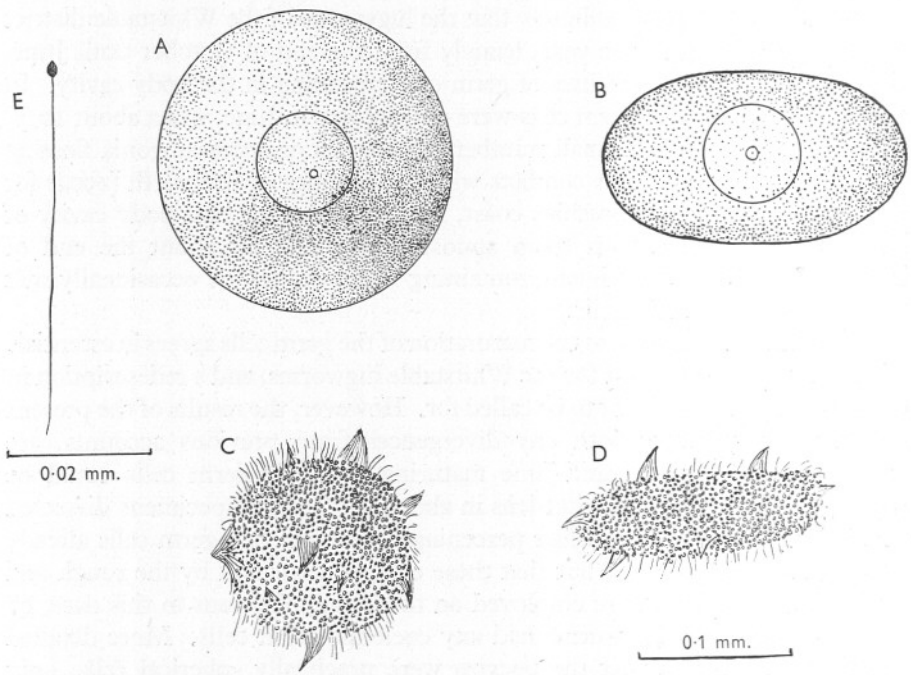

Fig. 4. A, fully grown coelomic oocyte. B, the same in side view. C, disk of mature sperms. D, the same in side view. E, mature spermatozoon. A, B, C and D approx. ×210. E approx. ×1000.

attached to the central mass of cytoplasm termed by Ashworth the blastophore (Fig 4, C and D).

By 28 September the oocytes had grown to have a diameter of 0·175 mm. and a depth of 0·095 mm. (Fig. 4, A and B). Little change was noticed in the male germ cells. The next detailed examination was made on 8 October, when the oocytes had attained a diameter of 0·18 mm., but apart from this had the same appearance. In the male worms about half the sperm masses consisted of spermatozoa. On 15 October most of the sperm cells had acquired tails and some of them had limited powers of movement. In many of the sperm masses the sperm tails were united by their tips and their slow undulations

had rather the appearance of a flagellar 'flame'. The significance of this is obscure. The oocytes by this time had attained a diameter of 0·19 mm. It is in this stage that both male and female germ cells are discharged.

Comparison with Ashworth's diagrams and figures of the dimensions of the oocytes reveals that the oocytes of the Whitstable worms are slightly larger (0·19 mm. as compared with 0·15 mm.). They also differ in shape being only very slightly biconvex or even biconcave and not strongly biconvex disks. Each oocyte is surrounded by a thin but tough vitelline membrane and after being left for some time in sea water this membrane acquires a certain stickiness and the eggs adhere quite firmly to the bottom of a glass vessel. They are appreciably heavier than water and this, combined with their adhesiveness, would tend to make them remain in the sand instead of being carried away in the plankton.

The spermatozoa of *Arenicola marina* have been described and figured by Ashworth, and those of *A. cristata* by Okada who also gives a detailed account of gametogenesis. Whilst Ashworth reported a distinct middle piece, Okada finds that this is incorporated in the head. The accounts of the two workers differ also in the shape of the head, particularly of the acrosome. The dimensions given in each account are of the same order of size if it is assumed that Ashworth's figure of 0·04 mm. for the length of the head should read 0·004 mm.

Spermatozoa collected in October 1947 had a total length of 0·055 mm., whilst the head measured 0·004 mm. in length. The general form is shown in Fig. 4 E. Very little detail could be made out and no distinct middle piece could be detected, the tail appearing to arise directly from the head.

Discharge of the Germ Cells

As far as is known there have been no direct observations of the discharge of the germ cells from the body in *A. marina*, but practically all workers are agreed that the gametes pass out through the nephridia. This is certainly true for *A. cristata* (Okada, 1941). Ashworth noticed germ cells distending the bladders of the nephridia, but dissections of many worms during the breeding period of 1947 failed to give confirmation of this observation. Nevertheless, the germ cells are discharged without any apparent rupture of the body wall, so that it is reasonable to infer that the nephridia do function as gonoducts, but that the gametes pass out through them very rapidly.

Sex Ratio

Difficulty in finding ripe males amongst an abundance of ripe female worms suggested that there might be a differential sex ratio. Counts on 300 worms showed that this was, indeed, true, the ratio being 3·7 females to 1 male in August and 3·8 females to 1 male in September. Okada, on the other hand, found a 1:1 sex ratio for *A. cristata*, so that in this as in other respects the Japanese differs from the British lugworm.

Artificial Insemination

It was found that mature spermatozoa, although still attached to the central mass of cytoplasm whilst they are in the body cavity and for a short time after they are discharged, rapidly gain their independence after a short time in sea water. Masses of coelomic sperm soon acquired motility and swam actively when transferred artificially to sea water, particularly if it was slightly hypotonic. There seems no obvious reason why sperm taken from the body cavity of ripe males and activated in sea water should not be capable of fertilizing what were apparently fully ripe oocytes from the coelom of ripe females. Yet all previous attempts at artificial insemination have come to nothing. In fact, Pirlot states definitely that the coelomic gametes are not viable until they have passed through the nephridia. Experiments carried out in October 1947 suggest that his statement is only partially true, for coelomic oocytes were induced to mature by artificial insemination with coelomic sperms to produce a fertilization membrane and undergo two cleavages. On another occasion sperm which had been shed in the natural way was collected from the sand and added to oocytes taken from a ripe female. The spermatozoa were fully active and yet the oocytes did not develop beyond the 4-cell stage. This tends to show that the inadequacy for development is a property of the oocytes rather than of the spermatozoa. Unfortunately, the converse experiment was not carried out because of failure to find unfertilized eggs naturally discharged on to the sand.

Early Development of the Egg

The eggs are fertilized on or in the superficial layers of the sand, presumably shortly after the discharge of the sperm near the time of dead low water. They are then covered merely by the shallow layer of water left by the retreating tide between the sand ripples. This timing certainly must increase the chances of fertilization, preventing as it does undue dilution of the seminal fluid. Tests carried out in the laboratory, however, show that spermatozoa remain motile for at least 18 hr. Observations on coelomic oocytes, to which had been added naturally discharged sperms, revealed that almost immediately the oocytes become surrounded by many hundreds of spermatozoa which cling to the vitelline membrane and by their activity often cause the egg to rotate. Sperm entry was not observed, but after $1\frac{1}{2}$–2 hr. most eggs had developed a 'fertilization membrane', and soon afterwards the first polar body was cut off. After 2–$2\frac{1}{2}$ hr. two polar bodies could be seen, both lying inside the egg membrane. Comparison of the diameters of unfertilized and fertilized eggs shows that the lifting clear of the fertilization membrane is due, in part at any rate, to shrinkage of the contents of the egg. With the formation of the fertilization membrane the egg loses its flattened shape and becomes practically spherical. Crossing the perivitelline space are what appear to be delicate threads of cytoplasm.

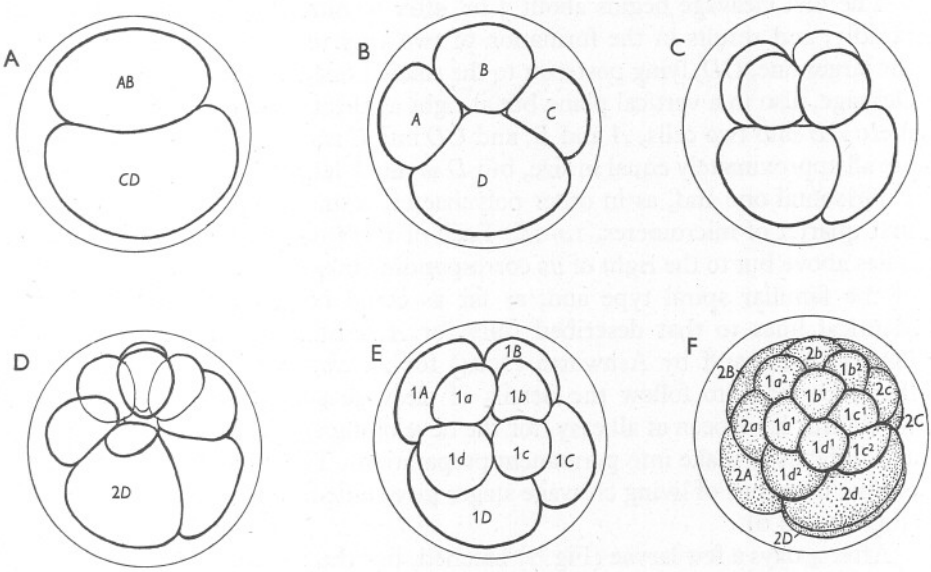

Fig. 5. Camera lucida drawings of cleavage stages. A, 2-cell stage. B, 4-cell stage from animal pole. C, 8-cell stage from the side. D, 2nd quartet of micromeres being formed. E, 8-cell stage from the animal pole. F, 16-cell stage from the animal pole.

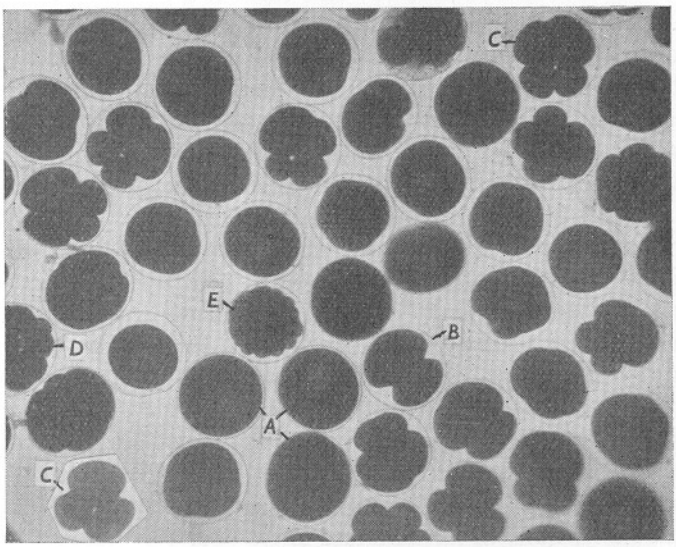

Fig. 6. Untouched photomicrograph of living cleavage stages. A, fertilized egg. B, 2-cell stage. C, 4-cell stage from the animal pole. D, 16-cell stage. E, blastula.

The first cleavage begins about 3 hr. after fertilization, is completed fairly rapidly, and results in the formation of two very unequal-sized blastomeres, the larger one, *CD*, lying posterior to the smaller one, *AB* (Fig. 5). The second cleavage, also in a vertical plane but at right angles to the first, divides blastomere *AB* into two cells, *A* and *B*, and *CD* into *C* and *D*. Of these *A*, *B* and *C* are all approximately equal in size, but *D* is much larger. The third cleavage is a horizontal one and, as in other polychaetes, results in the formation of the first quartet of micromeres, 1*a*–1*d*. Each of these is cut off obliquely so that it lies above but to the right of its corresponding megamere. Cleavage is, then, of the familiar spiral type and, as far as could be seen, it follows almost identical lines to that described fully for *A. cristata* by Child (1900) and Okada (1941) and by Ashworth (1904) for *A. claparedii*. No attempt was therefore made to follow the details of cleavage and gastrulation. Neither would this have been at all easy, for the developing eggs are singularly opaque and difficult to make into permanent preparations. The photomicrographs and outline drawings of living cleavage stages give some idea of early development (Figs. 5 and 6).

After 4 days a few larvae (Fig. 7) hatched, but the rest of the embryos died, since it was difficult to maintain satisfactory conditions in the small aquarium which alone was available. The larvae, like the eggs, are very opaque and creamy pink in colour. They are about 0·24 mm. long, and shaped rather like a radish. There is a well-defined prototroch encircling the thickest part of the body at about one-quarter of the way from the anterior end. A telotroch encircles the hinder end of the body and there is a prominent apical tuft of long cilia. Some distance behind the apical tuft, but on the dorsal side, is a pair of dark brown eye spots, whilst along the ventral surface, between the prototroch and the telotroch, is a band of shorter cilia. Neither mouth nor anus appears to be formed, but owing to the opacity of the larvae little could be seen of the internal structure, either in living larvae or in stained mounts. This is unfortunate, because only brief descriptions of early *A. marina* larvae are available. In fact, the only account that has been found is that of Blegvad (1923), who reared a few up to the time when three chaetigerous segments had differentiated. He also states that he found in September larvae with five chaetigerous segments, but gives no description of these nor does he mention where or how they were collected. Pirlot also found larvae with one chaetigerous segment in the sand, but neither describes nor figures them. Thorson (1946) mentions that E. Smidt has discovered early larvae, but again no description of them is given. He has, however, reasons for believing that from the first the larvae develop on the sand and remain there to develop further without ever becoming pelagic. Some confirmation of this view was found in the habits of the newly hatched larvae found in October 1947 for, unlike those of *A. cristata* (*vide* Lillie, 1905) or of *A. claparedii* (*vide* Ashworth, 1904), they often remained attached by their posterior end to the bottom of the dish and

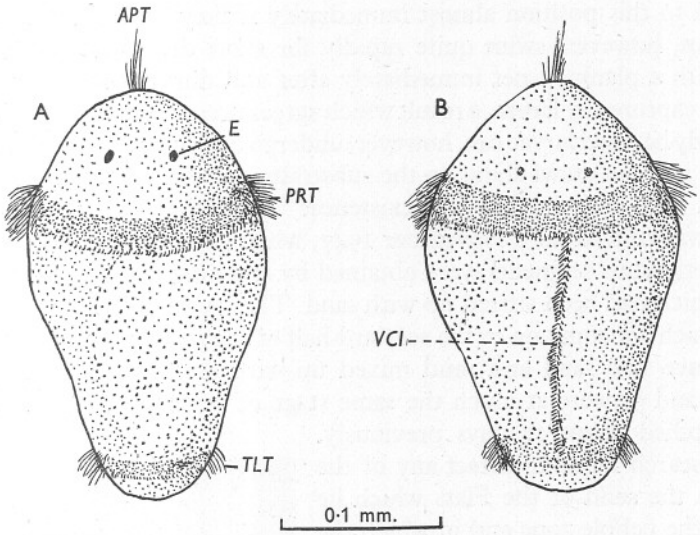

Fig. 7. Camera lucida drawings of newly hatched larvae. A, dorsal view. B, ventral view. *APT*, apical tuft; *E*, eye; *PRT*, prototroch; *TLT*, telotroch; *VCI*, ventral ciliated band.

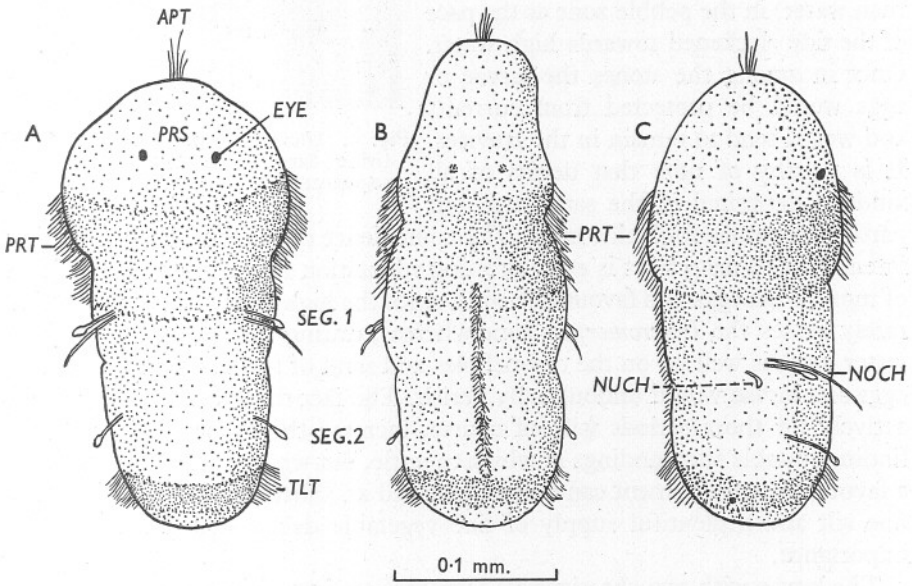

Fig. 8. Camera lucida drawings of living larvae with two chaetigerous segments taken from the *Fucus* zone. A, dorsal view. B, ventral view—prostomium extended. C, side view. *APT*, apical tuft; *EYE*, eye; *NOCH*, notopodial chaetae; *NUCH*, neuropodial chaetae; *PRS*, prostomium; *PRT*, prototroch; *SEG*, segment; *TLT*, telotroch.

returned to this position almost immediately if they were forcibly detached. They can, however, swim quite rapidly for short distances. Also, repeated hauls with a plankton net immediately after and during the breeding season failed to capture any larvae, a result which agrees precisely with that of Thorson. The newly hatched larvae can, however, undergo considerable and rapid changes in shape and can crawl about on the substratum, seemingly well adapted from the first to a bottom-dwelling existence. That Thorson was undoubtedly correct was proved on 8 November 1947, when large numbers of larvae with two chaetigerous segments were obtained by straining through a plankton net water which had been stirred up with sand. They were taken from the shallow pools which are common in the seaward half of the pebble and *Fucus* zone and which have fine sand and mud mixed up with the shingle. All the larvae (Figs. 8 and 9) were at much the same stage of development and must have been hatched about 14 days previously.

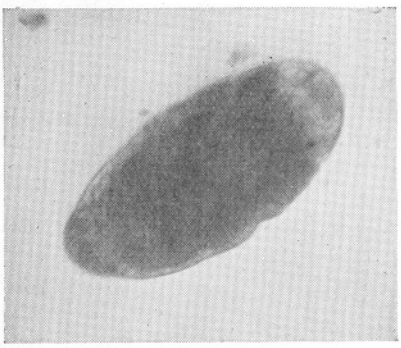

Fig. 9. Untouched photomicrograph of living larva with two chaetigerous segments.

Careful search failed to detect any of the larvae in the sand of the Flats which lie beyond the pebble zone and in which the spawning adult worms live, and it must be assumed that the fertilized eggs were carried towards the shore by the advancing tides and were deposited (being heavier than water) in the pebble zone as the pace of the tide slackened towards high water. Once in among the stones the larvae or eggs would be protected from currents and would tend to remain in the crevices. It is worthy of note that debris of all kinds is deposited in the same area but particularly at the high-tide mark. The coincidence of the maximum spawning intensity with neap tides is an interesting adaptation favouring the deposition of most of the eggs in a favourable zone, since the high-tide mark at these tides rarely passes the *Enteromorpha* zone whereas, during spring tides, the high-water mark is well up on the dry pebbles and sand of the beach proper where eggs and larvae would undoubtedly perish. The fact that the larvae can swim actively for short periods will, of course, increase the chances of the larvae finding suitable surroundings in which to settle, but what conditions constitute a favourable environment can only be guessed at. Shelter between the stones, fine silt and a plentiful supply of fine vegetable debris may perhaps be of importance.

The larvae with two chaetigerous segments are just visible to the naked eye as white specks about 0·25 mm. in length, and at first glance much resemble a small planarian. When at rest the body is bluntly conical, the broader end being anterior. Here is borne the apical tuft, whilst a little distance behind on

the dorsal side is a pair of dark brown eyes. Two rather indistinct grooves mark off the two segments. In the youngest of these larvae the anterior chaetigerous segment bears two notopodial chaetae, one of which is spoon-shaped and the other spear-shaped, but in some larvae this segment had also a single hooked neuropodial chaeta. The second chaetigerous segment bears a single chaeta only, which is spoon-shaped. Both prototroch, telotroch and ventral ciliated band are still present, but much wider, and it is by means of these that the larvae swim rapidly when detached from the bottom. Usually they crawl among the sand grains and detritus among which they live. They are extremely muscular little organisms, the prostomial region particularly being capable of a high degree of contraction and expansion. Reference to the descriptions of the larvae of *Arenicola cristata* given by Lillie (1905) and Okada (1941) and of *A. claparedii* by Ashworth (1904) will show that the larvae of *A. marina* are very similar to those of *A. cristata*, but hatch at a slightly earlier stage, having at first no chaetae. They are in this respect more like those of *A. claparedii*, but develop more slowly.

Apparently nothing is known of the structure and mode of life of larvae intermediate between those with three chaetigerous segments and the post-larval stages of Benham (1893) which are occasionally taken in plankton hauls in the spring.

During this investigation evidence has been found for the view that the larvae remain throughout the winter in the top centimetre or two of the sand in or bordering the seaward edge of the *Fucus* zone. By the following spring they have metamorphosed and grown into small worms resembling the adults in all essential features. Certain it is that small worms about 1·5 cm. long are found for the first time each year in enormous numbers in this region and not elsewhere on the Flats.

There is every reason to be hopeful that some of the so-far missing intermediate larval stages will be found during the coming winter.

Size Groups and Growth Rates

The very extensive samples taken from the lugworm population at fairly regular intervals over the whole year November 1946 to November 1947 provided material which was used to gain some idea of the growth rates and of the age and size groups. For these purposes the length of the body, excluding the tail, of freshly dug worms was measured. This gave a more reliable index of size than does total length of the body, since the tail (posterior achaetous region of the body) varies greatly in its proportion to the rest of the body, being frequently shortened by damage and often almost absent. Lengths were measured only to the nearest 0·5 cm., except on specimens of a year or less in age. The lengths refer to specimens in a moderate degree of contraction, a condition that they usually adopt a few seconds after being handled. The

TABLE III. AVERAGE LENGTH OF THE BODY (EXCLUDING THE TAIL) IN CM.

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
Young worms	—	—	—	—	—	0·8	1·5	2·0	2·4	3·75	4·3	4·0
Total worm population	6·4	5·5	5·3	4·8	5·9	6·1	8·2	8·1	9·2	9·1	9·8	8·7

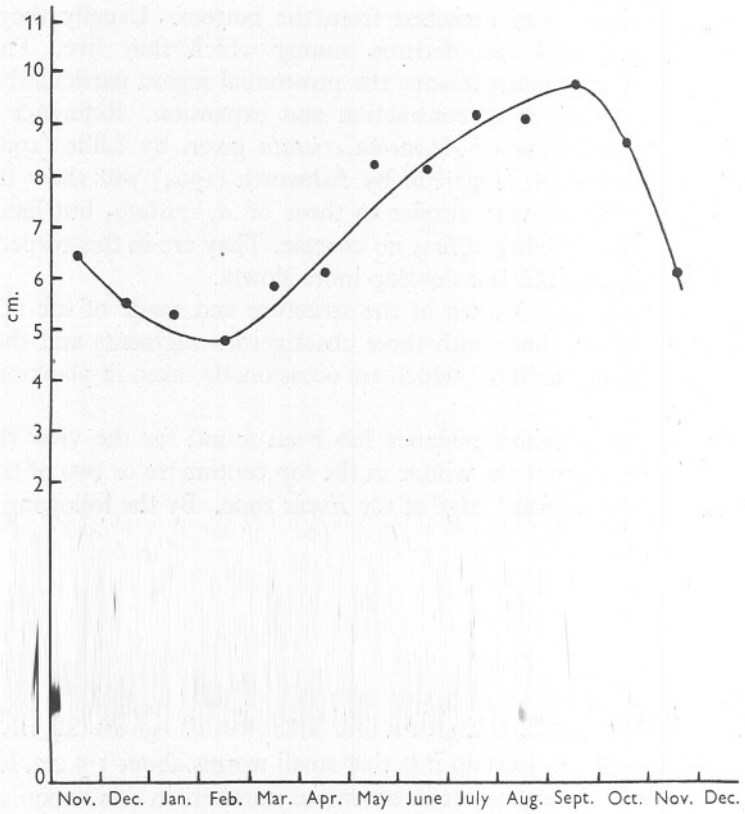

Fig. 10. Average length of body (excluding tail region) of adult worms.

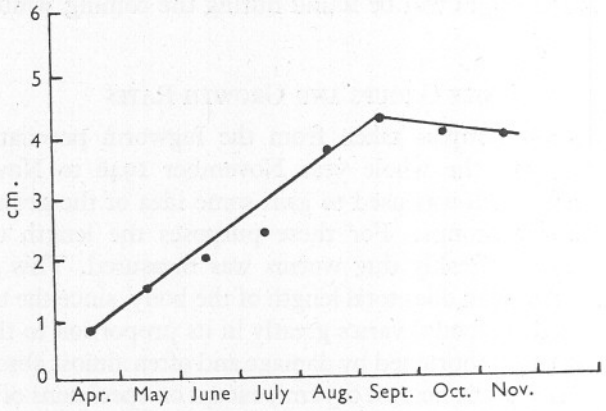

Fig. 11. Growth curve of young worms as shown by average monthly length of body (excluding tail).

results, although only approximate, gain in value from the very large number of worms which were measured.

The monthly figures for the average length of the body, excluding the tail, of all the worms collected are given in Table III and are expressed graphically in Fig. 10. Table III, also, and Fig. 11 show separately the average monthly lengths, excluding the tail, of young worms from eggs spawned in the autumn of 1946. These worms are easily separable from all others by their small size, pinkish colour and, usually, by being found nearer the shingle beach.

TABLE IV. CENTIMETRE SIZE GROUPS IN WORM POPULATION EXPRESSED AS OUT OF 200 WORMS

Size group (cm.)	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
2–3	—	—	3	3	1	1	—	—	—	—	—	—
3–4	4	20	21	26	11	7	1	—	—	1	1	2
4–5	16	25	40	43	31	15	1	7	1	2	8	2
5–6	38	85	61	73	62	33	12	21	3	8	2	7
6–7	63	55	47	36	47	59	27	23	12	14	11	21
7–8	58	15	29	16	31	31	48	48	37	24	20	43
8–9	20	—	5	3	11	23	39	46	38	35	13	41
9–10	—	—	3	—	5	15	34	19	38	33	22	21
10–11	—	—	—	—	1	7	18	18	16	30	45	24
11–12	—	—	—	—	—	4	12	7	20	23	28	21
12–13	—	—	—	—	—	3	5	5	19	12	20	13
13–14	—	—	—	—	—	—	1	3	7	14	11	5
14–15	—	—	—	—	—	—	1	—	7	3	8	3
15–16	—	—	—	—	—	—	—	2	1	1	—	—

The same figures were used to construct histograms (Table IV and Fig. 12) which show for each month the numbers of worms (to the nearest whole number) in a series of size groups which differ from one another by 1 cm. in length of the body, excluding the tail. Since the actual size of the samples was rather variable, the figures have been expressed as numbers out of 200. It should be mentioned that these figures all refer to worms obtained from the same general area of the Flats about 50 yd. seaward of the pebble and *Fucus* zone. They do not, until April, include any of the 1946 brood of worms and even after this time young worms are exceedingly rare in this area until November, and so are lacking from some monthly samples.

Discussion of Results

From Table III and Fig. 10 it will be seen that the average length of the worms decreases from about 6·4 cm. in November to 4·8 cm. in February, and then rises steadily to reach a maximum in September when the length index is 9·8 cm. This is followed by a fairly sharp decrease in October and November 1947 until the average length index is only 6·2 cm. Young worms, from eggs spawned in the previous autumn, grow from 0·8 cm. in April to 4·3 cm. in September and then decrease to a length index of about 4·0 cm., which probably remains fairly constant throughout the winter. By the

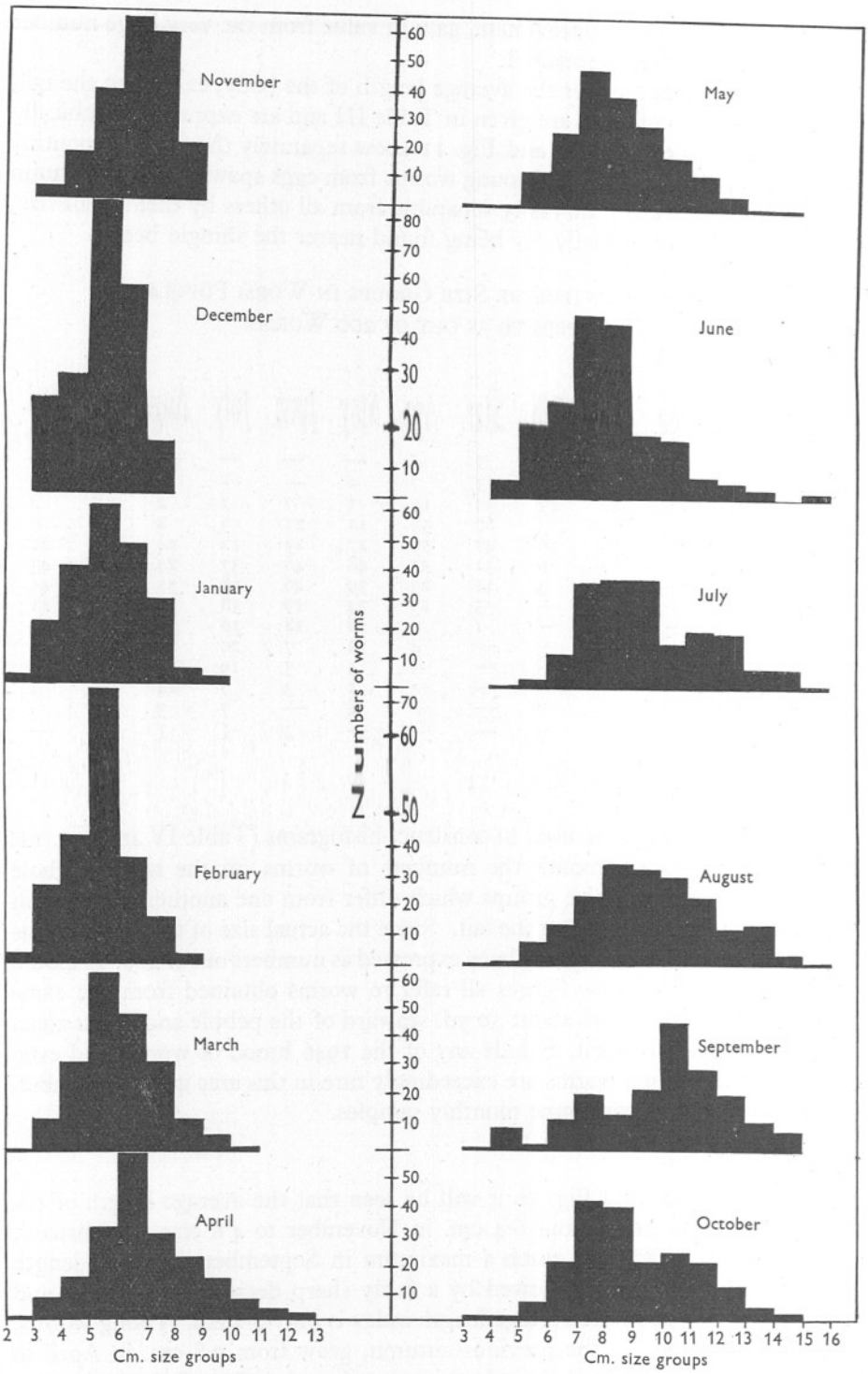

Fig. 12. Histograms showing numbers of worms in size groups differing by 1 cm. in length, November 1946 to October 1947.

following spring (April and May) the young worms which had attained a length index of 4 cm. in the previous September will have grown to a size which lies within the range of the adult size groups. Reference to Table I shows that in the autumn 98 % of the worms contain ripe germ cells so that it is clear that worms become sexually mature in their second summer and spawn 2 years after hatching from the egg. They can certainly spawn more than once, but how many times in not certain.

The histograms show a gradual change in the proportion of the various size groups. During the winter from December to March the 5–6 cm. group is the largest; in April it is the 6–7 cm.; in May the 7–8 cm. group is the largest; whilst in June the 7–8 and 8–9 cm. groups are about equal in size. By July the 7–10 cm. groups predominate and the 8–11 cm. in August. In September the 10–11 cm. group is the largest, but after October even worms exceeding 9 cm. in length are rare, whereas from May to October worms with a length index of up to 16 cm. are found. Now it has already been mentioned (p. 564) that at the end of October and during the first week of November there is evidence of a mortality of about 40 % of the adult worms. From the histograms it looks extremely probable that the worms which die are those in the larger size groups, that is, of 10 cm. and above. These presumably would be those which had reached a maximum size and had spawned for the last time. It will be seen that the size groups of 10 cm. and upwards for October represent about 37 % of the total—a figure which agrees well with the loss of 40 % estimated by another method.

This explanation is, however, inadequate to account completely for the decrease in size of the worms during the late autumn and winter. It can be seen that whilst the young (1946) worms grew steadily until September, yet from this time onwards they show a slight decrease in size. The same is true for the older worms as is shown by the decrease in average length from November to February. It seems that there is a period of 'degrowth' possibly due to the exhaustion of spawning and perhaps also because food is scarce at this time of the year. In this connexion I am indebted to Mr Wells for drawing my attention to the fact that lugworms kept in sea water alone remain alive and in good condition for long periods but become gradually smaller.

Migrations

Often regarded as an extremely sluggish animal, the lugworm is more active than is commonly supposed. It was repeatedly noticed that at all seasons of the year areas of soil from which all, or practically all, the worms had been removed by digging had been repopulated in the course of a few days to a normal density. It is possible that this repopulation was brought about by worms burrowing through the soil, but there is some evidence that worms leave their burrows when they are covered by the tide and swim to new situations and make fresh burrows. It has been noted that they can disappear into

the soil quite rapidly, in fact, in about 3–4 min. (Chapman & Newell, 1947). On many occasions worms have been seen swimming in the aquarium, whilst reports of this occurring in nature have already been mentioned (p. 556). It may be suggested that worms captured when free-swimming are in fact merely migrating to new burrows, and that this may take place quite independently of spawning or the season of the year. Thus Meek & Storrow (1924) found swimming lugworms in March, and yet Storrow (1925) brought forward strong evidence that the breeding season was in September.

A simple experiment carried out in the autumn of 1947 provides yet further evidence that the worms can and do swim under natural conditions. A bucket was filled with soil and partially buried in the Flats so that a few inches of its rim projected above the surface. Some weeks later it contained an active adult worm which must have come in over the top of the bucket and could have done so only by swimming when the tide was up since lugworms seem unable to crawl on the surface.

The occurrence of post-larval stages in the spring plankton would then perhaps be best explained neither as accidental (Thorson, 1946) nor as the end product of a very extended pelagic larval phase (Blegvad, 1923; Thamdrup, 1935), but as short migrations to places suitable for the continuation of the adult mode of life.

Whatever may be the normal method by which lugworms change the location of their burrows, it seems that this is a normal and often repeated process, and is responsible for the distribution of the animals throughout the habitat. It is, perhaps, of particular importance to the worms of less than a year old. These are first detectable in the spring (April in 1947) by the enormous numbers of minute castings along the shoreward edge of the *Fucus* zone where there may be as many as 250 per sq. yd. Here the small worms grow rapidly and then gradually migrate away from the shore to mingle with worms spawned in previous years.

Summary

The breeding season of the lugworms of the Whitstable area is a sharply defined one, extending for 14 days between the new moon and full moon spring tides in the second half of October. Spawning begins slowly and reaches a maximum at the intervening neap tides and then declines in intensity.

Both eggs and sperms are discharged from the burrows at extreme low water to lie on the surface of the sand. Here fertilization occurs.

No germ cells were detected in the body cavity from November to June, but from August onwards to the end of October 98 % of the adult worms are ripe.

At the end of the spawning period about 40 % of the adults die.

A brief description of gametogenesis and of the mature gametes is given.

Germ cells are discharged through the nephridia.

There is a differential sex ratio of 3·75 females to 1 male.

Coelomic gametes cannot be used for a completely successful artificial insemination, the eggs always dying after undergoing a few cleavages.

Fertilization and cleavage are briefly described. The eggs are fertilized as primary oocytes and undergo spiral cleavage in the way described by Child and others for different species of *Arenicola*.

Four to five days after fertilization the larva hatches. It is a very opaque trochophore 0·24 mm. long and usually rests sticking to the substratum, although it can swim actively. It has a broad prototroch, a telotroch and a mid-ventral tract of shorter cilia. There is an apical tuft and a pair of dark brown eyes. Mouth and anus do not seem to be open at this stage.

Larvae of about 14 days old and 0·25 mm. in length, and having two chaetigerous segments, are described. They were abundant in the silt between the pebbles of the *Fucus* zone, but no larvae were taken in the plankton nor in the sand of the Flats in which the adults spawned. It is suggested that fertilized eggs and larvae are carried inshore by the tide and are deposited in the *Fucus* zone where they live and develop into small worms in the winter and early spring of the following year. There is no extended pelagic larval phase, the modified trochophore larvae being demersal from the first.

Tables and graphs showing the growth of the young worms are given. The length of the body, excluding the tail, is taken as giving a true index of total length. The young worms hatched in 1946 were first noticed in April 1947 and by September had attained a length index of 4·3 cm.

The average length of the body, excluding the tail, for adults is also given in tabular and graphic form. This reaches its maximum (9·8 cm.) in September, but declines rapidly at the end of October and early November to the low level of about 5 or 6 cm. through the winter to rise again in the following spring.

From the histograms showing the numbers of worms in size groups differing by 1 cm. in length it is concluded that the sudden decrease in average length of the adult population at the end of October and early November is due to a mortality of adult worms (already mentioned) which have spawned for the last time. Worms spawn for the first time when they are 2 years old.

Further decrease in average length during the winter is due to other causes and affects the young as well as the adult worms.

Evidence is brought forward for the view that lugworms sometimes leave their burrows and swim for short distances probably to seek situations for new burrows. This kind of migration may be responsible for dispersing the animals throughout the habitat and accounts for its repopulation by young worms from the edge of the *Fucus* zone.

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THE GENERA *APOMATUS* AND *PROTULA* (POLYCHAETA, SERPULIDAE)

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(Text-fig. 1)

During an investigation of the blood systems of serpulids I have found that the pattern of the superficial blood vessels on the ventral surface of the thorax of the larger forms is a useful character for distinguishing the different genera, and sometimes is a reliable feature for distinguishing between the different species of a genus (e.g. *Serpula* and *Protula*). These blood vessels can easily be seen in living animals and are also visible in formalin-preserved specimens. Details of this matter will be published elsewhere.

Meanwhile, I wish to comment on the taxonomy of the genera *Apomatus* and *Protula*. The four western European species of these genera were obtained in the Gulf of Naples, and it was found that *Apomatus ampulliferus* Philippi, *A. similis* Marion and Bobretzky, and *Protula tubularia* (Montagu) all have the same type of superficial ventral thoracic blood system, whereas *P. intestinum* (Lamarck) is strikingly different in this respect. In *P. intestinum* (Fig. 1A) the trans-septal vessels (*tsv*) extend over the surface of the thorax and join the ventral vessel (*vv*); the vessels supplying the postero-ventral flange (*pvf*) of the thoracic membrane (*tm*) arise from the ventral vessel; the ventral vessel gives off other small vessels on to the surface of the thorax. In *P. tubularia*, *Apomatus similis* and *A. ampulliferus* (Fig. 1, B, C, D) the trans-septal vessels enter two ventro-lateral vessels (*vlv*) which terminate posteriorly in the flange of the thoracic membrane; the superficial blood system does not communicate with the ventral vessel. When specimens of these three species are handled they give off a strong odour which has never been encountered in *P. intestinum*; it resembles a mixture of machine-oil, oranges and iodine.

By taxonomists (e.g. Fauvel, 1927) the two genera are separated from each other by the presence of opercula in *Apomatus* and their absence in *Protula*. The most reliable feature distinguishing respectively *Apomatus similis* from *A. ampulliferus* and *Protula intestinum* from *P. tubularia* is the shape of certain adbominal chaetae. However, *Apomatus similis* has the same type of abdominal chaetae as *Protula tubularia*, and *Apomatus ampulliferus* has the same type of abdominal chaetae as *Protula intestinum*. The branchial crowns of these four species are readily autotomized when the animals are handled. When the crown with its opercula is lost *Apomatus similis* is indistinguishable from *Protula tubularia*; but the characteristic blood system of *P. intestinum* makes it easy to

distinguish from *Apomatus ampulliferus*. On two occasions I have found apparently intact specimens of *A. ampulliferus* without opercula. They were distinguishable from *Protula tubularia* by their abdominal chaetae and from *P. intestinum* by their ventral thoracic blood systems. Thus it seems necessary to reconsider the validity of using the operculum as the diagnostic character for separating the operculate genus *Apomatus* from the non-operculate genus *Protula*.

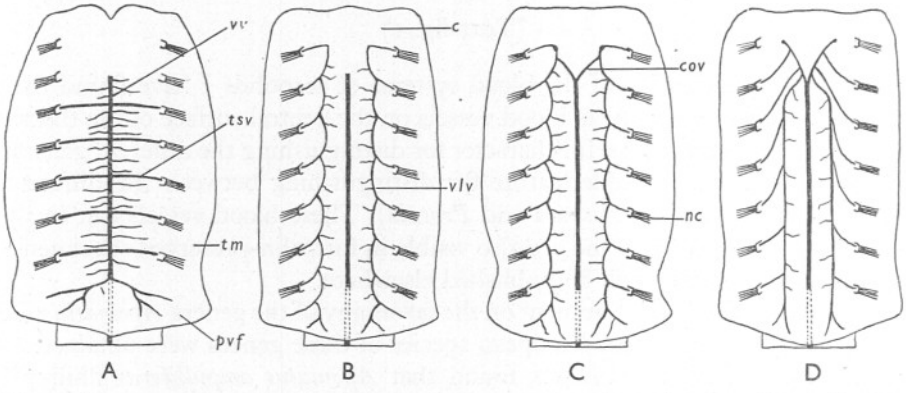

Fig. 1. Diagrams of superficial blood vessels on ventral surface of thorax. The collar has been turned forward. A, *Protula intestinum*; B, *P. tubularia*; C, *Apomatus similis*; D, *A. ampulliferus*. *c*, collar; *cov*, circum-oesophageal vessel; *nc*, notopodial chaetae; *pvf*, postero-ventral flange of thoracic membrane; *tm*, thoracic membrane; *tsv*, trans-septal vessel; *vlv*, ventro-lateral vessel; *vv*, ventral vessel.

The serpulid operculum and its peduncle represent a modified branchial filament. As Zeleny (1905) has shown, the existing serpulids can be arranged in a series reflecting the probable course of evolution of the operculum and its peduncle.

(i) Forms such as *Protula* without an operculum.

(ii) *Salmacina dysteri* with swollen tips to all its filaments. (Faulkner (1930) found that in her material the tips of the filaments were variable, some, none or all being swollen.) Similar swollen tips are noticeable on the filaments of the operculate species *Vermiliopsis infundibulum* (Philippi) and of the sabellid *Jasmineira candela* (Grube).

(iii) Forms such as *Filograna implexa* with two equally well-developed opercula, and *Apomatus* with a functional and a reserve operculum, all borne by filaments which in all other respects are just like non-operculate filaments.

(iv) Forms like *Pomatoceros* and *Hydroides* with one operculum, or with a functional and a reserve operculum borne by peduncles which are devoid of pinnules.

This series suggests that in the genera *Apomatus* and *Filograna* the filaments bearing opercula are in the process of evolving from ordinary branchial filaments. Hence less importance should be attached to the presence or absence of an operculum in the genera at the base of the series (*Protula*, *Apomatus*, *Salmacina*, *Filograna*) than in the genera later in the series (the rest of the serpulids). In the latter group of serpulids differences in opercular structure are accompanied by differences in other features and the opercula can satisfactorily be used for distinguishing genera. Within the former group of serpulids, however, *Apomatus* closely resembles *Protula*, and *Filograna* closely resembles *Salmacina* in most features, except that *Apomatus* and *Filograna* possess opercula whilst *Protula* and *Salmacina* do not. I suggest that a more natural scheme of classification would be obtained by combining *Apomatus* and *Protula* into one genus, and *Filograna* and *Salmacina* into another genus.

I suggest also that the genera *Apomatus* and *Protula* should be revised to reflect the close similarity between *P. tubularia* and the two species of *Apomatus*, and the dissimilarity of *Protula intestinum*. Fauvel (1927) has already commented on the similarity of *Apomatus similis* and *Protula tubularia* and has suggested that the former might be a young form of the latter. On the French coast (Fauvel, 1927) *Apomatus similis* is smaller than *Protula tubularia*; at Naples also this was usually so, but I found two specimens of *Apomatus similis* of the same size as *Protula tubularia*.[1]

The taxonomy of *Salmacina* and *Filograna* is similarly in need of revision. Faulkner (1930) has noticed operculum-like swellings at the tips of some or all of the non-operculate filaments of some specimens of *F. implexa* and *Salmacina dysteri*, and has agreed with McIntosh (1922–23) that the separation of the operculate genus *Filograna* from the non-operculate genus *Salmacina* is unsatisfactory, because in other respects they are closely similar. Faulkner considers that *Filograna implexa* and *Salmacina incrustans* are identical except that the former possesses opercula. According to Fauvel (1927), *Filograna* is bisexual, thus differing from *Salmacina* which may be hermaphrodite; but Faulkner has found hermaphrodite specimens of *Filograna implexa*.

I wish to thank the staff of the Zoological Station of Naples, the British Association for the Advancement of Science for the use of its Table, and the University of London for a grant towards travelling expenses.

Summary

It is suggested that the genera *Apomatus* and *Protula* should be revised to reflect the close similarity between *P. tubularia* and the two species of *Apomatus*, and the dissimilarity of *Protula intestinum*. It is further suggested

[1] McIntosh (1922–23) suggests that there is only one species of *Apomatus* (*A. ampulliferus*) and only one species of *Protula* (*P. tubularia*).

that the presence or absence of an operculum is not a sufficiently important character for distinguishing *Apomatus* from *Protula*, or *Filograna* from *Salmanica*; and therefore that these two pairs of genera should be fused into two genera.

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CLEANSING MECHANISMS AND THE FUNCTION OF THE FOURTH PALLIAL APERTURE IN *SPISULA SUBTRUNCATA* (DA COSTA) AND *LUTRARIA LUTRARIA* (L.)

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From the Marine Biological Station, Millport, and the Department of Zoology, University of Glasgow

(Text-figs. 1–8)

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Introduction

The investigations here recorded were the outcome of a preliminary study of *Lutraria lutraria* (L.) in connexion with a wider study on adaptation for deep burrowing in Lamellibranchiata. Examination of the ciliary currents concerned with the removal of waste material from the mantle cavity, which involved inquiry into the function of the fourth pallial aperture, revealed a variety of unrecorded facts. This led to an examination of conditions in *Spisula subtruncata* (da Costa) with which, on the basis of hinge characters, *Lutraria* is grouped in the family Mactridae (Thiele, 1935). Additional evidence of the close relationship between these two genera has been found.

This work was carried out at the Millport Laboratory, and it is a pleasure to record the kindness and help given by the Director, Mr R. Elmhirst, and by other members of the Staff. Thanks are also due to Dr H. F. Steedman for the preparation of sections.

Spisula subtruncata

External Appearance and Habits

Spisula subtruncata is a stoutly built bivalve which inhabits silty sand, into which it burrows quickly by means of a thick, somewhat pointed foot. The siphons (Figs. 1 and 2) are united and, in a specimen 3·4 cm. long by 2·6 cm. deep, extend to a length of not more than 8 mm., usually somewhat less. When buried only their tips project above the surface. The fused siphons are surrounded by a sheath of periostracum which arises in a groove immediately anterior to the outer ring of tentacles. The siphons thus represent the fusion of the inner and middle lobes, with the marginal (periostracal) groove of the outer lobe, of the mantle edge (Yonge, 1948). The middle (sensory) lobe is represented by a ring of tentacles which surrounds both siphons (Fig. 2). The inner (muscular) lobe is represented by a ring of large, with intermingled small, tentacles round the opening of the inhalant siphon, and by a membrane round that of the exhalant siphon. These tentacles are very mobile and act as strainers, preventing large particles from entering with the inhalant current, while the membrane constricts and directs the exhalant current.

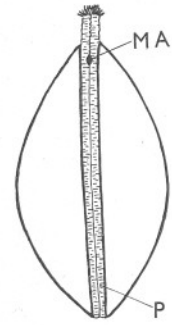

Fig. 1. *Spisula subtruncata*, animal fully expanded viewed from ventral surface. × 1. MA, mantle aperture, margins fused on posterior side only; P, periostracum covering exposed mantle surfaces and siphons.

When the adductors relax, the ventral margins of the shell valves separate for a distance of about 2 mm., but the mantle lobes remain closely applied as shown in Fig. 1. They are actually free from the region of the anterior adductor to the base of the siphons, so providing an exceptionally long pedal opening. But this only functions when the foot is protruded; at other times the ventral surface is closed, except for a small area immediately posterior to the fusion of the mantle edges at the base of the siphons. Here a spherical opening, about 1–2 mm. in diameter, can be seen when the animal is expanded (Figs. 1 and 2, MA). Similar local separation of the mantle edges in this region was originally noted by Kellogg (1915) in *Mactra solidissima* Dilwyn.

The Mantle Cavity

The appearance of the organs in the mantle cavity after removal of the right shell valve and mantle lobe is shown in Fig. 2. The flat and homorhabdic gills are large with the outer only about half the size of the inner demibranch. Their ciliation has been described by Atkins (1937 *a*, *b*). Small frontal cilia beat ventrally, carrying material into the marginal food grooves, except on the inner surface of the outer demibranch where they beat towards the gill axis.

But on this and on the adjacent surface of the inner demibranch there are additional long coarse frontal cilia which beat ventrally so that all large particles, such as sand grains, are carried into the food grooves, out of which they fall on to the surface of the mantle for extrusion with other waste material. Atkins associates the presence of these large cilia, which she notes are fully active only on mechanical stimulation, with life in silty sand. By their means many of the larger particles are removed from the gills, but mucus-laden strings of finer particles reach the long, strap-shaped palps by way of the food grooves and the gill axis. The palps function in the usual manner, further selection by them leading to the rejection of larger particles and masses from their tips.

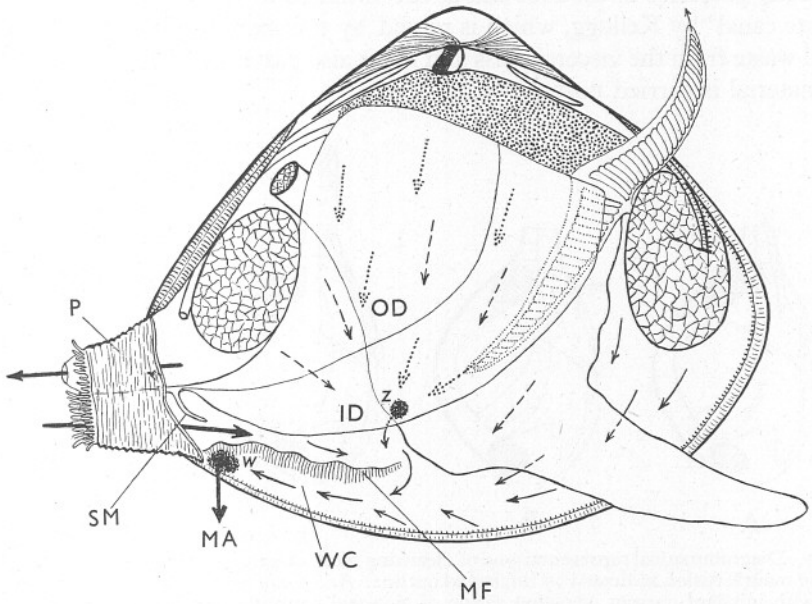

Fig. 2. *Spisula subtruncata*, animal viewed from right side after removal of right shell valve and mantle lobe, siphons intact. $\times 2\frac{1}{2}$. ID, inner demibranch; MA, mantle aperture with arrow showing direction in which waste (*w*) ejected; MF, mantle fold (left); OD, outer demibranch; P, periostracum surrounding siphons; SM, siphonal membrane; WC, waste canal; *z*, temporary accumulation of waste on visceral mass at base of the foot. Solid and broken arrows indicate course of ciliary currents on mantle (exposed or beneath other organs), dotted arrows currents on visceral mass. Currents on gills and palps (apart from rejection from tips of latter) not shown.

On the posterior third of the mantle surface a pair of horizontally extending mantle folds (Fig. 2, MF) form, by apposition, a roof over the applied mantle edges. Similar folds have been described by Kellogg (1915) in three other species of Mactridae, *Schizothaerus nuttalli* (Conrad), *Mactra solidissima* Dilwyn and *Spisula polynyma* Stimpson, although not in *S. planulata* (Conrad). Somewhat similar folds occur in various deposit-feeding Lamellibranchiata, species of *Scrobicularia*, *Abra* and *Macoma*, but they have a somewhat different

function. From the roof of the inner opening of the inhalant siphon a flap or siphonal membrane (Kellogg) hangs down (Fig. 2, SM). This, as shown below, is probably associated functionally with the mantle folds.

Removal of Waste Material

All currents on the mantle surface and visceral mass, but *not* on the gills, are shown in Fig. 2. The foot, as usual, is not ciliated. On the visceral mass the cilia (dotted arrows) carry material to an area (*z*) behind the posterior margin of the foot, which also receives matter rejected from the inner palps. On the mantle surface ciliary currents (broken and solid arrows) converge mid-ventrally posterior to the foot and at the entrance to the ventral tract, termed 'waste canal' by Kellogg, which is roofed by the mantle folds. The accumulated waste from the visceral mass and palps also passes into this canal in which all material is carried posteriorly.

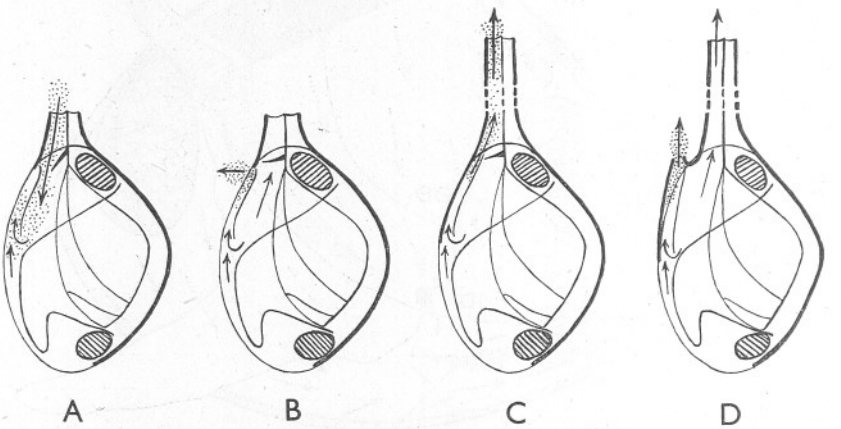

Fig. 3. Diagrammatical representations of cleansing mechanisms in various Mactridae. Extent of mantle fusion indicated by thickened outline. A, *Spisula subtruncata*, intake of sediment with inhalant current, showing action of siphonal membrane and passage of waste into canal guarded by mantle folds; B, *S. subtruncata*, ejection of waste ventrally through mantle aperture; C, *Schizothaerus nuttalli*, ejection of waste posteriorly through inhalant siphon owing to backward extension of waste canal behind siphonal membrane (based on Kellogg); D, *Lutraria lutraria*, ejection of waste posteriorly through fourth pallial aperture, mantle folds but *not* siphonal membrane being retained.

The siphonal membrane opens inward and so offers no resistance to the inflowing current. Kellogg suggests that 'its function is to throw the current downward on to the mantle edges, and away from the gills, when much sediment is present'. This view, implying that the membrane is an adaptation for life in silty water, appears correct. This deflexion of the water current necessitates some means of preventing the accumulation of waste at the base of the siphon from being swept forward. This, as Kellogg points out, explains the presence of the mantle folds which over-arch the waste canal. The action of both the membrane and the folds is shown diagrammatically in Fig. 3 A, B.

In *Schizothaerus nuttalli* the mantle edges, as Kellogg has shown, are fused as far forward as the anterior end of the mantle folds (see Fig. 3 C). But here the mantle folds and the waste canal terminate *behind* the siphonal membrane so that when the adductors contract for cleansing, the accumulated waste is ejected through the long inhalant siphon in the usual manner (Fig. 3 C). This animal, the Pacific horse-clam or gaper, is one of the largest of lamellibranchs, with a shell attaining a length of 8 and a breadth of 5 in. The fused siphons, encased in periostracum as in all Mactridae, are very long so that the animal often occurs at depths of up to 2 ft. or over (Quayle, 1941). But in the shallow burrowers, such as *S. subtruncata* and, judging from Kellogg's figure, in *S. polynyma*, these folds terminate, and the waste accumulates, *in front of* the membrane as shown in Fig. 2. This would appear to explain the local separation of the mantle edges in this region in *S. subtruncata*. Kellogg makes no mention of a similar opening in *S. polynyma*, but his account of this species is brief. In the former species a slow current of water is drawn in through this opening when the adductors are relaxed, but when they contract the waste is ejected through it. Back pressure of water will drive the siphonal membrane back and largely, if not completely, block the lumen of the siphon. The differences between this condition and that described by Kellogg in *Schizothaerus* are indicated in Fig. 3 B and C.

Conditions are somewhat different in *Mactra solidissima*, where Kellogg found that cilia and muscle combine to remove the waste ventrally. In the unrelated *Cardium corbis* Martyn all waste matter is so removed by ciliary action alone. In neither of these species is the posterior end of the animal buried, and this method of cleansing represents, Kellogg states, 'the usual procedure in forms with free mantle margins, and which are not completely buried in a burrow'. Waste could certainly not be removed ventrally by ciliary action in *Spisula subtruncata* which is completely covered with sand when it burrows.

The expulsion of waste ventrally following contraction of the adductors in *S. subtruncata* thus involves the presence of what is in effect, if not structurally, a fourth pallial aperture. This gives the key to the explanation of conditions here for the first time fully described in *Lutraria lutraria*.

LUTRARIA LUTRARIA

External Appearance and Habits

Lutraria lutraria (Fig. 4) is adapted for deep burrowing usually in rather shifting sands, although it also lives in mud where this is overlaid with sand. It occurs on the shore near low water of spring tides and in the sublittoral zone. The large oval shell with a wide posterior gape closely resembles that of the other genera of deep-burrowing lamellibranchs, *Mya* and *Panope*. This resemblance is the result of convergence due to similarity of habits. Attention

is here confined to the less obvious but fundamental relationship between *Lutraria lutraria* and the shallow burrowing species of the Mactridae, in particular *Spisula subtruncata*.

The shell attains a size of some 13 cm. long by 7 cm. broad. The massive, fused siphons extend for up to three times the length of the shell and, apart from their size, resemble in all respects those of *S. subtruncata*, being similarly covered with periostracum and fringed with tentacles and with a membrane round the exhalant siphon. There is also a true fourth pallial aperture. As shown in Fig. 4, the distended mantle edges extend for some distance beyond the margin of the shell and, at the base of the inhalant siphon, form a posteriorly directed papilla which marks the site of this aperture (FA).

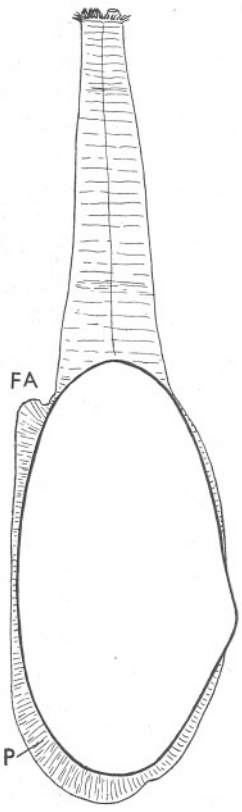

Fig. 4. *Lutraria lutraria*, fully expanded animal viewed from right side. $\times \frac{1}{2}$. FA, fourth pallial aperture; P, periostracum covering exposed mantle surfaces and siphons.

The Mantle Cavity

The disposition of the organs when exposed by the removal of the right shell valve and mantle lobe is shown in Fig. 5. Compared with *S. subtruncata*, they are extended longitudinally, especially in the posterior half of the body. The visceral mass is large, but the foot, though big for a deep burrower, is relatively smaller than in that species. The pedal gape is confined to the anterio-ventral surface. The gills are large and the outer demibranch only a little smaller than the inner one. Atkins (1937 *b*) describes them as plicate and homorhabdic, and has shown that currents run oralward along the marginal food grooves and along the gill axis, as in *S. subtruncata*. The long frontal cilia found in that species are absent. The palps are large but broad at the base which approaches in length the two free margins.

Between the wide pedal gape and the small fourth aperture, the mantle edges are fused for rather more than half the length of the ventral surface (between FA and PG). Atkins (1937 *c*) has shown that it is the cuticular linings of the applied epithelia that fuse, as shown in Fig. 8 (CF). She notes that, unlike *Ensis siliqua* (L.), *E. arcuatus* Jeffreys, and *Cultellus pellucidus* (Penn.), where cuticular fusion of the mantle edges also occurs, there is no rupture along the line of fusion when the animal dies and gapes widely. She thinks, therefore, that there may be fine cross-connecting strands of muscle in *Lutraria lutraria*. Owing to the folds into which the epithelia are thrown in fixation, she found it impossible to

determine this matter in sections. However, when examining stocks of specimens that had been preserved for several years in formalin it was found that the fused surfaces had either come apart or could be separated with the greatest ease. The exposed surfaces were perfectly smooth with no trace of any ruptured tissues. Apparently long exposure to formalin softens the cuticle along the line of fusion and this represents the only means whereby the two lobes are united. But they are certainly fused much more firmly than in *Ensis* or *Cultellus*.

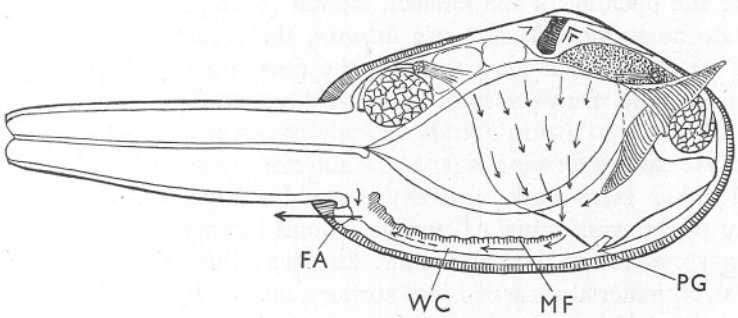

Fig. 5. *Lutraria lutraria*, animal viewed from right side after removal of right shell valve and mantle lobe, siphon cut longitudinally. $\times\frac{1}{2}$. PG, posterior end of pedal gape. Other lettering as before. Arrows indicate course of ciliary currents on the visceral mass and within the waste canal.

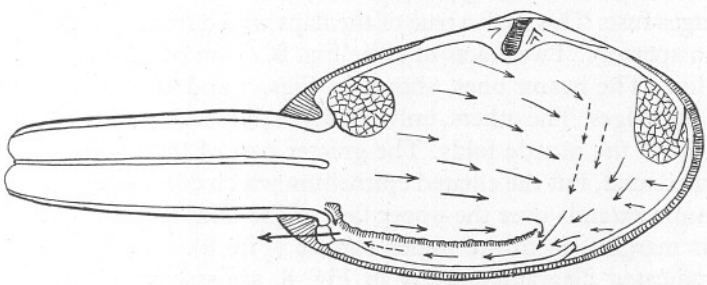

Fig. 6. *Lutraria lutraria*, as in Fig. 5, but with organs removed to expose the mantle surface and with arrows indicating the direction of the ciliary currents on this, weaker ones shown by broken arrows.

The fourth aperture is short, not more than 5 mm. long in an animal of shell length 11·5 cm. The mantle margins are here somewhat thicker, owing to a greater development of the pallial muscles. Well-developed mantle folds, shown in section in Fig. 8, extend from the base of the inhalant siphon, i.e. just posterior to the fourth aperture, to near the posterior margin of the foot and visceral mass, exactly as in *Spisula subtruncata* only for a relatively longer distance owing to the posterior extension of the body in *Lutraria lutraria*. There is no trace of a siphonal membrane.

Removal of Waste Material

The course of the ciliary currents on the visceral mass and of those on the surface of the mantle is shown in Figs. 5 and 6. On the former, material is carried ventrally to the posterior margin adjacent to the hinder surface of the foot. Conditions therefore resemble those in *Spisula subtruncata* and not in *Mya arenaria* L., where all currents beat towards vortices on either side of the posterior end of the more longitudinally extended visceral mass and nearly opposite the opening of the inhalant siphon (Kellogg, 1915; Yonge, 1923). There are no vortices in *Lutraria lutraria*, the accumulated waste material passing off the visceral mass to enter the posterior end of the waste canal (Fig. 5). On the mantle surface also, the direction of the ciliary currents is essentially similar to that in *Spisula subtruncata*. Over the posterior two-thirds, particles are carried forward as far as the anterior margin of the currents on the visceral mass. Here weak, ventrally directed, currents convey them to the entrance of the waste canal. Currents around the margin of the wide pedal gape carry material to the same point. In *Mya*, where the currents are more powerful, all material is carried into vortices, one on each side of the posterior end of the pedal gape.

The currents in the waste canal, when viewed from above with the mantle folds drawn apart, are shown in Fig. 7. All waste, as shown above, enters this canal. There are no cilia along the mid-line, where the cuticular surfaces of the mantle edges fuse. This is also true of the flaps which fringe the pedal gape and the fourth aperture. Two tracts of cilia (Fig. 8, *c*) are present on either side of the mid-line. The nearer ones, shown in Figs. 7 and 8, lie on the surface of a pair of low ridges. The others, only shown in the section (Fig. 8), are situated at the bases of the mantle folds. The greater part of the under surface of the folds is unciliated, but the ciliated epithelium which covers the general surface of the mantle extends over the upper face of the folds and for a short distance over their margins on to the under surface (Fig. 8). Subepithelial mucous glands, indicated diagrammatically in Fig. 8, are associated with all ciliated areas. The unciliated epithelium is much lower and almost devoid of glands.

Within the anterior half of the canal particles travel back with some speed, but behind this, in the region indicated by the broken arrows, the currents are very weak. More powerful currents exist between the base of the inhalant siphon and the fourth aperture towards which they carry particles. Conditions are thus very different from those in *Mya*. There an exceptionally powerful posteriorly beating tract of cilia occupies a broad mid-ventral area formed by the complete fusion of the mantle edges. Elongated areas of mucous cells on either side of the pedal opening (originally described by Vlès, 1909) supply mucus in which the waste particles are consolidated in masses at the base of the inhalant siphon through which they are periodically ejected. No such glandular areas are present in *Lutraria lutraria*.

The necessity for removing waste must be no less in *Lutraria* than in *Mya*, but the mechanism is certainly different. When fully expanded, as shown in Fig. 4, the fourth aperture is normally closed. But the immediate effect of contraction by the locally enlarged pallial muscles, which accompanies that of the adductors, is to pull the lips apart so that a longitudinal slit is converted

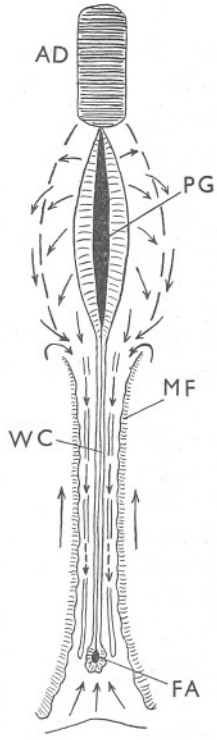

Fig. 7.

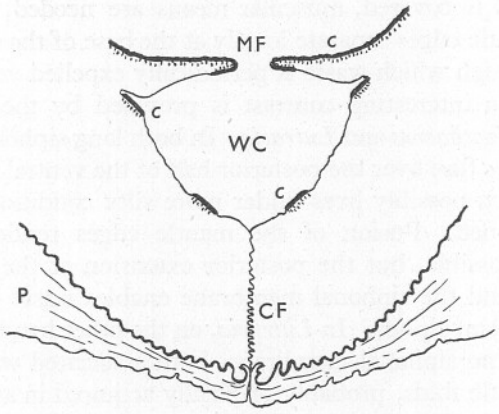

Fig. 8.

Fig. 7. *Lutraria lutraria*, mid-ventral region of the mantle viewed from above. $\times \frac{3}{4}$. AD, anterior adductor; PG, pedal gape. Other lettering as before. Arrows indicate direction of ciliary currents carrying material to fourth aperture.

Fig. 8. *Lutraria lutraria*, semi-diagrammatic drawing of section through the fused mantle edges and waste canal. $\times 2$. *c*, areas of ciliated epithelium with underlying mucous glands; CF, cuticular fusion of mantle edges. Other lettering as before.

into a circular opening. As already noted, this points posteriorly and is in line with the waste canal. Hence all material within this will be ejected through the fourth aperture. Bloomer (1903) noted that *Lutraria* uses this 'aperture frequently in suddenly ejecting water or any objectionable matter from the pedal cavity'. Atkins (1937 *c*) agrees with him. Neither, however, notes the presence of the pallial folds. The absence of a siphonal membrane in *Lutraria*, possibly correlated with the less silty environment, enables the greater part of

the water in the large inhalant chamber to be expelled at the same time through the inhalant siphon, as in the even larger *Schizothaerus* where the waste is carried out by this route. In Fig. 3 D conditions in *Lutraria* are shown diagrammatically in comparison with those in *Spisula subtruncata* and in *Schizothaerus*.

Discussion

It would appear from the foregoing account that a siphonal membrane has evolved in shallow-burrowing Mactridae, such as *Spisula subtruncata* and *S. polynyma*, as an adaptation to life in silty water. The long frontal cilia on the gills of the former, described by Atkins (1937 *a*, *b*), represent a further adaptation to these conditions. The protection of the waste canal by mantle folds is correlated initially with the presence of the siphonal membrane, as postulated by Kellogg. Where the hind end of the shell is not covered when the animal burrows, as in *Mactra solidissima*, ciliary currents may be adequate to remove the waste ventrally from the canal. But in *S. subtruncata*, where the entire shell is covered, muscular means are needed, and correlated with this the mantle edges separate locally at the base of the siphons, providing an aperture through which waste is periodically expelled ventrally.

An interesting contrast is provided by the two deep-burrowing genera, *Schizothaerus* and *Lutraria*. In both long siphons are formed while the mantle edges fuse over the posterior half of the ventral surface. But in *Schizothaerus*, which possibly lives under more silty conditions, the siphonal membrane is retained. Fusion of the mantle edges renders ventral ejection of waste impossible, but the posterior extension of the mantle folds and waste canal behind the siphonal membrane enables waste to be carried out through the inhalant siphon. In *Lutraria*, on the other hand, there are no long frontal cilia and no siphonal membrane, both associated with life in silty water, but the mantle folds, probably originally acquired in association with the membrane, remain. They retain their function because a true fourth aperture is present which, owing to the protrusion of the mantle edges, is directed posteriorly. The waste is thus expelled along a passage parallel to, but owing to the intervention of the mantle folds distinct from, the inhalant siphon. Owing to its descent from some form not unlike *Spisula subtruncata*, the cleansing mechanisms of *Lutraria* are very unlike those of *Mya*, despite the similarity of external form and of habit in the two genera.

A fourth aperture is present in a number of other Lamellibranchiata, in species of *Ensis* and *Cultellus pellucidus* and in many of the Anatinacea (Pelseneer, 1890, 1911). The nature of the opening in the former has been discussed by Bloomer (1903), Graham (1931) and Atkins (1937 *c*). In *Ensis* it lies in about the middle of the ventral surface, in *Cultellus* it is more anterior. The mantle edges between the fourth and pedal apertures are united only by cuticular fusion (Atkins, 1937 *c*), and very readily separate when the animals

are removed from the sand or mud which normally presses against the shell valves. Atkins considers that the function of the fourth aperture in these animals is to act 'normally as an additional inhalant aperture, and, on sudden closure of the valves, for ejection of unwanted particles'. The former function can be at best merely incidental; any opening into the inhalant cavity will admit water when the lateral cilia on the gills are beating. The same criticism can be made of the second function ascribed to it. Graham (1931) has shown that waste material is conveyed, in the usual manner, to the base of the inhalant siphon in *Ensis siliqua*. It appears more probable that the fourth aperture in these animals is essentially a safety valve which permits the ventral extrusion of some of the water in the mantle cavity when these rapidly burrowing animals make the sudden muscular contractions involved in downward movement. It is certainly not associated with special mechanisms concerned with collection of waste as it is in *Lutraria*.

In the Anatinacea the aperture lies, as in *Lutraria*, at or near the base of the inhalant siphon. The mantle edges are extensively fused along the ventral surface. Atkins (1937*c*) has shown that there is complete tissue fusion in *Thracia villosiuscula* F. & H., and this is probably true of all Anatinacea. Kellogg is the only worker to examine the mantle cavity in life, and he has shown that waste collects in the vicinity of the fourth aperture in *Mytilimeria nuttalli* (Conrad) and *Lyonsia saxicola* Baird. But there are no associated mantle folds, and he was unable to determine with certainty the significance of the opening. In the abyssal genera, *Asthenothaerus* and *Periploma*, Pelseneer (1911) describes a third ventral adductor immediately posterior to the fourth aperture. Such evidence as there is would therefore seem to indicate that the function of the fourth aperture in the Anatinacea is similar to that in *Lutraria*. But further study in life of species of this little-known group is needed.

Summary

Spisula subtruncata is a shallow-burrowing member of the Mactridae which inhabits silty sand. Adaptations to such conditions include long frontal cilia on the gills (Atkins), and the presence of a siphonal membrane with associated mantle folds over-arching a waste canal, as postulated by Kellogg for allied species.

The mantle edges are free ventrally, but are normally closely applied except for a short distance at the base of the inhalant siphon, an effective fourth pallial aperture being so formed. Through this opening material from the waste canal is ejected.

Lutraria lutraria is a deep-burrowing species belonging to the same family. The general resemblance to *Mya arenaria* is due to convergence. Cleansing currents resemble those of *Spisula subtruncata* and there is a similar waste canal, but the siphonal membrane and the long frontal cilia associated with a silty environment are absent.

The mantle edges are firmly united along the posterior half of the ventral surface by fusion of the bounding cuticle (Atkins), but there is a true morphological fourth aperture at the base of the inhalant siphon. This is directed posteriorly and all waste is probably ejected through it.

Schizothaerus nuttalli, described by Kellogg, is another deep-burrowing member of the Mactridae, but here the mantle edges are fused without leaving a fourth aperture. Waste is ejected through the inhalant siphon owing to the extension behind the siphonal membrane of the waste canal and mantle folds.

It is suggested that the fourth aperture in species of *Ensis* and *Cultellus* acts as a safety valve through which some of the water leaves the mantle cavity following the sudden contractions which occur in these rapidly burrowing species.

The fourth aperture in many Anatinacea has never been adequately studied. Existing data indicate that it may be concerned with the ejection of waste, but there is no associated waste canal with mantle folds.

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THE STRUCTURE AND LIFE HISTORY OF SOME MINUTE PROSOBRANCHS OF ROCK POOLS: *SKENEOPSIS PLANORBIS* (FABRICIUS), *OMALOGYRA ATOMUS* (PHILIPPI), *RISSOELLA DIAPHANA* (ALDER) AND *RISSOELLA OPALINA* (JEFFREYS)

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(Plate IV and Text-figs. 1–6)

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Introduction

Amongst the more common inhabitants of the seashore are a number of prosobranch molluscs which, owing to the smallness of their size, have escaped investigation. *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys) are some of the least known of these: their shells, and so much of their body as is exposed when the animal is creeping, have been described by Forbes & Hanley (1853) and Jeffreys (1867), but the internal anatomy and most of their habits are entirely unknown. The present investigation shows that in many respects these molluscs are highly specialized in correlation with their small size and their habitat. The more important features of structure and life history are described for each animal and, in the discussion, the features which they share because of their minuteness and their adaptation to a rock-pool habitat are dealt with.

Skeneopsis planorbis (Fabricius)

Skeneopsis is found abundantly all around the British Isles and is especially plentiful in coralline pools. The shell is roughly discoidal in shape, having an extremely depressed, blunt and rounded spire which is scarcely visible unless the shell be viewed edge-on (Fig. 1 A, B). There are four rather loosely coiled

whorls, with deep sutures, and the umbilicus is open and funnel-shaped. The last whorl is by far the largest. The mouth is almost circular, its lips projecting outwards, thin and entire in young specimens, though somewhat flexuous in older ones looking as if an original entire edge had been clipped. The only sculpture on the shell is due to the lines of growth (LG). The colour varies: typically, as in young specimens, the shell is reddish brown and glossy; older specimens may be dull and either a pale buff or olive green owing to algal

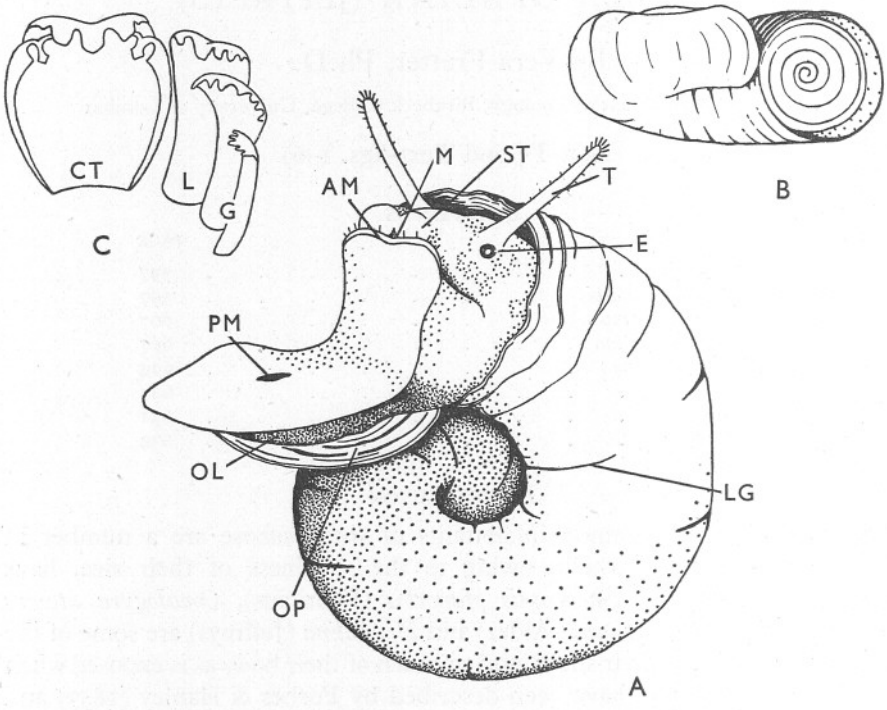

Fig. 1. *Skeneopsis planorbis*. A. Living animal seen from the left and below. ×45. B. Shell from the side. ×30. C. Half row of radula teeth. ×230. AM, opening of anterior pedal gland; CT, central tooth of radula; E, eye; G, marginal tooth of radula; L, lateral tooth of radula; LG, puckered lines of growth; M, mouth; OL, opercular lobe of foot; OP, operculum; PM, opening of posterior pedal gland; ST, snout; T, tentacle.

growth. As the mollusc grows to maturity algal spores gain a holdfast on the surface of the shell. These germinate and the small plants become embedded in a thick layer of mucus which they themselves secrete, and the layer may be added to by diatoms which are scattered in large numbers amongst the algal filaments. Thus in older specimens the shell is completely encased in a mucous covering from which arises a thick woolly coat of algal filaments.

When *Skeneopsis* crawls over weed or rock the shell is not carried erect but tilted sideways and may be rocked from side to side. The exposed parts of the

body have a ground colour of greyish white. On the metapodial (opercular) lobes (Fig. 1 and Pl. IV, fig. 1, OL) there is a mottling of deep grey or black, and patches of yellow occur on the body, all due to epithelial pigment granules. Two yellow patches lie between the eyes, each over a similarly pigmented region of the buccal cavity, with another of smaller size behind each eye, and a streak underlies the operculum. The two dorsal patches which lie close together are contiguous with a black streak extending for some distance beneath the shell. The head bears a pair of long cylindrical and widely diverging tentacles which may be waved slowly in the water as the mollusc creeps. Each is scantily covered with motionless cilia (Fig. 1, T), and the eye is situated on the outer side of the swollen base (E). The snout (ST) is broad with a mid-dorsal groove dividing it into two rounded lobes, between which lies ventrally the mouth (M). The foot is relatively short, truncated in front and tapering along the posterior third to a blunt point. Around the anterior edge a deep groove marks the opening of the anterior pedal mucous gland (AM), and a row of stiff cilia arises from the upper lip of the groove. The anterior pedal gland comprises three groups of mucous and mucoid cells set in a transverse row in the anterior tissues of the foot (Pl. IV, fig. 1, MG); the middle group is the most extensive, and the whole appears as a semicircular opaque white mass in the living animal. Gland cells of a similar nature are embedded in the tissues of the sole (GD) and open singly between the cells of the ciliated columnar epithelium. Yet another and still greater supply of mucus comes from a posterior pedal gland which opens as a mid-ventral longitudinal slit about a third of the pedal length from the posterior end (Fig. 1, PM). The opening leads dorsally into a ciliated duct (Pl. IV, fig. 1, D), which soon bifurcates into left and right branches, and each becomes surrounded by glandular tissue which extends into the haemocoel. On each side, at about the level of the pedal ganglia, this tissue then splits into two lobes, one passing dorsally (AL) and the other running back alongside the oesophagus and immediately above the columellar muscle (PL).

The animal is fond of crawling on the surface film of water and may suspend itself from this by means of a viscid thread issuing from the posterior pedal gland. The free end of the thread floats on the surface, and, as the animal slowly descends, it plays out the mucous rope: from the opening of the gland the secretion is directed into a longitudinal groove along the sole, where, in contact with the sea water, it hardens before leaving the posterior end of the foot. In such a manner *Skeneopsis* may finally reach the bottom of a shallow pool, or, if the thread be short, the mollusc may even reverse its course and climb along it to reach the surface again.

The mantle cavity extends along the whole length of the body whorl. On the left side is the well-developed, bipectinate osphradium, and dorsal to this the monopectinate gill, which has only nine finger-like filaments (Pl. IV, fig. 1, F) projecting downwards from a somewhat elongated axis. The hypobranchial

gland runs along the right wall of the cavity anteriorly. It passes back parallel to, and just above, the rectum as a single layer of mucous and mucoid cells, but near the level of the posterior end of the ctenidium the gland thickens, occupies a more dorsal position and the mucus is replaced by another type of protein. Posteriorly, the mantle cavity is much reduced in size, and, covered by the hypobranchial gland, pushes back over the kidney (K), which therefore opens on its floor. In the female the large glandular genital duct projects from the right wall of the mantle and partly obliterates the cavity on this side, the rectum running along its median side to open on a prominent papilla anterior to the genital opening. In the male the genital duct is far less conspicuous, and the anal papilla smaller. The penis (PE), which arises behind the right tentacle, is slightly compressed laterally and when fully developed extends the whole length of the mantle cavity.

The Alimentary Canal

The mouth leads dorsally into a short though very dilatable tube, a ventral extension of the buccal cavity which bears a cuticle, and this also spreads on to the floor of the main part of the cavity in which the odontophore lies. At the inner end of the buccal tube the cuticle is thickened to form two jaws laterally placed, each consisting of six transverse rows of teeth with about twenty in each row (Pl. IV, fig. 1, J); each tooth is secreted by a single epithelial cell. When the animal is feeding, the radula (R) works over the surface of the weed or other material to rasp off diatoms and algal cells, the jaws meanwhile gripping the substratum. The radula (Fig. 1 C) is made up of numerous

EXPLANATION OF PLATE IV

Fig. 1.

Skeneopsis planorbis. Right lateral view of whole animal seen as a transparent object. ×80. A, anus; AH, anterior region of stomach; AL, anterior lobe of posterior pedal gland; AM, opening of anterior pedal gland; BU, buccal ganglion; C, columellar muscle; CD, ciliated duct leading from vas deferens to mantle cavity; CE, cerebral ganglion; D, duct of posterior pedal gland; DI, digestive gland; DP, penial duct; E, eye; EX, spherules in excretory cells of digestive gland; F, gill filament; GA, parapedal ganglion; GD, mucous glands opening on sole of foot; H, heart; I, intestine; J, jaw; K, kidney; L, opening of digestive gland into stomach; LI, left salivary gland; MA, mantle; MG, anterior pedal gland; OE, oesophagus; OL, opercular lobe of foot; OP, operculum; P, prostate; PE, penis; PG, pedal ganglion; PH, posterior region of stomach; PL, posterior lobe of posterior pedal gland; PR, pleural ganglion; R, radula; RA, radular sac; RI, right salivary gland; ST, snout; T, tentacle; TE, testis; TO, statocyst; V, vesicula seminalis.

Fig. 2.

Omalogyra atomus. Right lateral view of whole animal seen as a transparent object. ×120. AB, albumen gland; AG, anterior lobe of digestive gland; B, buccal cavity; BC, bursa copulatrix; CG, capsule gland; DA, duct of albumen gland; FC, fertilization chamber; GA, genital aperture; HD, hermaphrodite duct; HL, head lobe; KM, large glands opening into mantle cavity near anus; MG, anterior pedal gland; MU, mucous gland; MT, muscular tube; O, ovarian duct; OD, muscles of odontophore; OM, opening of albumen gland into mucous gland; OPE, opening of sperm sac into prostate; OV, egg in ovary; PD, pallial vas deferens; PM, opening of posterior pedal gland; PO, pallial oviduct; SP, sperm sac; ST, stomach. Other letters as in fig. 1 above.

are removed from the sand or mud which normally presses against the shell valves. Atkins considers that the function of the fourth aperture in these animals is to act 'normally as an additional inhalant aperture, and, on sudden closure of the valves, for ejection of unwanted particles'. The former function can be at best merely incidental; any opening into the inhalant cavity will admit water when the lateral cilia on the gills are beating. The same criticism can be made of the second function ascribed to it. Graham (1931) has shown that waste material is conveyed, in the usual manner, to the base of the inhalant siphon in *Ensis siliqua*. It appears more probable that the fourth aperture in these animals is essentially a safety valve which permits the ventral extrusion of some of the water in the mantle cavity when these rapidly burrowing animals make the sudden muscular contractions involved in downward movement. It is certainly not associated with special mechanisms concerned with collection of waste as it is in *Lutraria*.

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Spisula subtruncata is a shallow-burrowing member of the Mactridae which inhabits silty sand. Adaptations to such conditions include long frontal cilia on the gills (Atkins), and the presence of a siphonal membrane with associated mantle folds over-arching a waste canal, as postulated by Kellogg for allied species.

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Lutraria lutraria is a deep-burrowing species belonging to the same family. The general resemblance to *Mya arenaria* is due to convergence. Cleansing currents resemble those of *Spisula subtruncata* and there is a similar waste canal, but the siphonal membrane and the long frontal cilia associated with a silty environment are absent.

The mantle edges are firmly united along the posterior half of the ventral surface by fusion of the bounding cuticle (Atkins), but there is a true morphological fourth aperture at the base of the inhalant siphon. This is directed posteriorly and all waste is probably ejected through it.

Schizothaerus nuttalli, described by Kellogg, is another deep-burrowing member of the Mactridae, but here the mantle edges are fused without leaving a fourth aperture. Waste is ejected through the inhalant siphon owing to the extension behind the siphonal membrane of the waste canal and mantle folds.

It is suggested that the fourth aperture in species of *Ensis* and *Cultellus* acts as a safety valve through which some of the water leaves the mantle cavity following the sudden contractions which occur in these rapidly burrowing species.

The fourth aperture in many Anatinacea has never been adequately studied. Existing data indicate that it may be concerned with the ejection of waste, but there is no associated waste canal with mantle folds.

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THE STRUCTURE AND LIFE HISTORY OF SOME MINUTE PROSOBRANCHS OF ROCK POOLS: *SKENEOPSIS PLANORBIS* (FABRICIUS), *OMALOGYRA ATOMUS* (PHILIPPI), *RISSOELLA DIAPHANA* (ALDER) AND *RISSOELLA OPALINA* (JEFFREYS)

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(Plate IV and Text-figs. 1–6)

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Introduction

Amongst the more common inhabitants of the seashore are a number of prosobranch molluscs which, owing to the smallness of their size, have escaped investigation. *Skeneopsis planorbis* (Fabricius), *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys) are some of the least known of these: their shells, and so much of their body as is exposed when the animal is creeping, have been described by Forbes & Hanley (1853) and Jeffreys (1867), but the internal anatomy and most of their habits are entirely unknown. The present investigation shows that in many respects these molluscs are highly specialized in correlation with their small size and their habitat. The more important features of structure and life history are described for each animal and, in the discussion, the features which they share because of their minuteness and their adaptation to a rock-pool habitat are dealt with.

Skeneopsis planorbis (Fabricius)

Skeneopsis is found abundantly all around the British Isles and is especially plentiful in coralline pools. The shell is roughly discoidal in shape, having an extremely depressed, blunt and rounded spire which is scarcely visible unless the shell be viewed edge-on (Fig. 1 A, B). There are four rather loosely coiled

whorls, with deep sutures, and the umbilicus is open and funnel-shaped. The last whorl is by far the largest. The mouth is almost circular, its lips projecting outwards, thin and entire in young specimens, though somewhat flexuous in older ones looking as if an original entire edge had been clipped. The only sculpture on the shell is due to the lines of growth (LG). The colour varies: typically, as in young specimens, the shell is reddish brown and glossy; older specimens may be dull and either a pale buff or olive green owing to algal

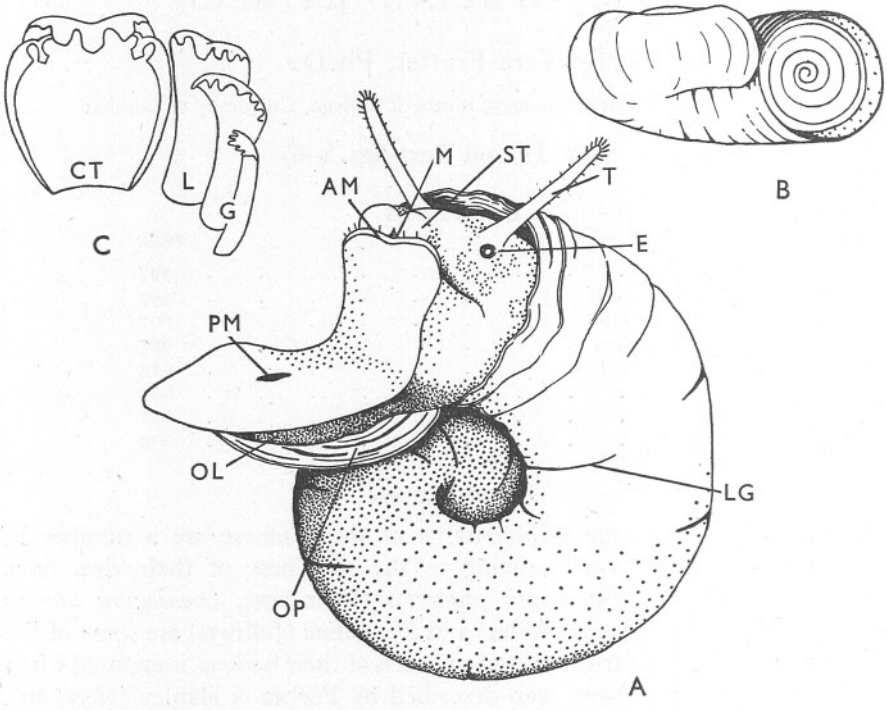


Fig. 1. *Skeneopsis planorbis*. A. Living animal seen from the left and below. ×45. B. Shell from the side. ×30. C. Half row of radula teeth. ×230. AM, opening of anterior pedal gland; CT, central tooth of radula; E, eye; G, marginal tooth of radula; L, lateral tooth of radula; LG, puckered lines of growth; M, mouth; OL, opercular lobe of foot; OP, operculum; PM, opening of posterior pedal gland; ST, snout; T, tentacle.

growth. As the mollusc grows to maturity algal spores gain a holdfast on the surface of the shell. These germinate and the small plants become embedded in a thick layer of mucus which they themselves secrete, and the layer may be added to by diatoms which are scattered in large numbers amongst the algal filaments. Thus in older specimens the shell is completely encased in a mucous covering from which arises a thick woolly coat of algal filaments.

When *Skeneopsis* crawls over weed or rock the shell is not carried erect but tilted sideways and may be rocked from side to side. The exposed parts of the

body have a ground colour of greyish white. On the metapodial (opercular) lobes (Fig. 1 and Pl. IV, fig. 1, OL) there is a mottling of deep grey or black, and patches of yellow occur on the body, all due to epithelial pigment granules. Two yellow patches lie between the eyes, each over a similarly pigmented region of the buccal cavity, with another of smaller size behind each eye, and a streak underlies the operculum. The two dorsal patches which lie close together are contiguous with a black streak extending for some distance beneath the shell. The head bears a pair of long cylindrical and widely diverging tentacles which may be waved slowly in the water as the mollusc creeps. Each is scantily covered with motionless cilia (Fig. 1, T), and the eye is situated on the outer side of the swollen base (E). The snout (ST) is broad with a mid-dorsal groove dividing it into two rounded lobes, between which lies ventrally the mouth (M). The foot is relatively short, truncated in front and tapering along the posterior third to a blunt point. Around the anterior edge a deep groove marks the opening of the anterior pedal mucous gland (AM), and a row of stiff cilia arises from the upper lip of the groove. The anterior pedal gland comprises three groups of mucous and mucoid cells set in a transverse row in the anterior tissues of the foot (Pl. IV, fig. 1, MG); the middle group is the most extensive, and the whole appears as a semicircular opaque white mass in the living animal. Gland cells of a similar nature are embedded in the tissues of the sole (GD) and open singly between the cells of the ciliated columnar epithelium. Yet another and still greater supply of mucus comes from a posterior pedal gland which opens as a mid-ventral longitudinal slit about a third of the pedal length from the posterior end (Fig. 1, PM). The opening leads dorsally into a ciliated duct (Pl. IV, fig. 1, D), which soon bifurcates into left and right branches, and each becomes surrounded by glandular tissue which extends into the haemocoel. On each side, at about the level of the pedal ganglia, this tissue then splits into two lobes, one passing dorsally (AL) and the other running back alongside the oesophagus and immediately above the columellar muscle (PL).

The animal is fond of crawling on the surface film of water and may suspend itself from this by means of a viscid thread issuing from the posterior pedal gland. The free end of the thread floats on the surface, and, as the animal slowly descends, it plays out the mucous rope: from the opening of the gland the secretion is directed into a longitudinal groove along the sole, where, in contact with the sea water, it hardens before leaving the posterior end of the foot. In such a manner *Skeneopsis* may finally reach the bottom of a shallow pool, or, if the thread be short, the mollusc may even reverse its course and climb along it to reach the surface again.

The mantle cavity extends along the whole length of the body whorl. On the left side is the well-developed, bipectinate osphradium, and dorsal to this the monopectinate gill, which has only nine finger-like filaments (Pl. IV, fig. 1, F) projecting downwards from a somewhat elongated axis. The hypobranchial

gland runs along the right wall of the cavity anteriorly. It passes back parallel to, and just above, the rectum as a single layer of mucous and mucoid cells, but near the level of the posterior end of the ctenidium the gland thickens, occupies a more dorsal position and the mucus is replaced by another type of protein. Posteriorly, the mantle cavity is much reduced in size, and, covered by the hypobranchial gland, pushes back over the kidney (K), which therefore opens on its floor. In the female the large glandular genital duct projects from the right wall of the mantle and partly obliterates the cavity on this side, the rectum running along its median side to open on a prominent papilla anterior to the genital opening. In the male the genital duct is far less conspicuous, and the anal papilla smaller. The penis (PE), which arises behind the right tentacle, is slightly compressed laterally and when fully developed extends the whole length of the mantle cavity.

The Alimentary Canal

The mouth leads dorsally into a short though very dilatable tube, a ventral extension of the buccal cavity which bears a cuticle, and this also spreads on to the floor of the main part of the cavity in which the odontophore lies. At the inner end of the buccal tube the cuticle is thickened to form two jaws laterally placed, each consisting of six transverse rows of teeth with about twenty in each row (Pl. IV, fig. 1, J); each tooth is secreted by a single epithelial cell. When the animal is feeding, the radula (R) works over the surface of the weed or other material to rasp off diatoms and algal cells, the jaws meanwhile gripping the substratum. The radula (Fig. 1 C) is made up of numerous

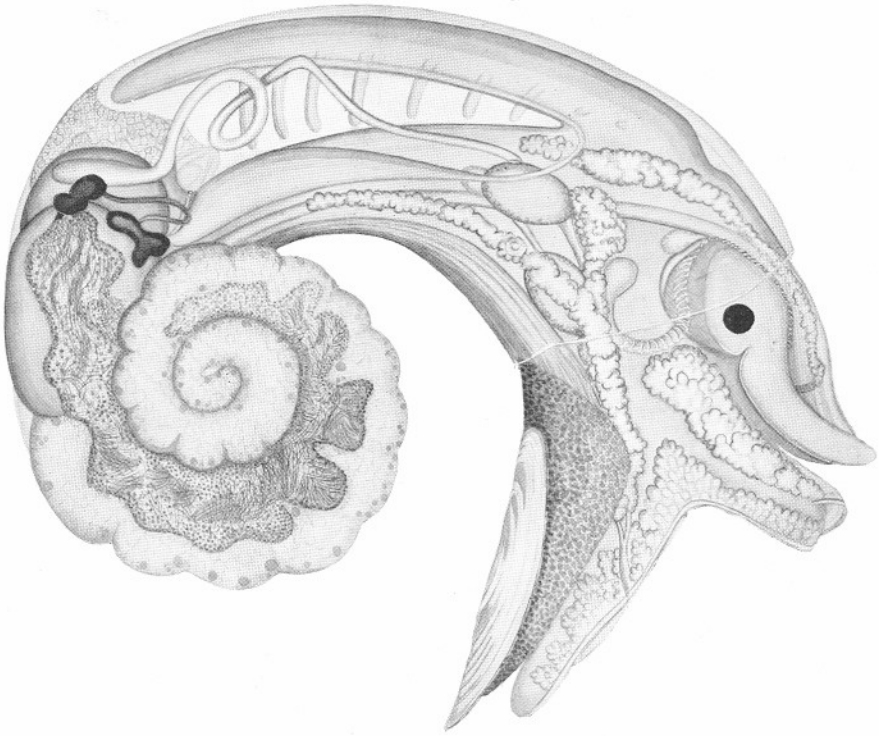
EXPLANATION OF PLATE IV

Fig. 1.

Skeneopsis planorbis. Right lateral view of whole animal seen as a transparent object. ×80. A, anus; AH, anterior region of stomach; AL, anterior lobe of posterior pedal gland; AM, opening of anterior pedal gland; BU, buccal ganglion; C, columellar muscle; CD, ciliated duct leading from vas deferens to mantle cavity; CE, cerebral ganglion; D, duct of posterior pedal gland; DI, digestive gland; DP, penial duct; E, eye; EX, spherules in excretory cells of digestive gland; F, gill filament; GA, parapedal ganglion; GD, mucous glands opening on sole of foot; H, heart; I, intestine; J, jaw; K, kidney; L, opening of digestive gland into stomach; LI, left salivary gland; MA, mantle; MG, anterior pedal gland; OE, oesophagus; OL, opercular lobe of foot; OP, operculum; P, prostate; PE, penis; PG, pedal ganglion; PH, posterior region of stomach; PL, posterior lobe of posterior pedal gland; PR, pleural ganglion; R, radula; RA, radular sac; RI, right salivary gland; ST, snout; T, tentacle; TE, testis; TO, statocyst; V, vesicula seminalis.

Fig. 2.

Omalogyra atomus. Right lateral view of whole animal seen as a transparent object. ×120. AB, albumen gland; AG, anterior lobe of digestive gland; B, buccal cavity; BC, bursa copulatrix; CG, capsule gland; DA, duct of albumen gland; FC, fertilization chamber; GA, genital aperture; HD, hermaphrodite duct; HL, head lobe; KM, large glands opening into mantle cavity near anus; MG, anterior pedal gland; MU, mucous gland; MT, muscular tube; O, ovarian duct; OD, muscles of odontophore; OM, opening of albumen gland into mucous gland; OPE, opening of sperm sac into prostate; OV, egg in ovary; PD, pallial vas deferens; PM, opening of posterior pedal gland; PO, pallial oviduct; SP, sperm sac; ST, stomach. Other letters as in fig. 1 above.



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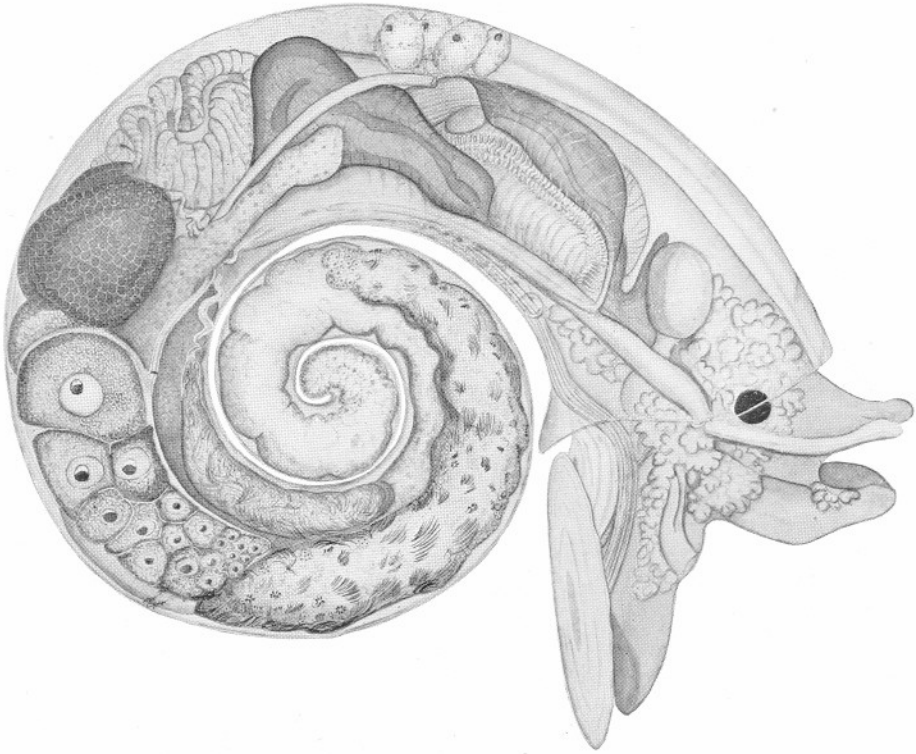

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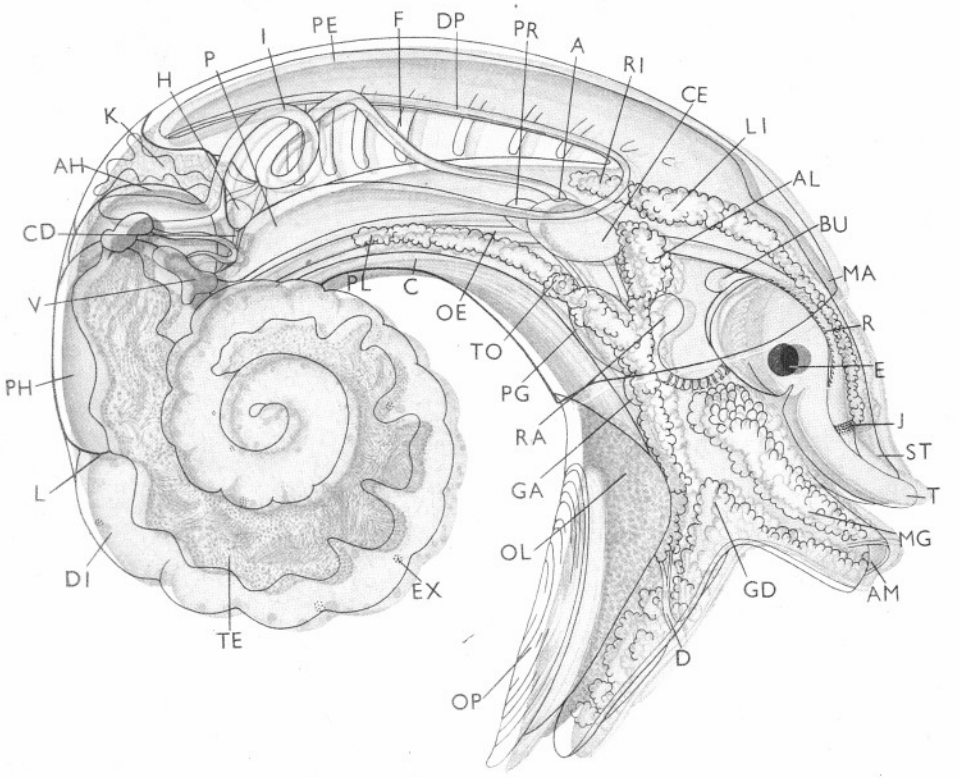
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Fig. 1.

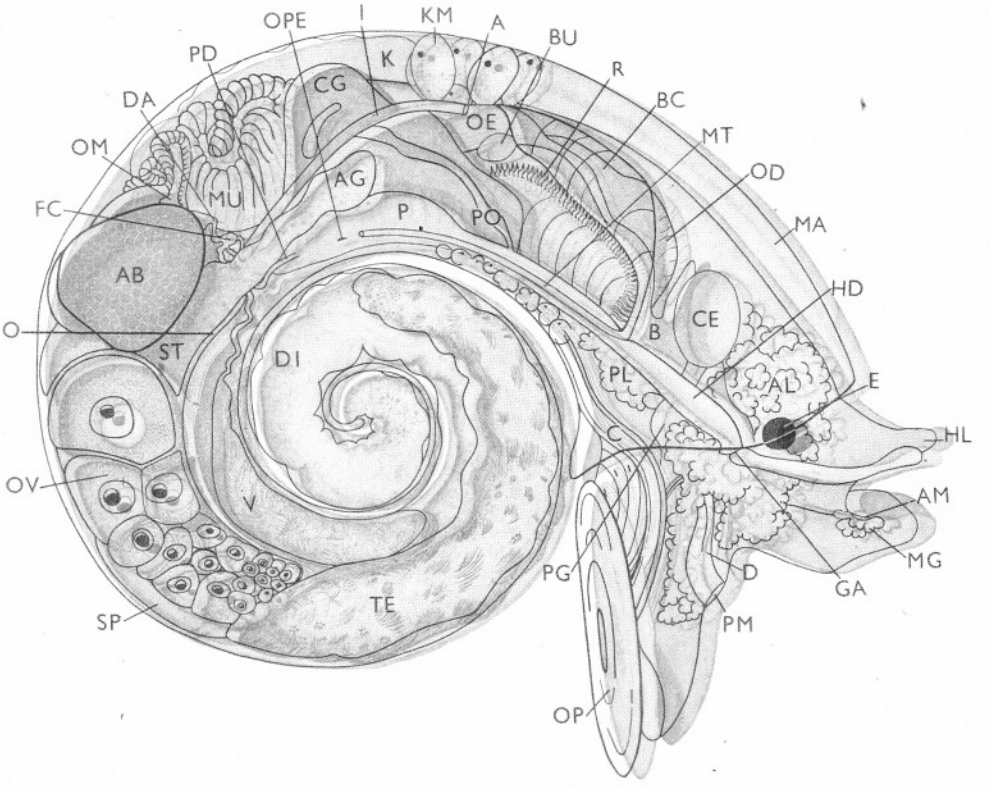
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Fig. 2.

transverse rows of sharply cusped teeth, each row comprising a large central tooth (CT) bordered on each side by one lateral (L) and two marginals (G).

Along the mid-dorsal wall of the buccal cavity is a deep ciliated channel along which the food is directed to the oesophagus. The salivary glands (Pl. IV, fig. 1, RI and LI) open at the extreme anterior end of this channel, one on either side. Their secretion lubricates the action of the radula and entangles the food particles which are drawn in by it. The glands run parallel with the oesophagus as far as the nerve ring, the one on the left side being slightly longer than that on the right. Mucous cells provide the greater part of the saliva. There is, however, a second type of secreting cell filled with protein spherules which swell and dissolve when expelled, probably liberating an enzyme.

The oesophagus (OE) is a straight, narrow, ciliated tube of about the same diameter throughout. From its origin at the posterior end of the buccal cavity it is directed ventrally and slightly to the left of the median line, and traverses the length of the body whorl. There are no glandular pouches along its course, as are common amongst herbivorous prosobranchs, and the only secreting cells are epithelial mucous glands.

The stomach is spacious and lies at the posterior end of the body whorl, at right angles to which it is elongated. It is divided by a transverse constriction into two regions: an anterior (AH), which is dome-shaped and lined by a columnar ciliated epithelium, the cilia being thick and closely set; and a more posterior one (PH), the wall of which is, in the main, cuticularized. The upper, anterior, chamber corresponds to the style sac of style-bearing prosobranchs and the lower, posterior, chamber to the part containing the gastric shield. The anterior wall of the posterior chamber is ciliated where it receives the opening of the oesophagus at the level of the transverse constriction. At the extreme posterior end is the opening of the single lobe of the digestive gland (L). The stomach, especially its anterior compartment, is conspicuous in the living animal since there is a heavy deposit of black spherules in the epithelial cells. The intestine (I) arises from the dorsal wall of the anterior chamber and bends abruptly to pass forward on the right side. For a short distance along its initial length can be traced a longitudinal groove bordered by a fold of epithelium. This gutter, with its accompanying fold, arises on the wall of the duct from the digestive gland, passes forwards to the anterior chamber of the stomach and so reaches the intestine. It affords a path by which waste from the duct may be conveyed to the intestine.

On histological grounds the intestine may be divided into four regions. The initial part, in which the columnar ciliated cells are heavily pigmented with black spherules, and along which the channel from the digestive gland can be traced, passes to a slightly wider and more muscular tube in which mucous cells alternate with ciliated cells. Here the faecal pellets are moulded: the particulate waste from the stomach, which consists of diatom cases, algal cells and detritus, is agglutinated by means of mucus and compacted into oval rods.

These are still further elaborated in the third section of the intestine, the longest of the four, which takes a somewhat sinuous course as it accompanies the genital duct along the right wall of the mantle cavity. In this section the mucous cells are replaced by another type of gland which is scattered somewhat sparingly amongst the ciliated cells—it is conical in shape, with a broad base, and tapering distally, and towards the base is a large round nucleus, with a prominent nucleolus. The cytoplasm is dense and contains small secretion spherules which swell in the lumen of the gut and presumably help to harden the outer rind of the pellet. In the terminal or rectal region the cilia are longer than elsewhere and mucous cells are scattered in the epithelium, increasing in number towards the anus.

The digestive gland (DI), together with the gonad (TE), constitute the visceral mass which occupies the smaller coils of the shell. The gonad, frequently the smaller of the two glands, lies on the right side. The digestive gland has a segmented appearance, since it is made up of a series of lobes which open into one another and increase in size towards the stomach, into which they ultimately open. The epithelium of the gland consists of three types of cells: the most frequent, the digestive cell, is narrow at the base and gradually broadens towards a rounded distal end where there is a dense layer of protoplasm containing innumerable small spherules. These have been seen to be discharged and are probably enzymatic. The rest of the cytoplasm, except around the nucleus, is filled with vacuoles which vary in size, and contain during life either a clear refringent liquid or agglomerations of fine particulate matter sometimes embedded in a mucoid substance. No diatoms, algal cells or any such particulate food has ever been found within the lumen of the digestive tubules. The stomach, however, may often be seen filled with such objects, and since only empty cases of diatoms and the walls of broken cells are to be found in the intestine, it may be assumed that the bulk of the digestive process occurs in the stomach and that only the resulting solution, with perhaps minute particles, enters the liver, and is taken up by the digestive cells for further treatment.

The two other types of cell, neither of which attains the height of that already described, occur in the crypts of the tubules. In one, which appears to be excretory in function, the protoplasm may be highly vacuolated and an irregular clump of brown or black granules be contained in each vacuole. A more frequent appearance is when the cell contains only one large vacuole filled with a single spherical mass of such granules. These can be seen through the shell of a living animal (EX). They have never been found in the lumen of the gland. Somewhat similar cells of undoubted excretory function are described in the digestive gland of tectibranchs (Fretter, 1939), and it is probable that, as in that group, waste matter is absorbed from the blood through the broad bases of the cells. This, however, has not been tested owing to the difficulty of injecting such small molluscs.

The third type of cell may be grouped in small numbers around the excretory cell, though sometimes it occurs alone in larger numbers. In longitudinal section it is triangular in outline with a broad base resting on the basement membrane and a tapering distal end which hardly reaches the surface of the epithelium. The spherical nucleus lies towards the base and has a large nucleolus. The protoplasm stains deeply with iron haematoxylin and is vacuolated. Each vacuole contains a colourless refringent spherule which gives a positive reaction for lime. The probable function of these cells is either to act as a storage of lime for shell formation, or for the purpose of controlling the reaction of the secretion from the digestive gland.

The Reproductive System

The male. The testis (Pl. IV, fig. 1, TE), situated on the right side of the visceral mass, consists of a linear series of lobes which open broadly into one another and lead finally to the gonadial duct. This acts as a vesicula seminalis (V) which is dilated with sperm from the onset of sexual maturity. It coils on the right side of the stomach and then leads into a short narrow tube with a straight course, conducting the sperm from the vesicula seminalis to the prostate (P). This tube, the renal vas deferens, is surrounded by a layer of circular muscles which closes the lumen except when spermatozoa are actually passing through it during copulation. It opens into the prostate gland on a small papilla. Alongside this is a ciliated duct (CD) which leaves the prostate and runs dorsally to open into the mantle cavity. Such an outlet to the mantle cavity has been described in certain Stenoglossa and in *Lamellaria*, and provides an escape for unwanted sperm (Fretter, 1941).

For the rest of its course the male duct runs straight along the right side of the mantle cavity to the penis (PE)—this section comprises the pallial vas deferens and along the posterior half the epithelium is tall and glandular and constitutes the prostate (P). The gland cells, which rest upon a basement membrane, are broad at the base and each tapers slightly towards the distal end. Wedged between the distal ends are ciliated cells which drive the prostatic secretion forward along the duct. The prostate is surrounded by a thin layer of connective tissue in which both circular and longitudinal muscle fibres occur. Anteriorly it ends abruptly, the duct narrows and is lined only by a ciliated columnar epithelium. The musculature, however, is greatly increased, for the circular muscle forms a layer which in thickness exceeds twice the height of the epithelial cells. Here, and along the penial duct, the histology of which is similar, the spermatozoa are conducted by peristaltic action.

The penis is somewhat compressed laterally and tapers to a point, the duct through it (DP) running near its ventral surface to open at the tip. Externally it is covered by a slightly cuticularized epithelium, except along the narrow dorsal and ventral walls where longitudinal strips of epithelial mucous glands occur, the secretion from which assists the passage of the penis through the

pallial groove of the female to reach the opening of the receptaculum seminis (Fig. 2, RE). Beneath the epithelium is a layer of circular and longitudinal muscle fibres, and through the thickness of the organ oblique and dorso-ventral fibres separate numerous blood spaces. These, when gorged with blood during copulation, so enlarge the penis that if the copulating partners be separated it is only after some minutes that the penis can regain its position of rest along the length of the mantle cavity.

The female. The ovary, on the right side of the visceral mass, occupies a position similar to that of the testis and extends as far as the posterior chamber of the stomach. From here a narrow ovarian duct (Fig. 2, O) passes towards the posterior end of the mantle cavity where it opens into the fertilization chamber (FC), placed at the posterior end of the pallial oviduct, and receiving a duct from the receptaculum seminis (DR), and another from the albumen gland (DA). Its walls are ciliated and muscular.

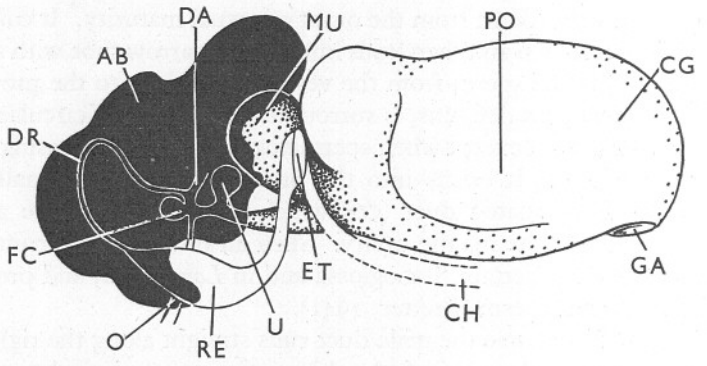

Fig. 2. *Skeneopsis planorbis.* Diagrammatic reconstruction of female genital duct. × 100. AB, albumen gland; CG, capsule gland; CH, channel along outer surface of mantle; DA, duct of albumen gland; DR, duct from receptaculum seminis; ET, entrance to receptaculum seminis; FC, fertilization chamber; GA, genital aperture; MU, mucous gland; O, ovarian duct; PO, lateral pouch of capsule gland; RE, receptaculum seminis; U, muscular sac.

The albumen gland is of considerable size (AB), and completely surrounds the fertilization chamber and the various ducts leading to it. The walls are thrown into a few deep folds, so that the gland has a lobed appearance, and they are lined throughout by a single type of cell in which the cytoplasm, except towards the base, takes up stains specific for mucus and contains somewhat large and irregularly shaped secretion masses of a protein nature, presumably albumen.

The oviduct extends along the right side of the mantle cavity. At first it is narrow and lined by ciliated cells, and, a short distance from the fertilization chamber, a muscular sac (U) opens into its dorsal wall. This sac is in the usual position for a receptaculum seminis, and might be its homologue, but it no longer functions as such and its use is unknown. The only point of interest

concerning it is the enormous length of the cilia on the walls—at least five times the height of the cells. The pallial oviduct then thickens, and, for the rest of its course, except for a narrow strip along the ventral wall, the plan of the epithelium is essentially the same: gland cells alternating with ciliated cells. The initial part of this glandular section is narrow and both mucous and mucoid cells occur. It then opens into the ventral wall of a mucous gland (MU) which produces the inner mucous layer of the wall of the egg capsule, and here the lumen is elongated dorso-ventrally, the lateral walls being thick and the dorsal and ventral ones moderately thin. The ventral is composed of a low ciliated epithelium with occasional mucous cells, and a similar thin ventral wall extends as far as the genital aperture; it corresponds to the ventral channel of the pallial oviduct of other prosobranchs. Anteriorly, the mucous gland leads into the final and largest section of the pallial oviduct, the capsule gland (CG), where the egg capsule is retained whilst the main thickness of its wall is deposited. Here the lumen on each side is extended laterally to form a pouch of considerable dimensions (PO), though towards the genital aperture the duct gradually narrows. Three types of gland cells occur in the epithelium. Around the opening from the mucous gland there is a ring of cells in which the cytoplasm is filled with small protein spherules of uniform size. Mucous cells occur at the posterior limit of each lateral pouch and a considerable number lie around the genital aperture (GA). Elsewhere, that is, over the main area of the wall, the cytoplasm of the gland cells produces a fluid which has the appearance and consistency of conchiolin. Within the cells the secretion droplets stain lightly with iron haematoxylin and pale blue with azan.

Perhaps the most interesting point in the female genital system is the structure of the receptaculum seminis (RE). Between the pallial oviduct and the underlying columellar muscle the outer surface of the mantle—that is, directly under the inner surface of the shell—is folded to give a fairly deep longitudinal groove, the mouth of which faces outwards. The anterior end of the groove is about one-third of the length of the pallial duct behind the genital aperture. As it passes back the groove deepens and is subdivided longitudinally by a fold of epithelium to give an upper channel (CH) which leads to the receptaculum seminis, and a lower or ventral one which eventually narrows and disappears. The upper or dorsal channel is lined by tall columnar ciliated cells, the lower one by a squamous epithelium. The former passes postero-dorsally up the side of the mantle, and therefore parallel to and alongside the genital duct, and, meanwhile, twists through 90° so that it now lies more towards the dorsal side of the duct, the mouth of the groove pointing in that direction too. At the level of the middle of the mucous lobe of the pallial duct the lips of the groove fuse to form the entrance (ET) to a ciliated tube which leaves the surface of the body and passes deeper to enter the receptaculum seminis (RE). The receptaculum is an elongated pouch on the right of the genital duct and its posterior end is surrounded, except on the median side,

by the albumen gland. Within it, the spermatozoa become orientated with their heads embedded in the epithelium. A narrow muscular duct (DR) leads from the posterior end of the receptaculum and takes a somewhat circuitous course to reach the fertilization chamber. The duct is surrounded by a thick layer of circular muscle, and only on rare occasions has sperm been seen in it. It would appear that during copulation the penis of the male is inserted between the shell and the mantle of the female on the right side, and directed along the course of the longitudinal groove. Its passage would be facilitated by the slight flattening of the penis and by the secretion from the mucous glands situated on its dorsal and ventral walls. The tip of the penis would then reach to the opening of the duct leading down to the receptaculum seminis. Sections of a female fixed immediately after copulation showed the receptaculum and the duct leading to it filled with spermatozoa. Such a specialized method of copulation is not known elsewhere in the Mollusca.

Reproduction and Life History

The egg capsule of *Skeneopsis* is described by Linke (1933). It is approximately spherical or ovate (0·45 mm. long, 0·35 mm. broad), though flattened along the surface by which it is attached to an algal filament. It contains one or two heavily yolked eggs which pass through a veliger stage within the capsule and hatch as miniatures of the adult. Each egg is surrounded by a layer of albumen which gradually diminishes as development proceeds, and the young molluscs come to occupy most of the space within the capsule. The wall consists of two layers, a fairly thin mucous lining, and a much thicker fibrous coat. The former is secreted by the posterior mucous lobe of the capsule gland, the latter by the anterior larger section of the pallial duct. Linke (1933) states that the full development takes from 3 to 4 weeks in sea water at a temperature of 12–15° C. At a slightly higher temperature (approximately 14·5–17·5° C.) eggs which were laid on weed in a finger bowl developed in $2\frac{1}{2}$ weeks. The young rasp their way through the wall of the capsule by means of the radula.

Lebour (1937) states that *Skeneopsis planorbis* breeds throughout the year at Plymouth. This statement, however, requires amplification. From an examination of animals in rock pools around Cawsand, Plymouth, it is found that the majority are spawning during spring. These adult individuals measure at their broadest diameter 1·55 mm. on the average, which is also about the maximum size to which they grow in this locality. By the first week in June innumerable young are present, exceeding, in most rock pools, the number of adults, and the average breadth of these is 0·48 mm. Egg laying continues throughout the summer months, though by September it is decreasing and only a few animals are spawning as late as the end of October. By the new year the typical individual found in the rock pools has a diameter of 0·85 mm. and is sexually immature. A few perhaps exceed a millimetre. The older generation has by this time died out—only one or two individuals have ever been found—

so that it is in the main an immature population which tides over the winter, a population produced by the late spawners.

It would thus appear that *Skeneopsis* is an 'annual' with a normal breeding season during the spring or summer. This, however, may be extended in two directions: (1) to the earlier months of the year if the weather be suitable, by precocious ripening of the snails which have survived from the previous year; or (2) it may be prolonged into late autumn, again if the weather is kind, by the arrival at maturity of young which were hatched during the summer months and which would otherwise have to wait for the coming of the next spring.

Omalogyra atomus (Philippi)

Omalogyra is one of the most minute of British molluscs, as is suggested by its specific name. The shell (Fig. 3), which resembles that of a miniature *Planorbis*, measures only about 1 mm. at its broadest diameter. It is reddish brown in colour, coiled in a plane spiral, and, since the umbilicus is widely open, the interior of the spire is exposed. The shell is thus concave on both sides and has a bilateral symmetry about the sagittal plane. There are three whorls, compactly coiled, with the outer one, the largest, enwrapping the others which are exceedingly small and diminish in size towards the apex. Each is rounded on the outside, but somewhat flattened on the inside; the sutures are strongly impressed and deep. The mouth, approximately circular in outline, projects slightly outwards and has a sharp and even edge. The surface of the shell is glossy and smooth except for fine striae marking the lines of growth. The operculum (Pl. IV, fig. 2, and Fig. 3, OP) is white, circular and flat, with a slightly thickened spiral line which coils outwards from the centre to give three or four turns of increasing diameter.

The body is a uniform yellowish white, though little is exposed as the animal creeps along; the shell is then held erect with the mouth parallel to the substratum. The mollusc has a steady gait and the shell is rarely tossed to and fro as in *Skeneopsis*. Projecting anteriorly from the mouth of the shell is the broad, flat, flexible snout which is notched medially so as to form on each side a flat semicircular lobe (HL); the two lobes are joined by a straight and thin intermediate membrane beneath which is the mouth. Around the outer edge of each lobe and along the intermediate membrane is a row of stiff cilia which are presumably sensory in function: when the animal moves about it frequently waves the lobes in the water or presses them against the weed or rock as though sensing its environment. The lateral and posterior margin of each lobe is thickly ciliated. On the upper surface towards the posterior extremity is the eye (Pl. IV, fig. 2, E), which is large for the size of the snail; it is only just exposed when the animal creeps. No tentacles are present; functionally they are replaced by the lateral head lobes.

The foot, with sides approximately parallel, is rounded or slightly bilobed in front and rounded posteriorly. It is short in proportion to the length of the shell, beyond the posterior end of which it does not project, and rarely is it seen to protrude beyond the snout anteriorly. Its epithelium is thickly ciliated except for a cuticularized band at the junction of the foot with the body. Projecting from this cuticular surface, immediately beneath the head lobe on each side, and on a level with the eye, is a small tuft of tall ciliated cells. Fibres from the pedal nerves pass to them, and they may therefore be epipodial sense organs. There are two pedal glands. The anterior one (MG) opens on the upper surface of the propodium, where, directly in front of the mouth, there is a median ciliated depression (AM). The gland consists of unicellular mucous cells which are embedded in the substance of the foot beneath this depression and open singly between the ciliated cells. The posterior gland, which is much more extensive, has a longitudinal slit-like opening at about a third of the pedal length from the posterior end of the foot (PM). The ciliated duct (D), which passes dorsally from the opening, soon bifurcates into left and right branches and each of these, as in *Skeneopsis*, drains the secretion from two main glandular masses: one lies in front of the nerve ring and extends forwards between the eyes (AL), whilst the other (PL), lateral and more posterior, runs back beneath the genital duct on the right side, and, on the left, extends up the side of the odontophore. The posterior part of the gland is composed entirely of mucous cells, except for a few large cells at its extreme posterior end. These are filled with spherules which are readily dissolved on fixation leaving an inconsiderable amount of vacuolated cytoplasm. In the anterior part of the gland a different type of secreting cell accompanies the mucous cell, with spherules staining lightly with iron haematoxylin and deep red with azan. All the cells of the posterior pedal gland are arranged in groups, and each group has its own individual duct which leads to one main branch of the collecting duct. The gland is a useful possession for animals inhabiting rock pools; for *Omalogyra* often creeps on the surface film of water and can employ a thread of secretion to lower itself gradually into the water should it be disturbed, in exactly the same way as *Skeneopsis*. Also, when the mollusc is creeping over weed, or occasionally over rocks, its path is lubricated by the viscid secretion, and this gives the firm anchorage which is so necessary on a wave-washed shore, and which in the larger rock-clinging gastropods may be given by the more muscular type of foot.

The mantle cavity extends to the posterior end of the body whorl. Anteriorly, for a short distance, it completely surrounds the body, as the left and right lobes of the mantle fuse with one another beneath the columellar muscle. Farther back, near the anterior end of the odontophore, and between this and the anus (A), it is restricted mainly to the right side, but also extends over the dorsal surface of the body. On the left, where in other prosobranchs the ctenidium hangs down from the roof of the cavity, the body wall is fused with the over-

lying mantle: in *Omalogyra* there is neither ctenidium nor osphradium. Posterior to the anus the presence of the genital ducts, and of the kidney, confines the mantle cavity to the left of the median line so that it comes to overlie the oesophagus. The anus opens far back on the right side, a position which is probably secondary. From it, two longitudinal strips of ciliated columnar cells, extensions of the rectal epithelium, pass forwards to the mouth of the mantle cavity (omitted, for simplicity, from Pl. IV, fig. 2). The dorsal strip, which is the longer, runs along the roof to its edge, the ventral one along the body wall, ending on a level with the nerve ring. This appears to constitute a tract along which faecal matter is led to the mouth of the mantle cavity. In a living animal faecal matter can be seen through the transparent shell to leave the anus and to be directed forwards in this way, apparently rotating on its route. Below each strip lie mucous glands which discharge into the mantle cavity, some between the ciliated cells. The dorsal layer of glands is broader than the ventral and extends towards the median line; it represents the hypobranchial gland. At its posterior limit, in the vicinity of the anus, the mucous cells are replaced by a group of about a dozen enormous cells of another type, the openings of which lie close together (KM). It is these large glands which have been mistaken for eggs by Jeffreys (1867) and Lebour (1937). Each is broadly elliptical in longitudinal section, with the nucleus, near the base, surrounded by a dense layer of cytoplasm. Elsewhere the cytoplasm is vacuolated. There may be one vacuole which fills the greater part of the cell or several smaller ones; in living material each contains a colourless fluid. The secretion of these glands appears to be concerned as much in the elaboration of faecal pellets as in lubrication, and thus compensates for the absence of glands in the intestine. The pellets are rod-shaped, often with rounded ends, and are not so compacted as in *Skeneopsis*.

The kidney (K), which lies in the mantle, extends back from the level of the anus to the heart, which is directed obliquely across its posterior wall, with the auricle in front of the ventricle. The kidney is a simple vesicle in which the epithelium is not folded, as is typical of other molluscs, to increase the excretory area. Along its left wall runs the main pallial vein which branches anteriorly over the mantle and leads posteriorly to the auricle. The inner wall of the mantle is covered for the most part by squamous epithelium which separates the blood vessels from the flow of water in the underlying cavity. This water current is presumably set up by the cilia on the longitudinal strips of epithelium passing forwards from the anus, which are constantly beating towards the mouth of the mantle cavity. The gaseous exchange which occurs through the wall of the mantle is apparently adequate for the respiratory needs of a gastropod of such small size, and so explains the absence of any specialized respiratory organ.

The Alimentary Canal

The lateral walls of the extreme anterior end of the buccal cavity are thickened by an epithelium of considerable height bearing a cuticle. These thickenings act as jaws which grasp the weed as the radula plays over its surface. The odontophore is far removed from the mouth owing to the elongation of the buccal cavity in an anterior direction to form a proboscis-like tube. This tube is very distensible and is also cuticularized. *Omalogyra* is a pendulum feeder (Ankel, 1938) with *Ulva* as its favourite food: as it creeps slowly over the surface of a thallus the head is swayed to and fro whilst the surface cells of the alga are rasped by the radular teeth. The animal thus leaves behind it a zig-zag feeding trail (Fig. 3, FT). During the spring, summer and autumn months the stomach, and especially the cells of the digestive gland, are coloured green with chlorophyll from the weed. The contents of the plant cells which are rasped by the radula, and perhaps some severed pieces of alga, are mixed with mucus from the anterior pedal gland, sucked up into the buccal cavity and passed along the dorsal ciliated channel which lies above the odontophore. At the extreme posterior end of this channel the salivary ducts open, one on each side; they are extremely narrow tubes and each passes back to a compact group of a few large secretory cells. The dorsal channel leads imperceptibly into the oesophagus (Pl. IV, fig. 2 OE) which is about the same diameter throughout its length. In animals which are collected during the summer, when food is plentiful, the oesophagus is broader than in the winter and spring. Moreover, there is a histological difference between them: in *Omalogyra* which live through the winter the oesophagus is ciliated at its extreme anterior end, along the whole length of its dorsal wall and for a narrow longitudinal strip along the mid-ventral wall. Laterally, however, in a region comparable to the oesophageal pouches of other prosobranchs, it is lined by digestive epithelium which is identical with the digestive cells of the liver, and also comprises the lining of the stomach. In animals which develop and breed during the summer, the longitudinal glandular tracts of the oesophagus are not present, though the stomach has the lining of digestive cells, reminiscent of the embryonic condition of gastropods in which the liver cells cover the wall of the stomach only to be constricted off at a later stage. In these forms, too, the salivary

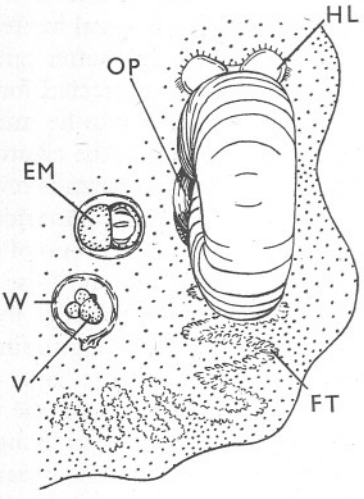

Fig. 3. *Omalogyra atomus*. Living animal feeding on *Ulva*. Two egg capsules are attached to the weed. ×45. EM, embryo at time of hatching; FT, feeding trail; HL, head lobe; OP, operculum; V, veliger; W, wall of egg capsule.

glands are relatively larger. The unusual distribution of the digestive epithelium in the adult is correlated with the type of food: the principal, perhaps exclusive, food is plant sap, and since this needs no mechanical treatment prior to digestion, the stomach is no longer necessary for this and can act as an extension of the digestive gland. Presumably in winter, when food is most scarce and when the animals are immature and undergoing slow development, the spreading of the digestive epithelium along the oesophagus enables a more thorough absorption of any food which may be obtained, or if the cells are capable of secreting enzymes it may permit a fuller utilization of the material. As the oesophagus passes back through the body whorl it is directed to the left and consequently gives ample space for the development of the voluminous genital glands on the right side; it opens at the extreme left of the antero-dorsal wall of the stomach. The stomach (ST), in proportion to the animal's size, is smaller than in *Skeneopsis*. The anterior wall not only receives the oesophagus, but the intestine (I) and anterior lobe of the digestive gland (AG) also open here. The intestinal aperture is median to that of the oesophagus, and a strip of ciliated epithelium, continuous with that of the oesophagus, runs across the stomach wall from oesophagus to intestine. The small anterior lobe of the digestive gland (AG) enters the stomach to the right of the intestinal opening. This lobe is not present in *Skeneopsis*, but only the much larger posterior one (DI), which leads from the posterior wall of the stomach and occupies the coils of the visceral mass. It would correspond with the left lobe of the digestive gland of other gastropods. This is always the larger of the two, since the right lobe—anterior in *Omalogyra*—is reduced as a result of torsion, and may be lost entirely. Each lobe in *Omalogyra* is a blind tube, constricted at regular intervals along its length, and the epithelium does not form the ramifications which are typical of the more solid construction of the liver of other gastropods. The digestive epithelium consists of two types of cells—digestive cells and rather infrequent lime cells. In the digestive cells the cytoplasm is vacuolated and the vacuoles seem to contain ingested food; no particulate matter has ever been found within them. The lime cells arise from a broad base and taper at the distal end; the cytoplasm is filled with large colourless spherules of calcareous matter.

The intestine is a short, straight tube which runs along the right side of the genital duct. Rather unusually there are no gland cells along its course. The cilia of the epithelium are so long that their tips meet across the tube and beneath the epithelium are a few circular and longitudinal muscle fibres embedded in a thin layer of connective tissue.

The Reproductive System

The gonad (Pl. IV, fig. 2, OV, TE) spreads over the surface of the digestive gland on the right side of the visceral mass. It is composed of two lobes lying alongside

one another, one a testis and the other an ovary. In animals which have been collected in the spring and which have developed slowly from late summer or autumn eggs the genital system is in the male condition; the female organs are developed, but are not as yet functional. The anatomy of such an individual is shown in Pl. IV, fig. 2, and its reproductive system will now be described. The testicular duct (V) acts as a vesicula seminalis. It leads, by a somewhat sinuous course, to the posterior end of the body whorl, on approaching which it narrows and is surrounded by a sphincter. The duct opens into the fertilization chamber (FC), a muscular pouch lined by ciliated epithelium, and into this there also passes (i) the ovarian duct (O) which at this stage is retarded in its development, (ii) the duct of the albumen gland (DA) and (iii) the pallial vas deferens (PD). The pallial vas deferens passes along the right side of the mantle cavity and is initially narrow and ciliated. Soon, however, it broadens and is surrounded, except on its ventral side, by numerous gland cells. The outer ends of these pass between the circular muscle fibres beneath the epithelium and form a thick subepithelial layer. In sections stained with iron haematoxylin and counterstained with mucicarmine, the differences between the epithelial and subepithelial parts of the cell are most pronounced. In the latter the cytoplasm stains rather deeply with iron haematoxylin, and spherules in the cytoplasm may be either a very pale grey, and slightly affected with mucicarmine, or a few small ones may be stained black. In the distal region the cytoplasm stains pink and the spherules may be either a deep pink or black. The latter occur towards the free tips of the cells and probably represent the final stage in the elaboration of the secretion. These glands constitute the prostate (P) and surround the pallial duct for about a third of its course.

Normally, in the mesogastropods, the pallial vas deferens leads to a penis which lies on the right side of the head, a muscular organ which is distended with blood during copulation. *Omalogyra*, however, has no such penis, and its method of copulation would appear to be unique amongst the molluscs.

Lying in the lumen of the prostate, and projecting back from an anterior origin, is a muscular tube (MT) which is open at its distal end to the prostatic cavity. Around the opening the walls are ciliated. Elsewhere, inside and out, the epithelium of the tube is covered by a thin cuticle; beneath the outer epithelium is a layer of circular muscles, and a layer of longitudinal muscles underlies the inner epithelium. The tube passes forwards beyond the anterior limit of the prostate, where the genital duct narrows, and it comes to occupy the greater part of the lumen of this part of the duct. Here the epithelium of the genital duct is also cuticularized and surrounded by circular muscles of considerable thickness. At some distance from the genital aperture the tube originates from the wall of the vas deferens. Closer investigation of this region shows that it actually passes through the dorsal wall of the duct, and enlarges into a muscular sac (BC) which lies in the haemocoel, and spreads over the right wall of the odontophore on to its dorsal surface. It is as though the lips of the

opening of this sac had been pulled out to form a long tube which lies in the duct to which the pouch connects, pointing towards the visceral mass. The histology of the sac is similar to that of the tube except that it lacks an outer epithelium. It is homologous with the bursa copulatrix of other forms. Strictly, the origin of the bursa is from an hermaphrodite duct (HD), since posterior to that point the pallial oviduct (PO) joins the vas deferens by way of an extremely minute opening surrounded by a sphincter. But obviously at this stage the oviduct is not functional and the main channel is, in effect, a male one. The hermaphrodite duct, which is extremely muscular, appears as a forward continuation of the vas deferens and opens anteriorly on the right side of the head (GA), just within the shelter of the mantle. It is lined by a slightly cuticularized epithelium in which there are a few mucous glands.

One other structure which is associated with the male genital system and which, like the elongated neck of the bursa, is only present in animals collected during the spring months, has yet to be described. It is a sac which lies against the left wall of the ovary (SP), and is connected to the posterior end of the prostate (OPE) by a narrow ciliated duct. The duct passes antero-dorsally on the left side of the stomach, and over the posterior end of the oesophagus to reach the thickly ciliated ventral wall of the prostate. The sac, which will be referred to as the sperm sac, is lined by an epithelium in which the protoplasm is highly vacuolated, and the nuclei are large with prominent nucleoli. In fixed material many vacuoles appear to contain a loose coagulum, and in the living state a somewhat watery fluid. The sac, and sometimes also the duct, may be distended with sperm and a mucoid secretion, presumably derived from the prostate.

The suggested mode of functioning of these male reproductive ducts is as follows. Animals collected in spring show the vas deferens as the principal pallial genital duct, and at this stage the opening of the pallial oviduct into the hermaphrodite duct is far too small to allow the passage of an egg capsule—in other words, the animal is purely male. Since the tube which extends from the opening of the bursa is an extremely muscular organ, and blocks the passage through the anterior end of the vas deferens, and since the bursa itself is also at this time extremely distensible, it may be assumed that, with the absence of the normal type of penis, these structures are concerned in copulation. The only means by which this seems possible is for the tube to suck up, by peristaltic action, sperm liberated from the vesicula seminalis, and prostatic secretion. These would then fill the bursa. The direction of the penial tube might then be reversed and it could be protruded through the muscular hermaphrodite duct so as to project from the genital aperture and pass into the duct of the copulating partner. Into this the sperm from the bursa would then be passed by muscular action. However, during the male phase no contents have been found in the bursa or in the penis. I do not know what part of the genital system receives spermatozoa, and have been unable to discover whether there is a mutual cross-fertilization or not.

The function of the sperm sac, which, it will be recalled, is found in the male phase only, is probably to clear the pallial vas deferens of sperm and prostatic secretion which have failed to enter the copulatory organ. Sections suggest that here the spermatozoa undergo disintegration: they appear to be digested and the final products absorbed by the vacuolated epithelial cells.

For the investigation of the female genital system it is necessary to examine animals collected in the months June to September. The eggs (Pl. IV, fig. 2, OV) in the ovary are relatively enormous even before the female system is functional, and appear to be out of all proportion to the size of the ovarian duct (O) along which they pass to the fertilization chamber (FC). From there the eggs are carried to the albumen gland (AB), which is divided approximately into two lobes lying side by side and communicating with one another along their adjacent walls. The short ciliated duct (DA) from the fertilization chamber opens into the anterior end of the right lobe, whilst at the anterior end of the left a narrow though muscular passage (OM) leads into the mucous gland (MU). Along this route the eggs are conducted. The epithelium of the albumen gland is composed of a single type of secreting cell. The mucous gland is of a rather irregular shape owing to the folding of its walls; the epithelium is high and the gland cells alternate with ciliated cells which are wedged between their distal ends.

The capsule gland (CG) is the next and last section of the pallial duct, and receives the eggs from the mucous gland; it lies on the right side of the pallial vas deferens and not above it as in the male phase (Pl. IV, fig. 2). Its secreting cells have a mucoid cytoplasm which is vacuolated and in the vacuoles are irregularly shaped protein spherules. Wedge-shaped cells, which lie between the distal ends of the secretory cells, are covered with closely set short cilia. The basement membrane is surrounded by a layer of circular muscles which thickens at the entrance to the hermaphrodite duct.

In all animals which have been collected in June and the succeeding months of the summer, that is, during the height of the breeding season, the reproductive system in all stages of maturity shows certain fundamental differences from the male phase: no tube extends from the lips of the bursa and no sperm sac is present; the capsule gland, now more voluminous, lies on the right side of the vas deferens, and not above it, and is broadly open to the hermaphrodite duct anteriorly; the pallial vas deferens is glandular along its whole length and its junction with the left wall of the oviduct, to form the hermaphrodite duct, is by way of a minute aperture surrounded by a sphincter. Certain changes have occurred in the structure of the bursa. It now opens by way of a muscular ciliated duct which is of considerable length, so that the sac itself appears to occupy a more posterior position and often lies behind the odontophore, between the oesophagus on the left and the male duct on the right. Its musculature is insignificant—in fact it is only with difficulty that any muscle fibres can be seen at all—and its epithelium is no longer cuticularized. The

cells are larger, with vacuolated protoplasm and the nuclei are spherical and have prominent nucleoli. The histology of the bursa in the female phase resembles that of the sperm sac in the male phase, and the function of these two structures appears to be similar, for within the bursa waste secretion from the genital ducts may accumulate and later be disposed of; the accumulation is greatest after an egg capsule has been deposited. On histological grounds the hermaphrodite duct may be divided into two distinct regions. The first is lined by a ciliated and glandular epithelium in which mucous cells alternate with ciliated cells, and there are a few subepithelial mucous glands. In the second, which leads to the genital aperture, the epithelium is low, cuticularized and thrown into slight longitudinal folds. Below it lies a thick coat of circular and longitudinal muscles, and a sphincter surrounds the genital opening.

Originally it was thought that every animal passed through a functional male phase with the genital structure as shown in Pl. IV, fig. 2, and later the reproductive system underwent certain changes associated with the adoption of the female phase—this would account for the differences noted above. This may indeed be true for the animals which survive the winter and are the early spring spawners. Although the transition has not been followed in any detail, some individuals collected in mid-April do show the capsule gland enlarging around the right wall of the vas deferens, and a reduction in the size of the sperm sac and of the penial tube. It is now known, however, that individuals which hatch from eggs of summer spawners fail to develop the full anatomical characteristics of the male, and pass directly into a state anatomically comparable with the completely feminized individual. This anatomical femaleness, however, does not prevent the formation of apparently ripe spermatozoa in the testis and their passage into such parts of the male system as are present, and although the lack of a penis and associated structures would appear inevitably to preclude copulation and cross-fertilization, it may not be incompatible with successful self-fertilization.

Reproduction and Life History

No description of the egg capsule of *Omalogyra* is known. Jeffreys (1867) states that capsules 'are occasionally found in the upper cavity of the last whorl in dried specimens', and Lebour (1937) regarded the large glands which open near the anus as egg capsules, and assumed, from the very young crawling stages she observed, that direct development occurred.

The capsules are laid during the spring, summer and early autumn. They are irregularly spherical or ovoid (Fig. 3), and only slightly flattened along the surface which anchors them to weed (*Ulva* and *Enteromorpha*). Each measures 0·2 mm. in diameter, or 0·17 × 0·20 mm., and contains one or occasionally two eggs surrounded by albumen and encased in a wall (w) which consists of two layers. The inner is a mucous layer, and the outer is thick, rather adhesive and

of a composite texture which gives a fibrous appearance and a somewhat wrinkled surface.

The eggs are fertilized either in the fertilization chamber or in the albumen gland: in a ripe female spermatozoa have been found in both of these. From the albumen gland the egg and albuminous secretion pass into the mucous gland, and here the inner layer of the capsule wall is added. The outer wall is manufactured by the capsule gland, to which the egg and its coverings is next transferred, and where it is detained for a much longer period. On two occasions a capsule has been found here, distending the duct to apparently abnormal proportions. The capsule is finally fixed to the weed, on which the adults are living, by pressure applied by the foot.

The development of the egg was studied during the month of August when the temperature of the sea water was high (15·0–18·5° C. day temperatures). A typical veliger (V) occurs, though the young develop to the crawling stage (EM) before they emerge. At this stage the individual practically fills the entire space within the wall of the capsule, the albumen being apparently used as food, and often it may be seen moving around the confined space with difficulty. Pressure thus exerted against the wall, together with the action of the radula, may assist hatching. The development is very rapid and is completed in about 10 days at the above temperature. On hatching, the small active molluscs, which measure about 0·16 mm. in diameter, begin to feed on *Ulva* and *Enteromorpha*, and appear to feed continuously. Their growth rate is rapid. In a week the size is doubled, after 17 days the average length is about 0·55 mm., and by the end of $5\frac{1}{2}$ weeks the reproductive organs appear to be functional.

Throughout the summer numbers of individuals of all sizes are abundant; during the autumn the numbers fall until in December and January it is frequently difficult to find more than half a dozen specimens in a rock pool which in summer contained hundreds. The specimens which have been collected during the winter months are immature, of an average length of 0·57 mm., and are apparently hatched from the eggs of late spawners; by March the average length of the individual is 0·77 mm. This would suggest that, as in *Skeneopsis*, animals which have bred do not survive the winter. There is no indication that they migrate elsewhere or choose another habitat. Thus immature individuals tide over the winter and their growth rate is exceedingly slow. In spring they attain maturity, copulation occurs, and egg capsules are produced. The rate of reproduction increases with the rise in temperature and prolific growth of weed in the early weeks of summer. From the anatomy of adult individuals in summer it would appear that self-fertilization may then be practised. Some indication of the rate of increase in numbers during August was obtained from sixty individuals which were kept in a finger bowl and supplied with *Ulva*: after 3 weeks 156 young were produced and there were 21 embryos.

Rissoella diaphana (Alder)

The two species of *Rissoella*, *R. diaphana* (Alder) and *R. opalina* (Jeffreys) occur in intertidal coralline pools, together with the two genera which have been described. Externally the species are readily distinguishable by the shape of the shell and by the tentacles and snout (Figs. 4 and 6), but on the whole their internal anatomy is similar.

The shell of *R. diaphana* has the appearance of a rather short oblique cone, whitish in colour, smooth except for the faint markings of the lines of growth (Fig. 4, LG). It is extremely thin and transparent so that the cream, brown and orange coloration of the underlying viscera are exposed to view. There are four and a half convex whorls separated by fine though well-defined sutures: the apical one is blunt and rounded, and they gradually enlarge towards the mouth, the last occupying three-fifths of the entire spire. The mouth of the shell is large with an outer lip which is incurved and somewhat expanded below. The inner lip is sinuate—it follows the curve of the pillar of the shell and is slightly reflected. The exposed parts of the body of *R. diaphana* are yellowish white with brown pigment patches occurring on the opercular lobes of the foot (OL), an isolated streak on each side of the foot anterior to these, and on the head, between the eyes, a narrow median longitudinal streak which expands anteriorly to the middle of the upper lip, and posteriorly along the neck. In some specimens the pigmentation is more intense, of a purple-brown colour, and covers all the exposed surfaces of the body. Through the transparent colourless shell, on the dorsal surface of the body whorl, wavy streaks of light brown pigment in the underlying mantle are conspicuous against a general background of deep cream. On the right a deep brown blotch, the outer pigmented covering of a group of glands, marks, approximately, the position of the anus. Through the coils of the spire may be seen the deep brown digestive gland, accompanied on the columellar side by the gonad, which is of an orange colour. The transparency of the shell is so great that even the different types of cells in the digestive gland can be distinguished: the excretory cells as black dots scattered throughout the gland, the lime cells with their colourless refringent spherules and, most frequently, the brown digestive cells.

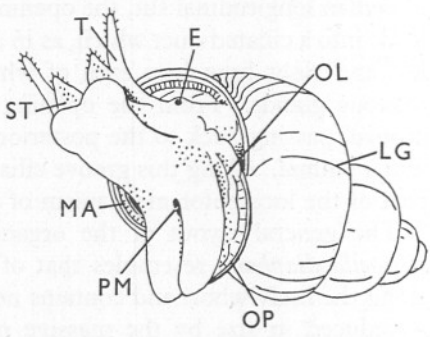

Fig. 4. *Rissoella diaphana*. Living animal. ×50. MA, mantle. Other letters as in Fig. 1.

The snout (ST) is bifid and forms two triangular lobes which diverge from one another at an angle of about 45°. These lobes are shorter and stouter than the tentacles (T) which arise one at the base of each, and the tentacles are

cylindrical and taper slightly towards a blunt tip. Each is covered, at least around the distal half, by stiff cilia, and these also fringe the margins of the snout. The eyes (E) are small and placed on slight protuberances far back on the neck, so that when the animal is creeping they lie beneath the shell and never emerge from its shelter.

The foot is more or less lanceolate, somewhat bilobed in front and rounded or bluntly pointed behind; the opercular lobe on each side projects beyond the lateral margins of the sole, which is covered by short thick cilia. Between the ciliated cells open the ducts of subepithelial mucous and mucoid glands. The pedal mucous gland opens on a ciliated V-shaped depression on the upper surface of the foot just in front of the mouth, the angle of the V being directed posteriorly. At about half the pedal length from the anterior end of the sole is a median longitudinal slit, the opening of the posterior pedal gland (PM). This leads into a ciliated duct which, as in *Skeneopsis* and *Omalogyra*, bifurcates into left and right branches, each of which receives the openings of unicellular mucous glands. From the opening of the gland a temporary longitudinal groove, passing back to the posterior tip of the foot, may be observed in the living animal. Along this groove cilia direct the secretion which is an essential part of the locomotor mechanism of the animal.

The general layout of the organs associated with the mantle cavity of *Rissoella diaphana* resembles that of *Omalogyra atomus*. The cavity extends along the body whorl and contains neither gill nor osphradium. Posteriorly it is reduced in size by the massive pallial section of the female duct which projects dorsally from the body wall. The anus is far back on the right side, and from it the dorsal and ventral walls of the rectum are produced anteriorly towards the head as two longitudinal strips of columnar ciliated cells—one along the roof and the other along the floor of the mantle cavity. The former extends farther forwards than the latter. Below each is a broad band of secreting cells which open in, and on either side of, the ciliated strip; the dorsal band is the broader and is composed entirely of mucous cells. It represents the hypobranchial gland. The ventral one is composed of mucous and mucoid cells, the former opening on the median and the latter on the lateral side of the ciliated epithelium. Faecal matter—diatom cases, pieces of algal filaments and detritus—is directed forwards between these ciliated strips and agglutinated by the secretion from the adjacent glands. Broad, oval pellets are thus expelled from the mantle cavity. Near the anus, and on its median side, is a group of large gland cells, about six in number, which open into the mantle cavity. They are surrounded by a thin coat of connective tissue in which dark brown pigment granules occur, and they constitute the conspicuous blotch which is always seen through the transparent shell. In each cell the cytoplasm is filled with very large vacuoles which contain secretion spherules: these dissolve rapidly in acid fixatives. On the median side of the ventral longitudinal strip of gland cells is a deep gutter into which the female duct opens at the

summit of a long papilla, and at the anterior end of which is placed the penis. The latter, when at rest, is folded back along the groove so that its tip lies immediately in front of the female aperture.

As in *Omalogyra* the kidney spreads forwards into the thickness of the mantle and opens near the anus. It is a simple sac lined by glandular tissue except for the dorsal wall where squamous cells occur. The glandular tissue is supplied by blood capillaries which are separated from the water current in the mantle cavity only by the squamous epithelium of the floor of the mantle. Through these capillaries the blood is filtered on its way to the efferent pallial vessel which passes along the left wall of the kidney.

Owing to the absence of a ctenidium, which is normally responsible for the setting up of a water current through the mantle cavity, *Rissoella* must depend upon other ciliated tracts for this purpose. Of these the longitudinal strips running forwards from the anus are the most powerful and maintain an exhalant stream. On the right side of the mantle is a band of columnar ciliated cells—a vestige, perhaps, of the ctenidium—where the direction of the effective beat of the cilia has not been determined, but together with a strip of similar epithelium on the underlying body wall they probably produce an inhalant current. Around the inhalant opening of the mantle cavity is a prominent tuft of ciliated cells which beat to the exterior and, as in other prosobranchs, they may expel the largest and heaviest particles which are drawn into the cavity with the stream of water.

The Alimentary Canal

The food of *R. diaphana* consists of diatoms, detritus and small algal filaments. These are collected by the radula whilst the object on which they occur may be held by the jaws. These comprise numerous teeth on the lateral walls of the buccal cavity, each secreted by a single cell and having a finely serrated edge. Anteriorly the buccal cavity is protected by a cuticle, and in the epithelium are a few mucous cells. The secretion from the anterior pedal gland, which opens immediately beneath the mouth, may assist in lubricating the action of the radula and agglutinating the small food particles. The radula is similar to that of *R. opalina* (Thiele, 1929) in that there is one central and two intermediate teeth, the lateral or marginals being absent.

The dorsal food channel, above the radula, conveys the food into the oesophagus. From its origin the oesophagus curves abruptly ventrally and to the left of the radula sac. Its displacement is due to the enormous growth of the reproductive ducts which fill the haemocoel dorsally; immediately behind the odontophore they cross to the right side to open into the mantle cavity. For the same reason the salivary glands, which open into the posterior end of the buccal cavity, are displaced; they are ventral in position, the left slightly

anterior to the right. Each gland is a small tubular structure consisting of a comparatively few large cells which are of two types occurring in about equal numbers. There are mucoid cells and glands which, perhaps, produce an enzyme. The oesophagus is lined throughout its length by a ciliated epithelium. It passes beneath the albumen gland to open ventrally into the anterior wall of the stomach.

The stomach, approximately spherical in shape, lies at the posterior end of the body whorl. Dorsally, along its anterior wall, it receives the opening of the intestine, and ventrally the opening of the oesophagus. There are two liver ducts, one dorsal, well behind the origin of the intestine, the other ventral and posterior to the oesophageal opening. The epithelium lining the anterior half of the stomach is ciliated, but posteriorly is an extensive gastric shield. The stomach usually contains a large quantity of food, apparently mixed with fluid from the digestive gland, and compressed into a bolus by the cuticle of the gastric shield.

The two lobes of the digestive gland are unequal in size. That opening into the dorsal wall of the stomach is the smaller and spreads forwards to the posterior end of the albumen and capsule glands. It corresponds to the smaller right lobe of the gland of other prosobranchs. The second lobe, which opens ventrally, constitutes the greater part of the gland and spreads through the smaller coils of the visceral mass with the hermaphrodite gland. The digestive epithelium consists of three types of cells: one, which may be termed the digestive cell, arises from the basement membrane to a broad club-shaped distal end. The cytoplasm is vacuolated and in the upper half of the cell lie spherules which are probably enzymatic and are frequently seen in the digestive tubules. In the lower half of the cytoplasm are greenish brown masses, circular or irregular in outline, which may be absorbed food. No particulate matter has ever been seen in the tubules of the liver, only the same greenish brown fluid as occurs in the stomach. Another irregularly scattered type of cell of varying shape is excretory in function and contains spherules usually of a deep brown colour. Frequently their base is broad and the cytoplasm contains numerous small spherules, those near the base staining moderately intensely with iron haematoxylin, whilst the more distal ones are unaffected. At what appears to be a later stage in their development, these fuse to give a brown homogeneous mass. None of these masses has been traced in the faecal matter. It may be that, since the mollusc is an annual, waste matter, extracted from the blood, is rendered harmless within these cells and accumulates throughout its life. The third type of cell in the digestive gland is of large size and contains spherules of calcareous matter.

The intestine is a short tube which from its origin passes posteriorly for a short distance and then runs abruptly forwards along the right side of the genital duct to the anus. It is lined by columnar ciliated epithelium in which there appear to be no gland cells.

The Reproductive System

The gonad, which lies on the columellar side of the visceral mass, is a hermaphrodite gland with sperm and ova developed in the same tubules. A single and very distensible gonadial duct leads to the posterior end of the body whorl. Proximally it acts as a vesicula seminalis which contains sperm even when eggs are passing through it. Simultaneous hermaphroditism occurs,

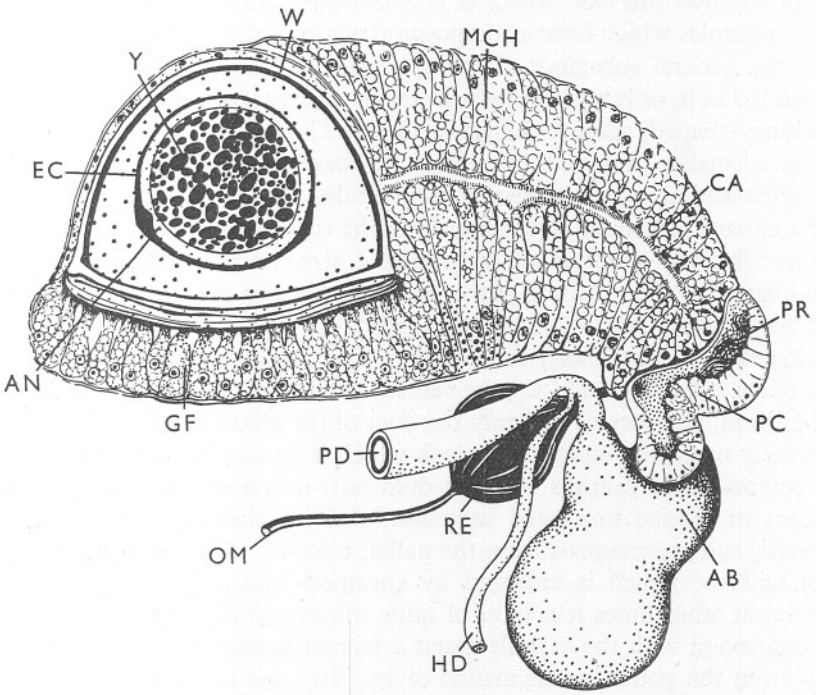

Fig. 5. *Rissoella diaphana*. Section through capsule gland and a reconstruction of the associated parts of the reproductive system. × 150. AB, albumen gland; AN, albumen; CA, gland cells producing a secretion similar to that of the albumen gland; EC, egg covering; GF, glands which thicken the floor of the egg capsule; HD, hermaphrodite duct; MCH, glands producing a mucoid-conchiolin fluid; OM, opening to mantle cavity; PC, posterior lobe of capsule gland; PD, pallial vas deferens; PR, spermatozoa; RE, modified receptaculum seminis; W, outer wall of egg capsule; Y, yolk granules of egg.

though, as is the usual rule, the male system is more precocious in its development than the female. The distal end of the gonadial duct (Fig. 5, HD) is lined by columnar ciliated epithelium, and on reaching the posterior end of the body whorl it divides into two branches which diverge from one another, one of these leading to the pallial vas deferens (PD) and the other to the albumen gland (AB).

The vas deferens passes forward beneath the pallial oviduct, that is, on the left of the median line, and during this part of its course it is ciliated and a few

circular muscles underlie the epithelium. Near the posterior end of the buccal mass the duct becomes glandular and turns at an obtuse angle across the dorsal surface of the body to the right side. It ends in a relatively short tubular penis, which, when at rest, lies folded back along the groove in the body wall. The glandular section of the duct constitutes the prostate. Here ciliated cells alternate with gland cells, one type of gland occurring posteriorly, and another along the anterior part of the duct. In the posterior glands the cytoplasm is vacuolated except towards the base where it is extremely dense. The vacuoles contain large spherules which have a composite structure; after the iron haematoxylin stain the general substance of the spherule is a rather yellowish grey, and embedded in it, or lying over its surface, are deeply staining bodies which may be kidney-shaped, comma-shaped or linear. The second type of gland, which covers a smaller area and extends to the base of the penis, contains small colourless and homogenous secretory spherules. No glands occur in the penis, and a ciliated columnar epithelium lines the tube.

The albumen gland is of considerable size, and is composed of a tall glandular ciliated epithelium of the usual type for this situation. It is probable that fertilization occurs within the gland, for during the breeding season spermatozoa are frequently found there. The gland opens into the posterior lobe of the capsule gland (PC), the ventral and anterior walls of which are thin and ciliated, and receive not only the duct of the albumen gland, but also the extremely narrow opening of a pouch which is presumably homologous with the receptaculum seminis (RE). It does not, however, function as such: it appears to receive unwanted secretion, such as albumen and excess shell material, and spermatozoa from the pallial oviduct. After an egg capsule has been laid the pouch is enlarged by enormous quantities of this material, whereas at other times it may be of quite minute dimensions. In addition to the connexion with the capsule gland a second narrow and thin-walled duct leads from the pouch to the mantle cavity (OM), and through this the surplus secretion and spermatozoa are passed to the exterior—there is no indication that the mollusc puts it to any profitable use. The glandular walls of the posterior lobe of the capsule gland (PC) produce a secretion of conchiolin-like consistency impregnated with mucus. Anteriorly the capsule gland leads forwards above the oesophagus and slightly to the right of the mid-dorsal line; it is a comparatively voluminous structure and projects from the dorsal body wall as an opaque white mass. It opens into the right side of the mantle cavity by way of a muscular papilla which is posterior to the root of the penis and well behind the tentacles.

Except in the region of the papilla, the walls of the capsule gland are thickened by tall epithelial secreting cells which alternate with wedge-shaped ciliated cells. In transverse section the lumen is approximately semilunar in shape, with the concavity directed ventro-medially. There are thus two longitudinal grooves along the duct: the outer or right one is the more pronounced,

is thin-walled, not glandular, and folds beneath the glandular tissue of the floor. It originates along the wall of the genital papilla and passes back to the posterior lobe of the capsule gland, near the opening of the albumen gland. On several occasions spermatozoa have been found along its posterior end, not orientated, but scattered in irregular masses, and it would therefore seem to be the path along which these travel to the site of fertilization. On a histological as well as a functional basis the secreting part of the duct, anterior to the posterior lobe of the capsule gland, may be divided into three regions. In the most posterior of these the gland cells form a complete band around the duct, and are similar in many respects to those of the albumen gland, though they stain deeper with mucicarmine and purple with toluidin blue (CA). The succeeding glandular belt resembles the posterior lobe in producing a mucoid conchiolin fluid (MCH). The final glandular section comprises, dorsally and laterally, only a very narrow band of cells, though along the floor it thickens and spreads towards the genital papilla. The glands produce a basophil secretion which is added chiefly to the floor of the capsule (GF). The muscular papilla is separated from the glandular duct by a sphincter; it is lined by ciliated cells and a few mucous cells.

Reproduction and Life History

The egg capsules are manufactured one at a time in the pallial oviduct. They are described by Lebour (1936). Each is hemispherical in shape and attached by the flattened base to green or red algae, the base measuring 0·48 mm. long and about 0·25 mm. broad. The capsule contains one or two eggs (Fig. 5, Y), each covered by a thin membrane, albuminous layer (AN) and egg covering (EC), and floating in a fluid which fills the capsule. The outer wall (W) is thick and semi-transparent. During early summer several individuals of *R. diaphana*, with capsules still in the process of formation, have been fixed and sectioned (Fig. 5), and from these the functions of the various parts of the capsule gland have been calculated. The egg is presumably fertilized and receives its supply of albuminous fluid as it passes through the albumen gland (AB), and in the posterior lobe of the capsule gland (PC), where excess spermatozoa are frequently found (PR), the egg covering is deposited. The staining properties of this covering, which isolates each egg from its neighbour, and those of the glands of the posterior lobe are identical. The fluid which fills the capsule is derived from the next section of the duct (CA) as the egg passes forward, and the outer wall (W) from the two ultimate glandular regions. The more posterior of these forms a substantial layer of conchiolin impregnated with mucus (MCH), and this is covered, especially along the base of the capsule, by secretion from the last glandular region (GF)—this stains with iron haematoxylin and is not mucus. It will be remembered that the glands of this last region are thick along the floor and few occur laterally and dorsally. Here the capsule appears to be retained for some time, and its floor is thickened, before it is passed into

the lumen of the genital papilla and finally deposited on the weed by the foot. Within the capsule the embryo passes through a veliger stage and hatches as a miniature of the adult.

The young at all stages of development are to be found with the adults in spring, summer and early autumn. During the winter the species is far from its summer abundance and the specimens which have then been collected are not fully grown, their reproductive organs being immature. It would thus appear that, as in the other two genera which have been described, *R. diaphana* is an annual. Its rapid development, which is completed within a fortnight, and its rapid rate of growth, enable it to take advantage of favourable climatic conditions, so that during the spring and summer several generations may be co-existent.

Rissoella opalina (Jeffreys)

The semi-transparent and highly glossy shell of *R. opalina* is globular in form (Fig. 6 A). There are three and a half whorls separated by broad deep sutures; from the first, which is low, the shell expands abruptly. The body whorl is rounded and its length is approximately twice that of the short, blunt spire. The mouth is broadly rounded anteriorly and gradually contracts posteriorly; the outer lip is sharp and thin, the inner flexuous and thickened on the lower part of the columella. The empty shell is a pale yellowish brown, though in the living animal it appears darker owing to pigmentation in the underlying tissues. When the animal is expanded, the short, tubular snout (ST) projects from under the anterior edge of the shell; above it, and on each side, is a deeply bifid tentacle (T) which is thickly ciliated. The upper surface of the body is mottled with purplish brown or black except for the tentacles, the V-shaped depression which lies immediately below the mouth and is the opening of the anterior pedal gland, and the periphery of the foot—these three regions are colourless. The eyes (E) are situated on slight protuberances and lie close together beneath the shell from which they are never extended. Each is surrounded by an unpigmented ring of tissue. In the living animal the brown pigment of the mantle can be seen through the shell, varied here and there by lighter wavy streaks and by cells filled with orange spherules. Three dark blotches lying within the mantle constitute one of the most characteristic features of the species and mark the position of groups of glands (PI), which are similar to the single group found near the anus in *R. diaphana*. In the upper coils of the spire the excretory cells of the digestive gland (P) can also be seen through the shell as scattered dark spots. The foot is large and triangular, slightly notched in front with the two anterior angles rounded, and bluntly pointed behind (PF). There are two pedal mucous glands resembling those of *R. diaphana*; the V-shaped depression on the propodium which marks the opening of the anterior one is, however, more pronounced.

The organs associated with the mantle cavity differ in some detail from those which have been described for *R. diaphana*. On the left of the mantle, and in the anterior position, is the rudiment of a ctenidium in the form of a few strongly ciliated folds of epithelium; these help to maintain the pallial water current, though they are of little importance in respiration. To the left of this, and washed by the inhalant stream, are the openings of two large multicellular glands, one at the edge of the mantle, and the other just within the mantle cavity, around them stretching a patch of epithelial mucous cells. Each opening leads back through a ciliated and glandular duct to the more posterior gland which lies where the mantle separates from the rest of the body. The gland which opens at the edge of the mantle is composed of mucous cells; the second, opening just within the mantle cavity, is surrounded by minute black pigment granules, and these may also be scattered between the large gland cells.

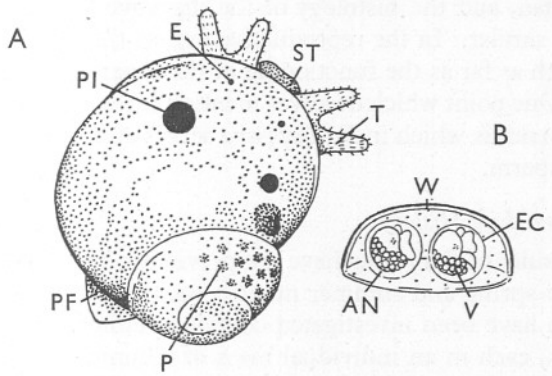

Fig. 6. *Rissoella opalina*. A. Living animal, ×40. B. Egg capsule, ×37. P, spherules in excretory cells of digestive gland; PF, posterior tip of foot; PI, pigmented group of gland cells; V, veliger. Other letters as in Figs. 1 and 5.

This gland is one of the three dark blotches which are conspicuous through the transparent shell. Median to the rudiment of the ctenidium is the anterior limit of the kidney which lies within the mantle, and is separated from the mantle cavity by a layer of squamous epithelium. This part of the mantle, within which lies the kidney with its rich vascular supply, is presumably the chief respiratory surface. The hypobranchial gland is, as in *Omalogyra* and *Rissoella diaphana*, displaced to the right owing to the interpolation of the kidney between the ctenidium and the gland. It stretches back from the opening of the mantle cavity to about the level of the anus—on the median side it abuts against the right wall of the kidney, and laterally against the columnar ciliated epithelium which lines the exhalant opening. Anterior to the anus opens the second of the three groups of large gland cells. This one, embedded in the mantle, is smaller and in a position comparable to the similar gland in *R. diaphana*. From just posterior to the anus a tongue-like projection of the mantle wall juts forwards ventral to the opening, so that the faeces are dis-

charged into a special compartment of the mantle cavity lying between this on the left side and the mantle itself on the right. Along each side of the compartment, on the surfaces facing one another, is a short strip of ciliated epithelium which drives the faecal matter forwards. Unlike *R. diaphana* the strips are short, since the anus is farther forward, and they do not enter the rectum itself. Embedded in the projection, and opening on its ventral surface posterior to the anus, is the third group of large pigmented glands. The only apparent function of these glands is to compensate for the reduced size of the hypobranchial gland and the lack of intestinal glands to consolidate the faeces. Posteriorly the mantle cavity is filled by the pallial oviduct, which projects from the dorsal wall of the body.

The internal anatomy of *R. opalina* is sufficiently similar to that of *R. diaphana* for a description to be unwarranted. The alimentary canal is built on the same plan, and the histology of the digestive gland, and its mode of functioning, is similar. In the reproductive organs there are some differences in detail, though as far as the functioning of the organs is concerned these are insignificant. One point which deserves mention is the absence of the modified receptaculum seminis which in *R. diaphana* serves as a reservoir for unwanted secretion and sperm.

Reproduction and Life History

The egg capsules of *R. opalina* have not previously been described. They are laid during the spring and summer months on green and red algae. The ten capsules which have been investigated contained either two, or rarely (twice) three, embryos, each in an individual mass of albumen which is surrounded by an egg covering. The embryos, with these protective layers, float in a common fluid which fills the capsule. The capsule is hemispherical, with the flattened surface, attached to the weed, measuring approximately 0·65 × 0·4 mm.; the height is about 0·5 mm. The wall is thick, semi-transparent and of a fibrous texture, being composed of conchiolin threads in a mucoid substrate. It is produced by the composite secretion from the capsule gland. The method by which the capsule is manufactured in the pallial oviduct is similar to that of *R. diaphana*.

The embryos pass through a veliger stage and develop to a replica of the parent before they hatch. The full development in the summer months takes about a fortnight. During this time the embryo comes to occupy the entire space within the egg covering, which appears to be stretched during its growth; the covering is not broken until the young are ready to escape from the capsule. The veligers can be recognized by the early appearance of the groups of large pigmented gland cells which lie in the mantle. Also through the mantle, at a later stage in embryonic life, the kidney tissue can be seen.

Young, which hatched from capsules during August, ranged from 0·18 to 0·27 mm. long. They adopt the same feeding habits as their parents and

within a fortnight their size is more than doubled (0·43–0·68 mm.). Breeding is continuous throughout the warmer months when individuals at all stages of maturity can be found in the rock pools in comparative abundance. The adults with very few exceptions do not survive the winter, when the number of the species is low, and an immature, slow-growing population is characteristic.

Discussion

Skeneopsis planorbis, *Omalogyra atomus*, *Rissoella diaphana* and *R. opalina* are amongst the smallest British marine molluscs and are inhabitants of rock pools below the level of mid-tide, especially those which have an abundant growth of algae. They are rarely found elsewhere on the shore. As compared with the more familiar and larger intertidal prosobranchs these small forms show in some respects a simplicity of structure, and in many others a high degree of specialization. The latter may be correlated both with their habitat and their smallness.

All four species are herbivorous, feeding on diatoms, algal filaments and some detritus, and during the warmer and lighter months of the year, when conditions favour plant growth, they feed continuously, even at low tide when other herbivores, uncovered by water, are less active. There appears to be no cellulase in the digestive system, since uninjured plant cells pass through the gut undigested, and add to the abundant faecal matter. Nevertheless, unlike other herbivorous intertidal prosobranchs, the intestine is extremely short: in *Omalogyra* the length is one-third the length of that part of the gut lying anterior to the ducts of the digestive gland, whereas in the limpet the corresponding proportion is 8:1. The limpet is uncovered by the tide for a considerable number of hours each day, and the faecal matter must then be stored in the long glandular intestine where it is elaborated to prevent fouling of the mantle cavity later (Graham, 1932). Molluscs like *Skeneopsis*, *Omalogyra* and *Rissoella*, which live predominantly in rock pools, need none of these precautions, since there is a continuous flow of water through the mantle cavity to carry away the faeces, and a short and histologically simple intestine suffices when its function is simply one of transport. The intestine does not enter the coils of the visceral mass, but, from the anterior region of the stomach, at the posterior end of the body whorl, it passes directly along the right side of the mantle to the anus. Moreover, in *Omalogyra* and *Rissoella diaphana*, and to a lesser extent in *R. opalina* and *Skeneopsis*, it becomes shorter still because of the posterior position of the anus, which lies deep in the mantle cavity instead of at its opening.

It is a well-known fact that certain prosobranchs lose their ctenidium. In *Pomatias elegans*, and perhaps also in *Acicula lineata*, this is associated with a change from an aquatic to a terrestrial habitat. It would seem that smallness

is a factor leading to the same result, since in the Omalogyridae, Rissoellidae and Pyramidellidae there is no gill. The loss of a special respiratory surface in the minute representatives of a phylum is, of course, a common occurrence. It is probable that a certain amount of respiratory activity is normally carried out by the mantle in any mollusc, and it would appear that this is adequate for the respiratory needs of animals of such small size as those which are mentioned above. Three of the four species which have been described show other changes in the organs associated with the mantle cavity, which may accompany this loss. *Skeneopsis*, which is larger than the others, retains to a greater extent the typical arrangement of organs in the pallial cavity: it still possesses a ctenidium, though the number of filaments is reduced to nine, the kidney lies near the posterior end of the mantle cavity and the hypobranchial gland extends far back along the right side. In *Rissoella diaphana* and *R. opalina* the ctenidium is represented only by a patch of ciliated columnar cells, and in *Omalogyra* it is lost entirely. In these three the kidney has grown forwards mid-dorsally into the mantle, and brings with it a rich vascular network, which is separated from the water current in the mantle cavity only by a squamous epithelium. This, perhaps, increases the chances for the oxygenation of the blood. It is tempting to imagine that the similar forward thrust of the kidney in the other gastropods without a gill—the pulmonates and *Pomatias elegans*—may confer a similar benefit upon the animal. In *Omalogyra* and *Rissoella* the hypobranchial gland does not spread far beyond the anus, but its small area may perhaps be compensated for by the relatively enormous size of some individual cells. Accompanying the gland are longitudinal strips of columnar ciliated epithelium which pass forwards from the anus and produce a strong exhalant current. This current induces the inhalant flow of water along the right side of the mantle cavity, which is normally maintained by the ctenidium.

The ability of these gastropods to produce vast quantities of mucus from the foot would appear to be associated with their habitat. In the calm waters of a rock pool at low tide, they can utilize the mucous rope played out from the posterior pedal gland to lower themselves through the water in a caterpillar-like fashion. When the tide is high, and the water more turbulent, the viscid secretion from the gland, as well as from the general surface of the sole, helps them to maintain a firm hold. The posterior pedal gland has already been described in the rissoids (Johansson, 1939), and it occurs in other small, intertidal gastropods such as *Bittium*, *Cerithiopsis* and *Triphora* (personal observation). As a result of this excessive demand for mucus the glandular tissue has become too extensive to be accommodated entirely within the foot, and spreads into the haemocoel along each side of the buccal cavity and the anterior oesophagus.

As far as the internal anatomy is concerned there are two main points worthy of notice: the simplicity of the gut, and the complexity of the reproductive organs. The oesophagus differs from that of the typical prosobranch

in being devoid of oesophageal glands. In the related Rissoidae the explanation of this seems to be the presence of a crystalline style in the stomach. None of the creatures under consideration possesses such a structure, so that the simplification of the oesophagus must be due to something else. Now this part of the alimentary canal runs through the connexion between head, foot and visceral hump, where space has to be made for large and complex reproductive ducts which spread into all available corners, and it is probable that the presence of these limits the size of the oesophagus. Digestive tissue is, therefore, confined to the digestive gland which completely fills the visceral hump, except for the gonad, and its extent in *Omalogyra* is increased by spreading on to the gastric wall, and in the winter form—a particularly small animal—on to the lateral walls of the oesophagus as well. The epithelium in the digestive gland is composed of (*a*) digestive cells, (*b*) lime cells, and, except in *Omalogyra*, (*c*) cells which appear to act as deposits for excretory material. I have never observed this to be eliminated, and it would appear that these cells act as a kidney of accumulation, which is a perfectly feasible arrangement in an annual mollusc. This would also have the effect of relieving the kidney itself of a great deal of its normal work, leading to a simple sac-like structure, suggesting, in fact, that the organ has become more important from the respiratory than the excretory point of view. It may still, however, be required for osmoregulatory purposes, which may, at times, be a matter of prime importance to an inhabitant of a rock pool.

The survival of these rock-pool prosobranchs depends upon their ability to take advantage of conditions which favour their rapid growth and reproduction. These are fulfilled during the warmer months of the year by the high temperatures and ample food supply. The population is then at a maximum, and several generations of each species may be co-existent. With the fall in temperature during the autumn both growth and reproduction are retarded, and the mature population gradually dies out, so that only perhaps an occasional individual will survive into the winter. The population is then at a minimum: it is typically immature, having been derived from eggs laid by late spawners, and the growth of the individual is extremely slow compared with that during the summer. The necessity for a rapid increase in numbers is reflected in the hypertrophy and complexity of the reproductive organs to provide for the protection and feeding of the embryos. Relatively large egg capsules are produced; each is fixed to the weed on which the animals live and contains one to three heavily yolked eggs, surrounded by albumen, and protected by a thick wall. The development takes about a fortnight during a favourable summer and the young hatch as miniatures of the adult. If conditions are good, they grow rapidly, mature, and reproduce in the same season—*Omalogyra* may develop from the egg and reproduce in about 7 weeks. The life of such individuals is short and may be reduced to less than 6 months.

A similar maximum of numbers during the summer is found in *Rissoa parva*

(da Costa), and probably many other rissoids. In these, however, some mature animals may live through the winter, spawning the while.

Rissoella and *Omalogyra* are hermaphrodite and ripe spermatozoa and ova occur simultaneously. Simultaneous hermaphroditism is a fairly common phenomenon within the prosobranchs, and is found in quite unrelated forms—*Valvata*, *Velutina*, *Cerithiopsis* (personal observation) and in all the Pyramidellidae. Little is known of the extent to which self-fertilization is practised. It seems likely that it takes place in *Omalogyra*, and there is no morphological bar to its accomplishment in *Rissoella*. In *Omalogyra* there does not appear to be anything which could act as a copulatory organ in the summer population, in which the development of the reproductive organs is different from that of winter forms, yet, despite this, reproduction goes on rapidly, and the explanation may be self-fertilization or parthenogenesis, but the latter seems far less probable. In individuals which develop slowly during the winter months and which come to maturity in the spring, the male system is the first to become functional, and it seems likely that copulation will then occur, but, as I have never seen this taking place, I do not know whether it is a reciprocal act or not.

If the hermaphrodite reproductive system be neglected, it would appear that the anatomy and life history of the molluscs under discussion indicate a relationship with the Rissoidae. Many of the rissoids are intertidal, or inhabit shallow waters, and they also possess a posterior pedal gland which extends from the foot into the haemocoel of the head; to them such a gland is as useful an aid to locomotion as it is to *Skeneopsis* and *Rissoella* and enables them to exploit the surface film as well as the substratum. The food and feeding habits are also similar—except in *Omalogyra*. The food consists of algal filaments, diatoms and detritus. It is passed down a simple oesophagus, which lacks glandular pouches, and is partly digested in the capacious stomach. Amongst the rissoids several species (Graham, 1939; Johansson, 1939) possess a crystalline style, which, however, is not present in *Skeneopsis* and *Rissoella*. In *Omalogyra* the radula is reduced to three teeth in each row (Ankel, 1936) which puncture the algal cells from which the sap is sucked. Pruvot-Fol (1926) points out the similarities between the structure and function of this radula and that of the ascoglossan nudibranchs, and even goes so far as to suggest the presence of an ascus sac for used teeth in *Omalogyra*, though I have never seen anything of this nature. Her final conclusion is that the similarity is entirely due to convergence. The egg capsules of the rissoids are fixed on weed and are similar in most respects to those of *Skeneopsis*, though they contain relatively smaller and more numerous eggs which escape as free veligers (Lebour, 1934). Thus in the rissoids the general parallelism is maintained between lack of specialization in bodily structure and simplicity of larval history. Related to the rissoids are the hydrobiids amongst which *Hydrobia jenkinsi* Smith is peculiar in practising parthenogenesis. In other species of *Hydrobia* the sexes

are separate, so that parthenogenesis in *H. jenkinsi* would appear to have arisen by the loss of the male. *Omalogyra* may indicate a different way in which a purely parthenogenetic species may evolve—that is by the reduction and final loss of the male stage in the reproductive activities of a hermaphrodite.

Summary

The external features of *Skeneopsis planorbis* (Fabricius) are described and compared with those of *Omalogyra atomus* (Philippi), *Rissoella diaphana* (Alder) and *R. opalina* (Jeffreys).

The foot has a large posterior mucous gland (Figs. 1 and 4, PM; Pl. IV, figs. 1 and 2, AL, PL), its secretion forming a thread on which the mollusc can climb from one level to another.

Correlated with their small size are modifications of the pallial organs. *Skeneopsis*, the largest and least specialized, has a bipectinate osphradium, but the gill is reduced to nine filaments; the anus lies well within the mantle cavity. In the other genera osphradium and ctenidium are lost, though the latter may be represented in *Rissoella* by a small tract of ciliated epithelium. In the absence of a ctenidium the animals depend entirely upon pallial respiration and the stream of water through the mantle cavity is maintained by other means: from the anus strips of ciliated epithelium pass forward to the mouth of the mantle cavity, causing a strong exhalant stream and carrying away the faecal pellets. There is a compensating inhalant flow. The kidney (Pl. IV, figs. 1 and 2, K), with its rich vascular supply, has migrated into the tissues of the mantle, increasing its respiratory efficiency.

In the internal anatomy the simplicity of the gut and the complexity of the reproductive organs are the most outstanding features. One may be the cause of the other (pp. 628–29).

The animals are abundant during the warmer months and scarce in winter, when an immature slow-growing population is found. The opportunity for rapid increase in numbers during spring and summer is given by the hypertrophy and complexity of the reproductive organs which provide for the protection and feeding of the embryos.

Omalogyra and *Rissoella* are hermaphrodite. It seems likely that self-fertilization may occur in the summer animals of *Omalogyra* in which there appears to be no copulatory organ. Summer individuals differ in other structural details from the winter animals. In *Rissoella* there is no morphological bar to self-fertilization, but it has never been observed.

Egg capsules (Figs. 1 and 6) are fixed to weed and contain from one to three eggs, which hatch in about a fortnight at summer temperatures. The young escape in the crawling stage, and, if conditions are favourable, become mature in 6 weeks or less and reproduce in the same season. Thus one generation follows rapidly upon another.

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THE GONADS, LARVAE, AND BUDDING OF THE POLYSTYELID ASCIDIANS *STOLONICA* AND *DISTOMUS*

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(Text-figs. 1–6)

Stolonica socialis (Hartmeyer) and *Distomus variolosus* Gaertner are two species of styelid ascidians with a capacity for budding and colony formation, found on both sides of the western end of the English Channel. *Distomus* occurs immediately below the level of extreme low spring tides, commonly encrusting the sides of rocks and laminarian bases. *Stolonica* is more usually found by dredging in deeper water, on the upper sides of stones or gravel bottom. Their external appearance and general internal anatomy have been well described and beautifully illustrated in the monograph of Lacaze-Duthiers and Delage (1892), while the process of budding has been investigated by Selys-Longchamps (1917).

In spite of their local abundance and striking appearance, little attention has been given them by English biologists and much of general interest has been overlooked, while an over-emphasis of the importance of the pattern systems of botryllid colonies has masked the close relationship of all the budding styelid-like ascidians. This relationship is discussed further, after descriptions have been given of the breeding cycles of *Stolonica* and *Distomus*.

Stolonica socialis (Hartmeyer)

Mature colonies (Fig. 1 A) consist of loosely associated individuals from 10 to 15 mm. high, of a bright yellow-orange when alive, each with independent branchial and atrial siphons.

With regard to the internal anatomy (Fig. 1 B) the main points of interest are that the branchial sac has three true moderately well-developed branchial folds on each side. The heart has one end opening, as in many other ascidians, at the posterior end of the endostyle. A considerable part of the tubular heart extends anteriorly and mid-ventrally, immediately below the endostyle.The neural gland is dorsal to the ganglion. The most striking feature, however, is the distribution and nature of the gonads.

Gonads

The gonads (Fig. 1 B—D) are arranged in three rows, one along each side of the endostyle, and one on the left following the outer course of the intestine. They are essentially hermaphrodite organs imbedded in the atrial or mantle

wall. Each testis and ovary has its own duct extending as part of the atrial lining, opening into the atrial cavity.

The fully formed gonad consists of a testis divided into from six to a dozen lobes all emptying into a common sperm duct which projects into the atrial

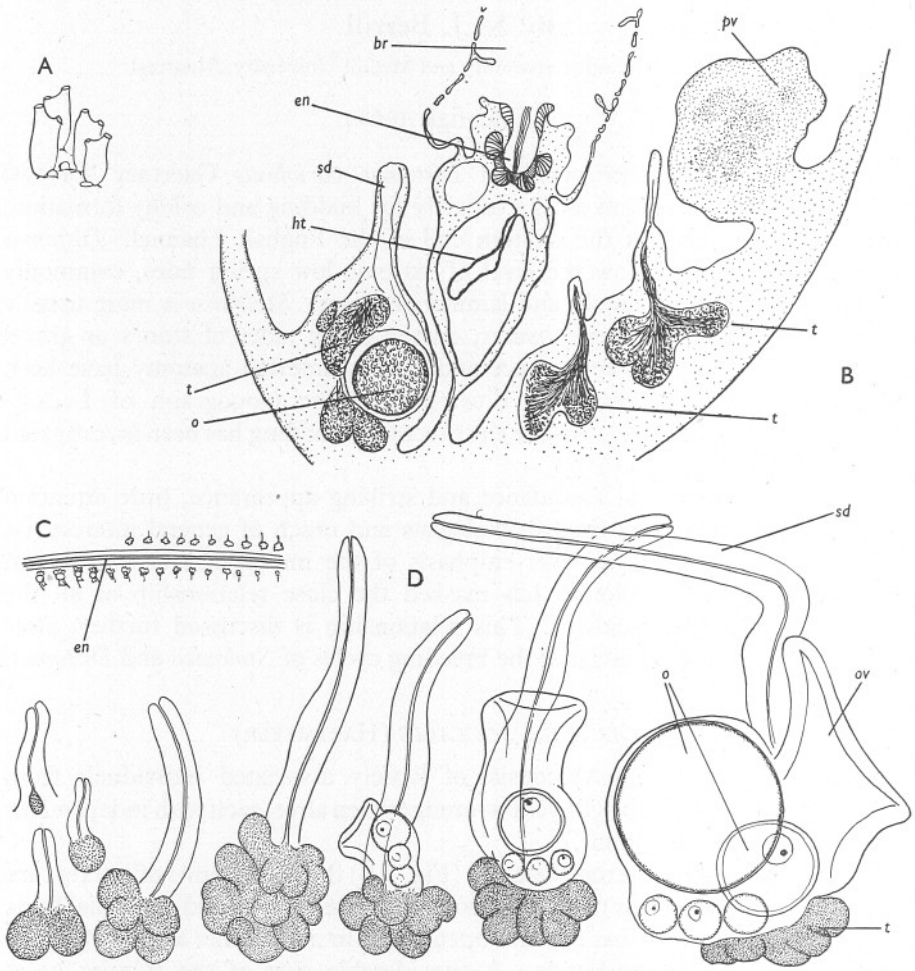

Fig. 1. *Stolonica socialis*. A, zooids. B, cross-section of mature zooid to show position of heart ventral to the endostyle, and gonads in the mantle wall on each side of the mid-ventral line. C, endostyle with male gonad series on one side and male to hermaphrodite series on the other. D, graded samples of hermaphrodite series. *br*, branchial sac; *en*, endostyle; *ht*, heart; *o*, ripe egg; *ov*, oviduct; *pv*, parietal vesicle or endocarp; *sd*, sperm duct; *t*, testis.

cavity within a long slender extension of the inner atrial wall, and an ovary with a single large ovum and several small oocytes, with a very short and very wide oviduct opening to the atrial cavity.

The gonads, however, are not all alike. The series along the right side of the endostyle and the series following the course of the intestine on the left side each consists of testes only, essentially the same as the male component of the hermaphrodite unit just described; while the series along the left side of the endostyle is a graded one, and at its posterior end from four to six units are hermaphrodite, each with a fully grown ovum (Fig. 1 C). At the anterior end only male components are present, those at the extreme anterior end being relatively extremely small. Intermediate units occur along the middle range of the series.

As the male gonads become progressively smaller it is evident that the number of the testis follicles is correspondingly reduced, the size of the individual follicle remaining unaffected until the number is reduced to one, and only further diminution results in a reduced follicle size. Also the length of the sperm tube is directly proportionate to the number of follicles or mass of testis tissue.

The size of the male gonad increases until a maximum is reached approximately midway along the side, after which it remains virtually the same size, although there is some indication of further but slight increase. The female gonad first appears about halfway along the series as a group of small partly grown ova associated with a relatively small oviduct. The size of the unit increases progressively, passing towards the posterior end, until a maximum size is reached about one-quarter the length of the series from its end. The maximum units have a fully grown ovum, one partly grown, and several oocytes showing no sign of growth at all. The smaller units may have a partly grown ovum and undeveloped oocytes, but no fully grown ovum.

The series, which is illustrated in Fig. 1 D, may accordingly be regarded as a single series of increasing unit sizes, progressive size increases giving rise to progressively larger male gonads until a maximum is attained, further size increases resulting in first rudimentary and finally large functional female gonads.

The male series on the right of the endostyle and alongside the intestine exhibits less of a size gradient and its members do not attain the tissue mass of the hermaphrodites. It is believed that unless the initial rudiment of a gonad exceeds a certain critical size, it will not grow to a size capable of forming or segregating oocytes, and unless oocytes are formed no oviduct will develop.

The majority of the middle zone hermaphrodites probably do not mature as female gonads, since, shortly after the maximum gonads have shed their eggs and the tadpoles developed, the parent zooid becomes senescent and is sloughed off. As far as can be determined the maximum gonads at the posterior end of the series each yield two ripe eggs in the course of the breeding season, three at the most and one at a time. The submaximal gonads produce but one ripe egg coinciding with the shedding of the last egg of the larger units, while the smaller units near the beginning of the hermaphrodite series fail to produce any. Whether, given sufficient time, they could do so is not known, for their time is cut short by the death of the whole organism.

Development of the Egg

Development of the egg as far as the formation of the active tadpole larva takes place within the atrial cavity. The mature eggs are the largest, though not the yolkiest, known among ascidians, with a diameter of approximately 0·70 mm. They are equalled in size only by those of *Ecteinascidia turbinatum* Herdman.

Cleavage is unmodified, with the same sequence of pattern established for *Styela* by Conklin (1905). Gastrulation occurs between the sixth and seventh cleavage as in all other ascidians and is typically embolic. In spite of the large size of the egg and its rather heavy yolk content, the yolk is distributed as in smaller and less yolky eggs and has no apparent affect upon either cleavage or gastrulation, other than a general retardation of developmental rate (Fig. 2 A).

At 16° C. the tadpole hatches by digestion of the egg membrane about 5 days after fertilization, although at that time it is still inactive. It continues development for another 4 days within the atrial cavity of the parent before it attains functional differentiation and is liberated. During this last period there is considerable growth of the trunk, while the changes in the tail are mainly those of fine differentiation of the locomotory tissues. The free-swimming period usually lasts about 2 days, but may be shorter or considerably longer. It may be greatly affected by the length of time the fully formed tadpole has been retained within the parental atrial chamber. The heart commences beating about 4 days after the tadpole first becomes attached, the four rows of gill slits function 2 days later, and the gut functions fully after another 5 days. It is this last state (Fig. 2 B) that should be regarded as the end of egg development, and not the attainment of the active tadpole stage.

Tadpole Larva

The tadpole (Fig. 2 B) is about the largest and most effective swimmer among ascidian larvae. The trunk is approximately 1 mm. and the tail, exclusive of the cuticular fin, 2 mm. long. At a temperature of 16–17° C. the tadpole has a free-swimming period of from 24 to 48 hr. for the great majority. Swimming is somewhat intermittent under laboratory conditions, depending greatly upon external stimulation. At this temperature the stroke of the tail is about 8–12 per sec., and progress about 25–30 mm. per sec. Tadpoles show response both to light and gravity, being positively heliotropic and negatively geotropic during the first few hours at least.

During the active phase the trunk remains ovoid and streamlined. The tail fin, a cuticular secretion, is vertical, retaining the primitive position in spite of the large size of the egg, and as the result of the developing tail being coiled horizontally around the trunk rather than vertically. Both branchial and atrial invaginations are formed at this time, the atrial being median and single from

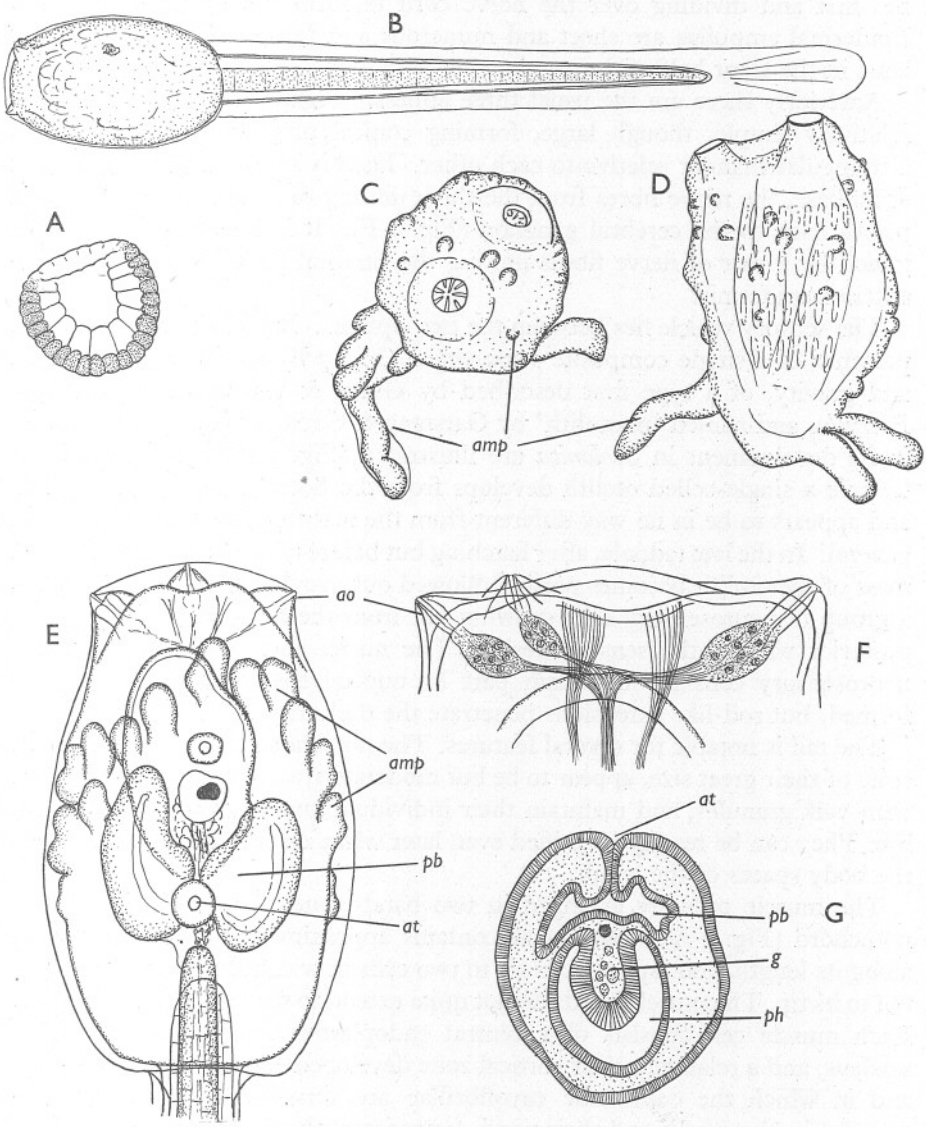

Fig. 2. Development and tadpole structure of *Stolonica*. A, gastrula. B, active tadpole. C, metamorphosed individual with siphons open. D, fully developed oozooid with four rows of gill slits. E, trunk of tadpole from dorsal side showing adhesive organs, ampullae, sensory vesicle and peribranchial sacs. F, anterior region of tadpole showing nerves and ganglia to adhesive organs and anterior epidermis. G, cross-section of tadpole through atrial invagination to show ectodermal origin of peribranchial sacs. *amp*, ampulla; *ao*, adhesive organ; *at*, atrial siphon; *g*, ganglion; *pb*, peribranchial sac; *ph*, pharynx.

the first and dividing over the nerve cord to form the peribranchial sacs. Epidermal ampullae are short and numerous and form an irregular circular zone in the front half of the trunk.

Anteriorly there are the usual three adhesive organs (Fig. 2 E). They are relatively simple, though large, forming conical projections distributed in a triangular manner relative to each other. Each is supplied with a ganglion at its base, the nerve fibres from the three uniting to form a single fibre that passes back to the cerebral ganglion (Fig. 2 F). It is accompanied but not joined by a pair of nerve fibres uniting the cerebral ganglion with the mid-anterior epidermis.

The sensory vesicle lies between the two siphons. It is characterized by the presence of a single composite sense-organ (Fig. 3 E) sensitive to both light and gravity, of a type first described by Grave & Woodbridge (1924) for *Botryllus* and named 'photolith' by Garstang & Garstang (1928). Two stages in its development in *Stolonica* are illustrated (Fig. 3, C–F). In the early tadpole a single-celled otolith develops from the floor of the sensory vesicle and appears to be in no way different from the otolith of ascidian tadpoles in general. In the late tadpole, after hatching but before liberation, the pigmented mass of the otolith becomes partly hollowed out, partly extended, to embrace a group of neurosensory cells growing out from the sensory ganglion at the posterior wall of the sensory vesicle. The nuclei and cell bodies of these neurosensory cells for the main part lie outside the pigmented cup thus formed, but rod-like extensions penetrate the dark mass.

The tail is notable for several features. The notochord cells, about forty, in spite of their great size, appear to be but moderately vacuolated, are congested with yolk granules, and maintain their individual integrity throughout larval life. They can be readily identified even later when resorbed and separated in the body spaces of the trunk.

The muscle cells are arranged in two bands, one along each side of the notochord (Fig. 3 A). Each band contains approximately twenty-four cells along its length, and tapers from six to two cells in width from the base of the tail to its tip. The muscle bands do not quite extend to the tip of the notochord. Each muscle cell consists of a central endoplasmic region containing the nucleus, and a relatively clear cortical zone developed equally well on all sides and in which the contractile myofibrillae are formed. Even after metamorphosis, these cells and their zones are recognizable in the resorbed tissue. The most striking feature is the continuity of the myofibrillae from cell to cell (Fig. 3 B). The myofibrils pass as continuous structures, following a slightly spiral course, from the broad base to the narrow tip of the muscle band as a whole, and there is no doubt that the band functions as a unit. The fibrils pass from cell to cell in the cortical or ectoplasmic zone, and there is a definite superficial syncitial or symplasmic state of the tissue. A similar condition has been described by Caswell Grave (1921) for *Amaroucium*, and by Conklin

(1931) for *Styela*. *Stolonica* tadpoles are exceptionally favourable for demonstrating this condition, owing to the large size of the muscle cells and relatively enormous thickness of their hyaline zone.

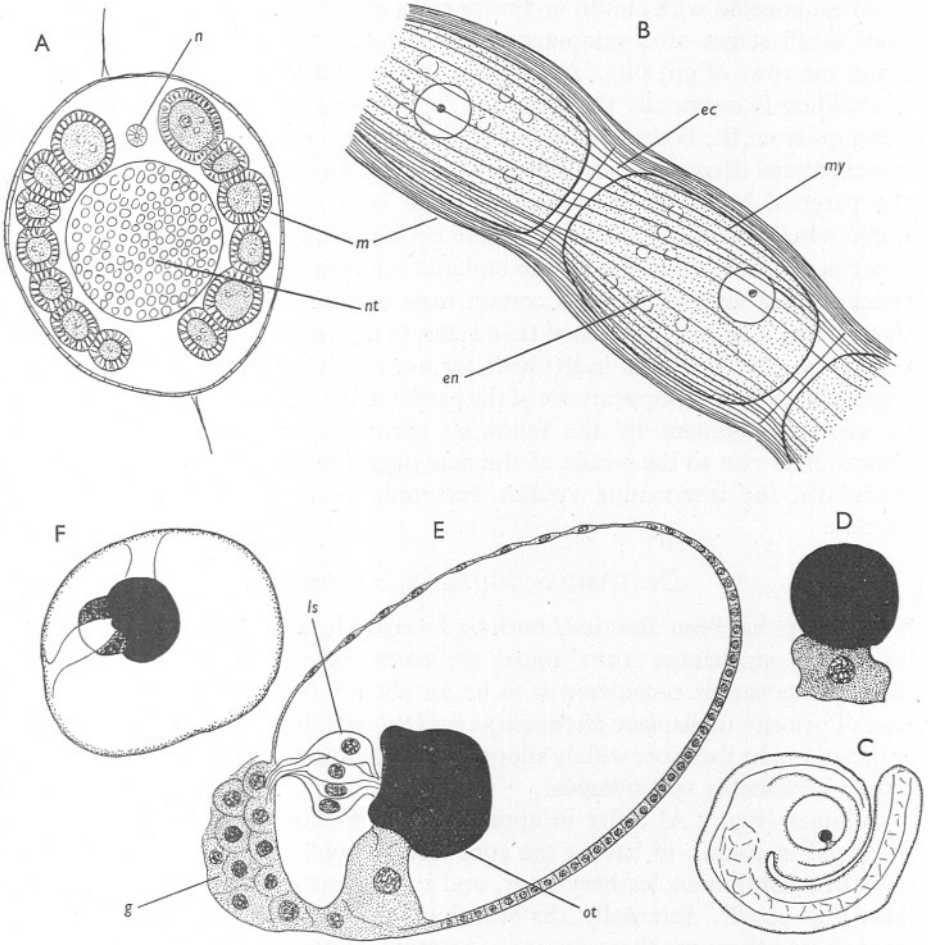

Fig. 3. Tail and sensory vesicle of *Stolonica* tadpole. A, cross-section of tail showing organization of muscle cells. B, adjacent muscle cells showing thick ectoplasmic zone and continuity of myofibrillae from cell to cell. C, embryonic tadpole with newly formed otolith. D, otolith of C at same magnification as figure E. E, sensory vesicle with otolith invaded by light-sensitive neurons to form 'photolith'. F, dorsal view of vesicle showing extension of otolith pigment. *ec*, ectoplasm; *en*, endoplasm; *g*, ganglion; *ls*, light-sensitive cells; *m*, muscle cell; *my*, myofibril; *n*, neural tube; *nt*, notochord; *ot*, otolith.

Budding

The process of budding has been described at length by Selys-Longchamps (1917), to which little can be added. There is no sign of budding in the oozooid when it first functions with the primary four rows of gill slits (Fig. 2 D, G),

nor for several weeks after, during which growth occurred, though not enough to increase the number of rows of gill slits. Selys-Longchamps, however, figures (1917, plate III) a young colony from dredged material consisting of a central oozooid with eleven or twelve rows of gill slits, and with about eight buds at all stages of development from initiation to functional zooids with about ten rows of gill slits. Apart from size it seems evident that the process of budding is essentially the same for colonies old or young. An outgrowth develops from the body wall involving the epidermis, the atrial lining, and the mesenchymal tissue between. The process extends a considerable distance from the parental body, while reserve nutritive cells of the circulating system, pseudovitelline cells, accumulate at the tip between the outer epidermal and inner atrial tubes. The tip of the stolonic outgrowth constricts off after the accumulating vitellus attains a certain mass and cuts off circulation through that region. The bud so isolated then starts to develop, although the process is very slow. Fully mature individuals form a relatively large bud of this type which survives the disappearance of the parent in the late summer and completes its own development by the following spring. The internal atrial vesicle always gives rise to the whole of the new organism with the exception of its epidermis, the intervening vitellus becoming progressively utilized in the process.

Distomus variolosus Gaertner

This species has been described both by Lacaze-Duthiers & Delage (1892) and by Selys-Longchamps (1917) under the name *Heterocarpa glomerata* Alder. Selys-Longchamps considered it to be an absurd obedience to intransigent laws of priority to displace *Heterocarpa* by *Distomus*, but this last name appears at present to be the more widely adopted. The *Allaeocarpa apolis* of Michaelsen (1904) is probably synonymous.

Colonies (Fig. 4 A) differ in appearance from those of *Stolonica* in being brick red in colour, in having the constituent zooids closely packed together to form a continuous leathery layer, and in the smaller maximum size of the individual zooids. Internally, the branchial sac is without true folds, although on each side there are three groups of internal longitudinal bars, undoubtedly the remnants of what were originally three branchial folds (Fig. 4 B). The neural gland is dorsal to the ganglion, while the heart extends anteriorly beneath the endostyle as in *Stolonica*, and as in *Stolonica* the gonads are unique, though in their own way.

Gonads

The zooids, as in almost all ascidians, are functional hermaphrodites, but are peculiar in possessing only testes on the right side and ovaries on the left.

The testes (Fig. 4 C, G) are comparatively simple, the smallest being more or less pear-shaped, larger ones becoming relatively elongated, a maximum

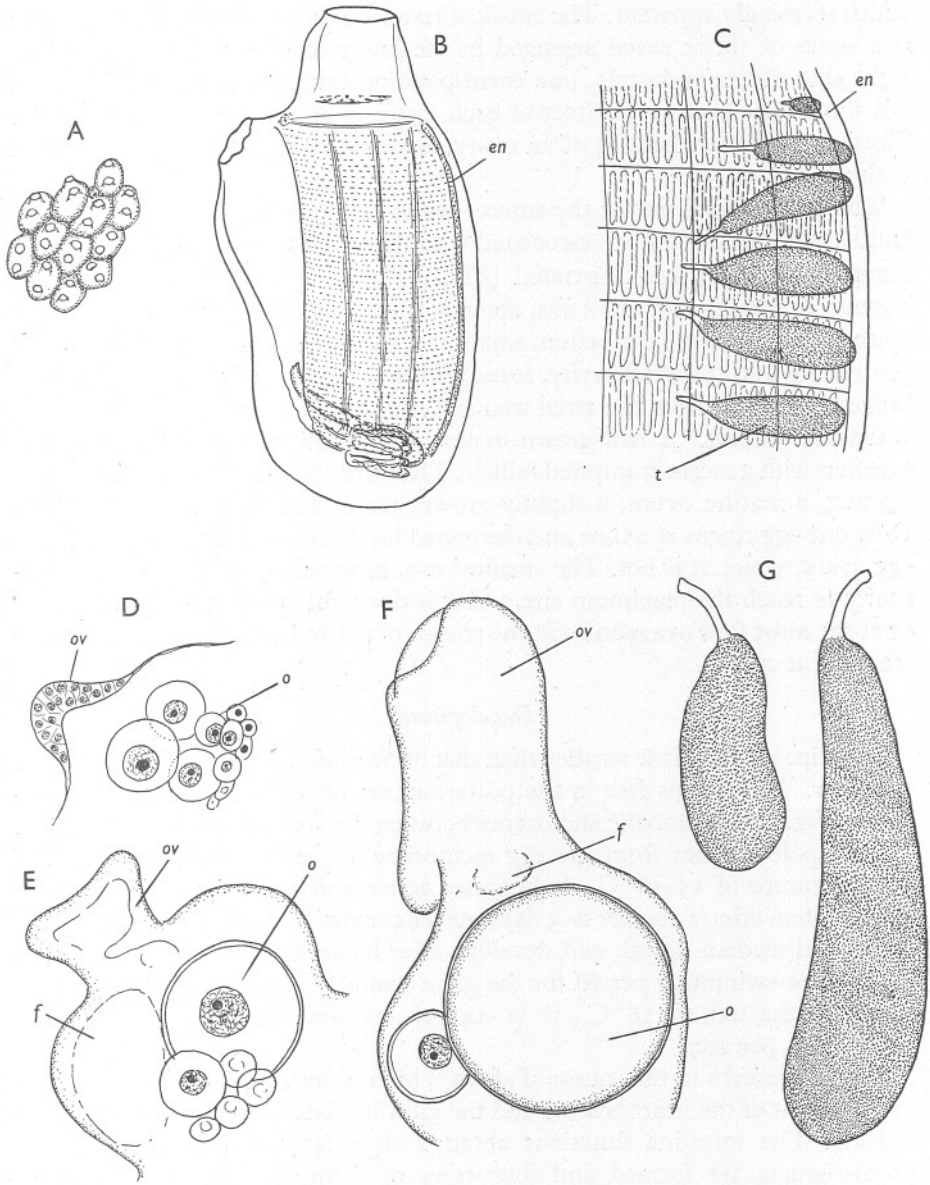

Fig. 4. *Distomus variolosus*. A, zooids. B, zooid enlarged. C, part of ventral branchial sac showing relative position and number of testes. D, young stage in development of ovary and oviduct. E, ovary with one egg discharged, and numerous oocytes. F, typical mature ovary with ripe egg. G, minimum and maximum sized testes. *en*, endostyle; *f*, empty follicle; *o*, ova; *ov*, oviduct; *t*, testis.

width seemingly apparent. The smallest testes occur anteriorly. Usually there is a series of six or seven arranged in the lower mantle wall parallel to the right side of the endostyle, one corresponding fairly closely to each row of gill slits. The short sperm duct of each testis opens towards the dorsal side. There is no trace whatever of an ovary, however rudimentary, in association with the testes.

The ovaries are found in the antero-dorsal mantle wall of the opposite side, and have no trace of a testis associated with them. Three stages in the development of an ovary are illustrated (Fig. 4 D–F). The youngest consists of a group of oocytes and small ova, about a dozen in all, lying beneath the atrial epithelium. The atrial epithelium adjacent to the ovary shows a local thickening protruding into the atrial cavity, foreshadowing the oviduct. The second stage bulges as a whole from the atrial wall and has a moderately large though short and wide oviduct. A half-grown ovum, with a few small ova, are present, together with a recently emptied follicle. The third stage has the fully developed oviduct, a mature ovum, a slightly grown ovum, and an old empty follicle. Only one egg ripens at a time and the gonad has been considered to be a single egg ovary, which it is not. The smallest ova, however, do not have an opportunity to reach the maximum size and it is doubtful whether more than three or at the most four ova mature in the course of the individual zooid's breeding season and cycle.

Development

The ripe egg is a little smaller than that of *Stolonica*, approximately 0·6 mm. diameter. It develops free in the posterior part of the atrial cavity. Gastrulation (Fig. 5 A) is embolic and occurs between the sixth and seventh cleavage. The tadpole hatches from the egg membrane 4–5 days after fertilization at a temperature of 15–16° C. It becomes active and is liberated through the atrial siphon after a further 2–3 days' development. The atrial invagination is single and median-dorsal, and develops after hatching and before liberation.

The free-swimming period for the great majority is from 18 to 30 hr. The stroke of the tail, at 16° C., is 11–14 per sec. and the tadpole progresses 20–25 mm. per sec.

The tail resorbs in the course of about 8 hr. and metamorphosis is complete to the extent of the heart beating and the gill slits functioning 10–12 days after settling. The intestine functions about 2 days later. As in *Stolonica* no protostigmata are formed and four rows of definitive stigmata appear as independent perforations from the beginning (Fig. 5 C).

The tadpole (Fig. 5 B) is large, though not so large as that of *Stolonica*, and is brick red. The cuticular fin of the tail is vertical, the developing tail being coiled horizontally around the embryo, so that it does not become twisted through ninety degrees as it would if the tail retained the primitive vertical position in the limited perivitelline space. A pair of flukes extend postero-

laterally from the trunk. They may conceivably have some stabilizing function in swimming. In the anterior half of the trunk a ring of sixteen epidermal ampullae, rarely more, encircle it. The ring is very regular compared with the same feature in tadpoles of *Stolonica*. Three adhesive organs, arranged triangularly, are formed at the anterior tip. During metamorphosis the tail resorbs, the tail cuticle is thrown off, and the trunk shortens along its main axis. At the same time the ring of ampullae extend individually, secreting test substance and making fast to the substratum, taking over the function of the transient adhesive organs.

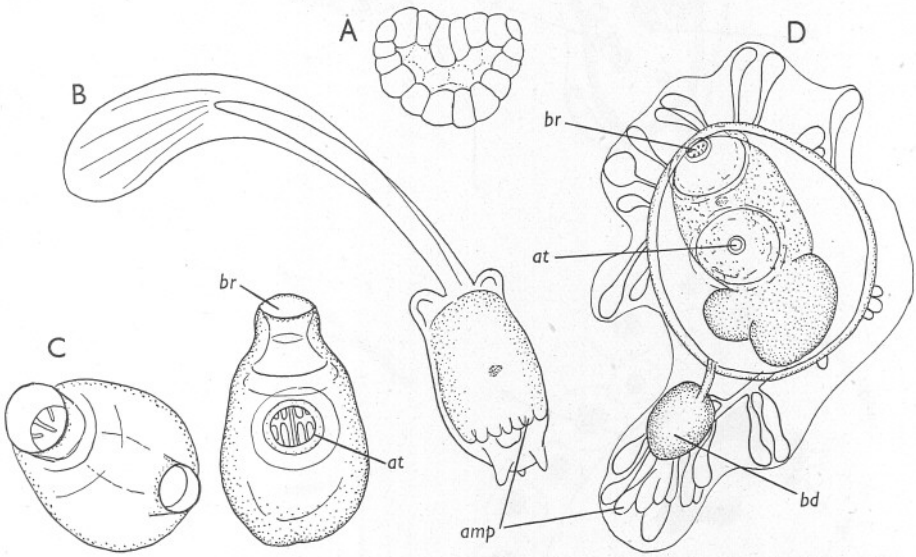

Fig. 5. Development of *Distomus*. A, gastrula. B, active tadpole. C, functional oozooids. D, oozooid after several weeks' growth with first bud and numerous ampullae. *amp*, ampulla; *at*, atrial siphon; *ao*, adhesive organ; *bd*, bud; *br*, branchial siphon.

The adhesive organs are large but simple, consisting of conical epidermal projections containing a hollow core of glandular cells that secrete the adhesive substance. Each has a nerve ganglion associated with its base and a nerve fibre connecting with the central neural ganglion (Fig. 6 E). The fibres remain separate from each other until they reach the sensory vesicle region. Two lateral nerve fibres pass from the central ganglion to a pair of lateral larval ganglia.

The sensory vesicle contains a single sense organ, a typical 'photolith' as in *Stolonica* and *Botryllus* (Fig. 6 D). As in these forms, it develops early as a unicellular otolith from the floor of the sensory vesicle, and late in the course of tadpole development a group of neuro-sensory cells project from the postero-dorsal wall of the vesicle and enter the hollowed-out and extended mass of otolith pigment. The tadpoles are responsive both to light stimuli and gravity.

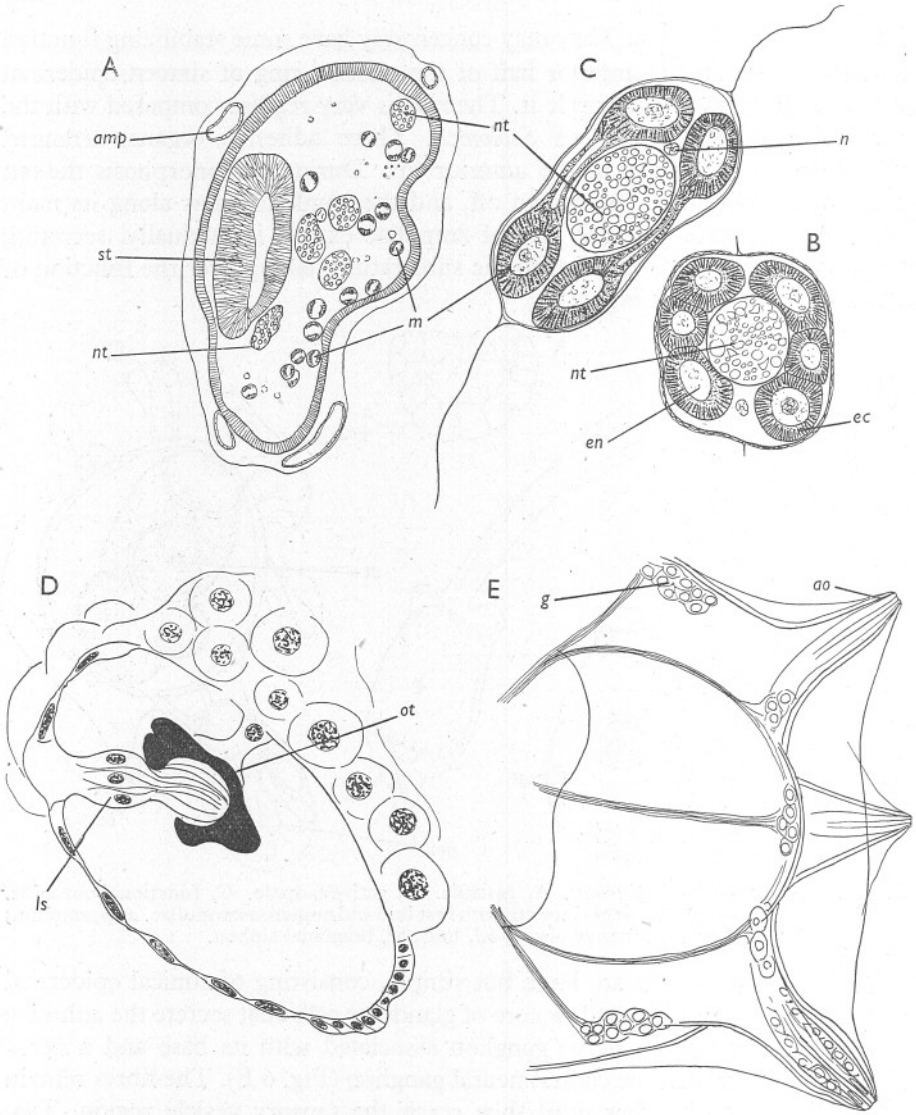

Fig. 6. *Distomus*. A, section through metamorphosed tadpole to show muscle cells and yolky notochord cells scattered through body cavity. B, C, sections of tail through middle and posterior part to show nature and arrangement of muscle cells. D, sensory vesicle with typical photolith. E, anterior region of tadpole showing nerves and ganglia associated with the adhesive organs and anterior ectoderm. *amp*, ampulla; *ao*, adhesive organ; *ec*, ectoplasm; *en*, endoplasm; *g*, ganglion; *ls*, light sensitive cells in photolith; *m*, muscle cell; *n*, neural tube; *nt*, notochord; *ot*, otolith; *st*, stomach.

The notochord consists of approximately forty yolk-laden cells arranged in single series. The muscle cells (Fig. 6 B, C) are arranged in two bands, one on each side of the notochord, each band consisting of three cells in cross-section at the base of the tail, two near the tip. The notochord extends

posteriorly slightly beyond the muscle bands. Myofibrillae are continuous from cell to cell throughout the length of the band, taking the same somewhat spiral course as in *Stolonica*. They are confined to the relatively enormously thick hyaline zone. After resorption of the tail, notochord cells still richly laden with yolk granules and muscle cells now isolated and with the fibrilla zone obvious are clearly recognizable scattered through the primary body cavity (Fig. 6 A).

Budding

Buds are produced in essentially the same manner as in *Stolonica*. Local regions of the posterior and ventral body wall, involving epidermis, mesenchyme, and atrial lining, grow out to form the bud stolon. Usually the outgrowth is extremely short and the bud develops at its tip in close conjunction with the parent and without severing its connexion. Winter buds, however, are produced similar to those of *Stolonica*, with large accumulations of pseudovitelline cells between the epidermis and the inner atrial tube. These masses survive the dissolution of the parents after the sexual breeding season and themselves develop to functional maturity by the following spring.

The first buds appear relatively early, from the wall of the oozooid, a few weeks after the settling of the tadpole, at the time the most anterior of the primary four rows of definitive stigmata is dividing into two rows (Fig. 5 D).

Selys-Longchamps (1917, plate III) shows two partly fused young colonies each with an oozooid with about a dozen rows of stigmata, giving rise to five or six buds at various stages. There is evidently a considerable accumulation of reserve cells between the epidermal and atrial layers even in the buds of these early colonies and this appears to be the main source of bud nutrition rather than the communicating stalk with the parent zooid. The epidermis contributes only epidermis, and all other tissues and organs are derived from the atrial epithelium forming the internal vesicle.

The Polystyelid and Botryllid Ascidians

The most recent systematic treatise on ascidians is the monograph by Van Name (1945) on North and South American forms. In this account the Botryllidae are assigned full family status, but are described as belonging to the same stock as the Styelidae, and as quite closely related to some of the compound members of that family. Van Name is not in favour of separating the compound from the simple Styelidae as a separate family (Polyzoidae, syn. Polystyelinae), as Ärnbäck-Christie-Linde (1923) and others have suggested. Any discussion of such forms as *Stolonica* and *Distomus* therefore involves the botryllids on the one hand and the non-budding styelids on the other.

Van Name's setting apart of the Botryllidae in their old accepted status is based on the presence of zooid systems and common cloacal apertures, and

on differences he believes to exist with regard to gonads and budding. His refusal to separate polystyelids from simple styelids is based on the close relationship of *Polyandrocarpa*, a polystyelid, and *Polycarpa* (a simple styelid), when only adult features of the mature isolated individual are contemplated. If only adult characters are considered, there is little doubt that the two forms merit merely a generic distinction.

It is evident that much of the diversity of opinion is due to varying interpretation of similarities in adult and reproductive features. If the classification is to reflect actual relationships, it is important to decide whether similarity of adult structure is basic and other characters convergent, or whether budding and larval characters can be used to unify a group. It is considered here that the last is possible and there is a natural group of styelid ascidians set apart from other styelids by two unique characters, a type of budding and a larval sense-organ not to be found elsewhere among tunicates.

Botryllids and polystyelids are the only members of the order Pleurogona (= Stolidobranchia = Ptychobranchia) that bud. Since no member of this order possesses a posterior abdominal or post-abdominal extension of the body, and the epicardium survives only in one family and as a highly specialized renal organ, there is no possibility of the strobilating epidermal-epicardial budding processes of the Enterogona (= Phlebobranchia + Aplousobranchia), nor is there any structure comparable to the budding stolon of the Perophoridae. The styelid-botryllid type of budding is always fundamentally an outgrowth or outgrowths of the whole body wall at the level of the pharynx, consisting of a hollow protrusion of both epidermal and atrial epithelia with mesenchymatous tissue enclosed between them. It is usually called 'palleal' budding, and the atrial epithelium is invariably the primary morphogenetic tissue. Nothing comparable to this type of budding occurs among any other forms. It accordingly remains to be shown that the marked variability of budding among the botryllids and polystyelids is that of one basic type. There are differences in the number of buds produced; and while in some genera buds may form from a relatively extensive region of the body wall, in others they are localized within a small area on each side. In some forms buds are produced slowly during the long period of growth of the parental individual as a functioning organism, in others either a single pair or a series are formed only during the developmental period of the parent. These variations can be regarded only as specializations in area and time, and do not affect the essential morphology of the process. Morphological differences are not great. They relate to the distance a palleal outgrowth extends before its tip starts to develop as a bud, whether separation of the tip from its stalk is necessary before development starts, and whether nutrition of the buds is effected by a secondary reattachment to a colonial vascular system or is met by accumulation of reserve material between the inner and outer vesicle of the bud. The bud proper always consists of an outer epidermal vesicle enclosing an inner vesicle

derived from the atrial epithelium, the latter giving rise to all structures except epidermis.

It is simpler, and therefore more reasonable, to assume that this method of budding has been acquired on a single occasion by the group that exhibits it, than either that it has been acquired more than once or that all pleurogonid ascidians at one time possessed it, and the majority have lost it at different times.

The conclusion that all styelid and botryllid ascidians exhibiting palleal budding comprise a natural group is reinforced by a study of the tadpole larvae. Without exception, every species so far known that forms buds from the atrial body wall produces tadpoles with a 'photolith'. On the other hand, a photolith is not developed in the tadpole of any other ascidian species. All photoliths consist of a single-celled otolith developing from the floor of the sensory vesicle, the pigmented mass becoming hollowed out as a deep cup to receive the distal ends of a group of neurosensory cells growing out from the neural wall of the vesicle in the region where the ocellus occurs in other forms. The organ is responsive both to light and gravity. It is hardly conceivable that parallel evolution would so occur that two or more groups with palleal budding independently evolved a photolith. The coextension of the two features definitely indicates the existence of a single natural group.

At the same time, on the basis of adult structure, the relationship of *Polycarpa* and *Polyandrocarpa* is very close and hardly justifies anything greater than the generic distinction Van Name assigns them. This raises the question whether the Styelidae should be divided into two subfamilies, or whether the budding forms should be raised to full family status. This last may seem more logical, for the polystyelids as a whole exhibit great variability and as a group seem to have been launched on an independent evolutionary career of diversification, but it ignores the obvious relationship with the simple polycarpid styelids. There seems to be little justification for the maintenance of the botryllids, i.e. the genera *Botryllus* and *Botrylloides*, in a separate category, whether family, subfamily or any other, purely on the basis of the presence of zooid systems in the colonies. No such value is given to the presence or absence of systems in other families, e.g. Polyclinidae, and as Brien (1937) has shown they depend on buds being at equivalent developing stages and relatively close together. The striking end-result is out of proportion to the character leading to it. Accordingly the stand taken here is that there is a single natural group, the subfamily Botryllinae, characterized by palleal budding and the presence of a photolith in the tadpole larvae, combining with the Styelinae to form the Styelidae.

It is interesting within this group to try and determine the divergent paths of specialization. Species of *Polyandrocarpa* form a logical starting-point since there is reason to believe the genus is in every way, other than in budding and in the tadpole photolith, merely a slightly dwarfed edition of the styelinid

genus *Polycarpa*. In species of both genera there are four well-developed folds of the branchial sac on each side as in styelids generally, and the gonads are hermaphrodite units developing on both sides in the atrial or mantle wall, with eggs and testis follicles numerous in each gland in *Polycarpa* species and the larger species of *Polyandrocarpa*. *Polycarpa* species do not bud, and the tadpoles of all species investigated merely have the unicellular otolith, the ocellus and light responsiveness being absent. *Polyandrocarpa* species produce palleal buds, but belatedly and slowly, so that colonies consist usually of a small number of relatively large zooids. Eggs and tadpoles are larger than those of *Polycarpa* species but smaller than in other polystyelids. In both the smaller *Polycarpa* species (e.g. *P. gracilis*) and larger *Polyandrocarpa* forms (*P. zorritensis*, *tincta*, *gavei*, etc.), the hermaphrodite glands, or polycarps, develop as a series in the mantle wall along each side of the endostyle.

From such a beginning, specializations have occurred more or less independently in three directions, with regard to branchial structure, number and nature of gonads, and time and place of budding.

Budding inevitably leads to a reduction in the size of the zooids, and the more efficient the budding process the smaller the zooids become, since growth is directed more toward zooid multiplication than individual size increase. Colonies with small zooids may therefore have arisen several times within the family, and the secondary simplifications of body structure correlated with size reduction do not necessarily indicate an exclusive close relationship among such forms. In these, the four well-formed branchial folds of *Polyandrocarpa* species are reduced to various degrees.

In the subgenus *Eusynstyela* of *Polyandrocarpa*, zooids do not exceed 10 mm. in length, and reduction is noticeable in the number of longitudinal bars constituting each of the four branchial folds. In *Stolonica* and *Gynandrocarpa* they are similarly reduced, but in addition the number of folds is reduced from four to three. In *Distomus* the three folds are reduced to three groups of longitudinal vessels corresponding to, but not actually forming, folds. Where zooids are even smaller, not more than 5 mm. long, all trace of folds as such is gone, but they are represented by evenly spaced inner longitudinal branchial vessels, 8 in *Polyzoa opuntia*, 5–6 in *Alloeocarpa bacca* and *Metandrocarpa dura*, 4 in *Kukenthalia borealis* and *Symplegma viride*, and 3 in *Polyzoa translucida*, and the species of *Botryllus*, *Botrylloides*, and *Chorizocarpa*. Since there is such a correlation of branchial reduction with reduction in zooid size as a whole, branchial structure by itself cannot be used as a basis for relating species or genera.

With regard to the reproductive organs a somewhat similar situation exists. The first sign of a reduction effect in both *Polycarpa* and *Polyandrocarpa* species is a limitation of polycarps from a scattered arrangement to two rows parallel to the endostyle. With further reduction in the size of the zooids to the small dimensions of those in colonies of *Symplegma*, *Botryllus*, *Botrylloides*

Kukenthalia and *Chorizocarpa*, a single polycarp is all that can be accommodated on each side of the body. In all of these forms there is further an increase in the size and reduction in number of ova produced by the ovarian component of the polycarp, when compared with a polycarp of species of *Polyandrocarpa*. These genera, accordingly, may form a natural subdivision, or again may merely show converging structure due to a comparable degree of body size reduction.

The gonads in *Polyandrocarpa* are undoubtedly the least modified within the group, with regard to the distribution, number, and nature of each. In *Polyzoa* conditions are similar, except that the units are smaller, both the number of ova and testis follicles being greatly reduced. *Stolonica* has changed little in number and distribution, but the acquisition of a relatively enormous egg size results in the ovary becoming functionally a virtual one-egg ovary, even though other oocytes may be present. The formation of anterior male and posterior hermaphrodite polycarps can be interpreted on the basis of an antero-posterior gradient in the size of the polycarp rudiments at the initiation of their development. In *Metandrocarpa* (s. *Goodsiria*) polycarps are of a single sex, and on both sides there are female gonads with large eggs in the anterior part and male gonads consisting of a single testis in the posterior part (Ritter, 1896); while in *Distomus* (s. *Alloeocarpa*) ovaries with no trace of testis are found in the anterior part of the right side, and testes alone in the posterior part of the left side. Eggs are large and mature singly in both *Metandrocarpa* and *Distomus*.

A comparison of budding has to be less complete since too little is known in some cases, especially concerning the time and localization of the young buds. In general, however, the different genera comprise two groups, one in which budding is essentially a process performed by functional zooids during their later growth phase, and in which buds may grow out from various parts of the posterior and ventral atrial wall; and the other in which there is a small single bud-producing area in the latero-ventral wall.

The interrelations of the various genera therefore are complex and obscure. There has apparently been diverse evolution independently in the three features, branchial structure, nature of gonads, and time and place of budding. Much more detailed information is needed for all but *Botryllus*, *Botrylloides*, *Symplegma* (cf. Berrill, 1940), *Stolonica* and *Distomus*. At the same time *Botryllus*, *Botrylloides*, *Symplegma*, *Kukenthalia* and *Chorizocormus* do have in common the following characters: three inner longitudinal vessels in the branchial sac, a single polycarp on each side, with eggs of a comparable size, and on one side or both budding is confined to a very small area of the lateral wall immediately anterior to the gonad. This may be an instance of parallel evolution, but coincidence of the three features is considerable and it is difficult to avoid the conclusion that at least these five genera form a natural subdivision of the polystyelids.

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STUDIES ON BRITISH LAMINARIACEAE. I. GROWTH IN *LAMINARIA SACCHARINA* (L.) LAMOUR.

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(Plates V–XIII and Text-figs. 1–10)

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INTRODUCTION

Very little information was available at the beginning of the Second World War on the growth and behaviour of the common British Fucaceae and Laminariaceae when a need for this knowledge arose for economic purposes. An investigation was started, therefore, on these groups at the request of, at first, a private firm, Messrs Cefoil Ltd., and later the Ministry of Supply.

This first paper deals with *Laminaria saccharina* (L.) Lamour. and gives the results of observations made from 1941 to 1945 on the south coast of Devon, in the neighbourhood of Plymouth, and on the coast of Argyll, off the island of Luing. At both places low water of spring tides occurs in the middle of the day and middle of the night.

Most of the literature on the Laminariaceae can be obtained from the references given by Fritsch (1945), but the following Russian papers not included by him give some detailed information on the growth of *L. saccharina* in the northern seas: Kireeva & Schapova (1933, 1938) and Tikhovskaya (1940) deal with the seasonal variation of this species in the Kola Fjord and Barents Sea, working from the size and weight variation of the species throughout the year.

There is no precise information available, however, on the variation in the rate of growth of either the frond or the stipe of individual plants of this species with change in age of the plant and season of the year. Precise information is lacking on the regenerative and propagative powers of this species; also on the variation in the time of production, growth, reproduction, depopulation rate, and longevity of populations growing in different geographical positions, at different bathymetric levels and in different types of habitat.

From the results of the present work some information has been obtained on the above points and, in addition, the results have shown the influence of bathymetric zone and habitat on the behaviour of the gametophyte generation (microscopic) in relation to the time and period of production by it of the sporophyte generation (macroscopic plant).

Many workers, in particular Kjellman (1883), Foslie (1890), Setchell (1900), Børgesen (1903), Killian (1911), Printz (1926), Zinova (1929), Flerov & Karsakoff (1932), have stressed the outward variation in the form of *L. saccharina* plants growing in different types of habitat and have given descriptions, some giving measurements, of the many varieties of this species. Foslie (1890) and Flerov & Karsakoff (1932) have suggested also a possible internal structural variation depending on the latitude at which growth occurs, particular mention being made of the mucilage canal system of the frond.

The variation in the length, width, texture and bullations of the frond, in the shape, length and diameter of the stipe, in the design of the holdfast, and in the size, shape and position of the reproductive tissue on the frond that has been found in this species during the present work can be related to the

variation in the rate of growth with changes in age, season, habitat and geographical position (Pls. V–VIII). Not only can growth forms of *L. saccharina* be classed as varieties of the species, some of the forms obtained agree even with the descriptions of distinct species. For instance, second-year plants in very exposed habitats in the intertidal zone agree with Agardh's (1867) description of *L. hieroglyphica*, whilst summer-developed plants at the northern station, in the late spring and summer of the following year, in sheltered habitats in the sublittoral zone, agree with Børgesen's (1903) description of *L. faeroensis*; this species with more rapid stipe growth would resemble *L. longicruris* De la Pylaie of the north-eastern coast of North America if Setchell (1900) is correct in stating that mucilage canals are absent from the stipe.

It would be of great systematic interest if the chromosome numbers were known and transplanting experiments from one latitude to another could be carried out on the following species of *Laminaria*: *L. agardhii* Kjellman, *L. faeroensis* Børgesen, *L. groenlandica* Rosenvinge, *L. longicruris* De la Pylaie, *L. hieroglyphica* J.Ag. and *L. saccharina* (L.) Lamour. Evidence could then be obtained to show whether they are really distinct species or all growth and latitude forms of the one species.

In this work three zones are distinguished on the shore, the intertidal, the sublittoral fringe and the sublittoral.

The *intertidal zone* is regarded as extending from extreme high water of spring tides down to just above low water of mean spring tides.

The *sublittoral fringe zone* is that zone distinguished by Stephenson (1937, 1939) 'to designate the part of the sublittoral zone which extends above extreme low water of spring tides. The fringe remains submerged at low water of neap tides, its degree of emergence at low water of springs depending very much upon variations in wave action.' This zone extends above extreme low water of the lowest spring tides to approximately 0·1 m. above low water of mean spring tides at the southern station and 0·5 m. at the northern station.

The *sublittoral zone* is the region below extreme low water of spring tides in which the attached algae are permanently submerged.

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PRODUCTION OF THE SPOROPHYTE

Schreiber (1930) found that the gametophyte generation of *L. saccharina* growing in culture was perennial but was fertile only during the winter and spring; he attributed the loss of fertility during the summer to the increase in temperature. He found that fertility could be induced during the summer in strains of gametophytes, started during the winter and spring, growing at a temperature of 16–18° C. by lowering the temperature to 6° C. He therefore concluded that there was no inherent seasonal alternation of sterile and fertile periods, but that the power of gamete production was at all times released by the action of suitable external conditions quite independently of the time of the year. As he found young sporophytes in nature only in the spring he believed that, although the gametophyte could be perennial in nature, it was fertile only during the winter months.

The results obtained by Harries (1932) disagree with those of Schreiber, since she states that oogonia develop on female gametophytes in temperatures up to 16° C. She does say, however, that when the temperature is raised above a certain degree it inhibits reproduction although it accelerates growth. She concludes from her experiments that, when there is a suitable light intensity and sufficient phosphate, fertility of the gametophyte varies with the nitrate concentration, but that when there is a sufficient quantity of nitrate and phosphate present in the medium then the fertility varies with the light intensity.

The present investigations have shown that sporophytes of *L. saccharina* can be produced in nature during all months of the year at some level on the shore, on both normal untouched areas and on experimental areas from which the original population had been removed. The gametophyte generation of this species must, therefore, be capable of reproduction during all months of the year.

TABLE I. PRODUCTION OF THE SPOROPHYTE OF *LAMINARIA SACCHARINA* IN RELATION TO BATHYMETRIC ZONE AND HABITAT

Type of habitat	Locality	Names given to experimental areas	Nature of substratum	Observations commenced	Observations ceased	Monthly record of sporophyte production in *L. saccharina*												No. of months sporophytes produced in the year
						Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	
Floating at surface:																		
Permanent submergence at shallow depth at all times	P.	Floating raft	Tarred wood	14. xi. 41	3. viii. 44	×	×	×	×	×	×	×	×	×	×	×	×	12
	A.	Buoys—inner channel	Painted metal	10. i. 42	3. ii. 43	×	×	×	×	×	×	×	×	×	×	×	×	12
Lower intertidal to sublittoral fringe zone:																		
Permanent submergence in pools at M.L.W.S.T.	W.	Inlet—cleared area	Rock	3. iv. 42	1. x. 44	×	×	×	×	×	×	×	×	×	×	×	×	12
	W.	Cloustoni cleared III	,,	26. iii. 44	2. x. 44	·	·	·	×	×	×	×	×	×	·	·	·	
	A.	*Blocks (6)—lobster pond	Concrete blocks on soft mud	20. iv. 42	19. viii. 43	—	—	—	—	—	—	—	—	—	—	—	—	0
Periodical emergence at spring tides	W.	Bay—cleared area	Rock	6. ix. 41	4. x. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	W.	Digitata cleared I	,,	23. x. 41	4. x. 44	×	×	×	×	?	—	×	×	×	×	×	×	10–11
	W.	Digitata cleared II	,,	10. xi. 42	4. x. 44	×	×	×	×	?	—	×	×	×	×	×	×	10–11
	W.	Digitata cleared III	,,	26. iii. 44	30. ix. 44	·	·	·	—	—	—	×	×	×	·	·	·	
	W.	Cloustoni cleared I	,,	24. ix. 41	2. x. 44	×	×	×	×	?	—	?	;;	×	×	×	×	9–11
	W.	Cloustoni cleared II	,,	27. ix. 42	3. x. 44	×	×	×	×	?	—	×	×	×	×	×	×	10–11
	M.	Cloustoni cleared area	,,	22. x. 41	31. x. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	M.	Digitata cleared area	,,	22. x. 41	31. x. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	A.	Digitata cleared I	,,	5. xi. 41	5. ix. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	A.	Digitata cleared II	,,	30. v. 42	4. ix. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
	A.	Cloustoni cleared I	,,	12. ix. 42	4. ix. 44	×	×	×	×	—	—	×	×	×	×	×	×	10
Sublittoral zone:																		
Permanent submergence at depths from 1 to 4 m. below E.L.W.S.T.	A.	Ropes—inner channel, 1 m.	Tarred-manilla	10. i. 42	3. ii. 43	—	?	×	×	×	×	×	×	×	×	—	—	8–9
	A.	Blocks (3) shallow, 1 m.	Concrete on gravel	20. xi. 41	7. ix. 44	—	?	×	×	×	×	×	×	×	×	—	—	8–9
	A.	Blocks (1), 1 m.	,,	16. viii. 43	7. ix. 44	—	—	×	×	×	×	×	×	×	×	—	—	8
	A.	Blocks (6), 2 m.	,,	23. iv. 43	16. viii. 43	·	·	·	·	—	×	×	×	·	·	·	·	
	A.	Blocks (4), 2 m.	,,	26. iv. 44	5. ix. 44	·	·	·	·	—	×	×	—	·	·	·	·	
	A.	Blocks (3) deep, 4 m.	,,	20. xi. 41	3. ii. 43	—	—	—	—	×	×	×	×	×	?	—	—	5–6
	A.	Blocks (6), 1–4 m.	,,	16. viii. 43	5. ix. 44	—	?	×	×	×	×	×	×	×	—	—	—	7–8
	M.	Blocks (6), 4 m.	Concrete on rock	27. iii. 44	20. xi. 45	—	—	—	—	×	×	×	×	×	×	—	—	6
Permanent submergence at depths from 6 to 12 m. below E.L.W.S.T.	A.	Blocks (6), 6–8 m.	Concrete on rock	10. vii. 44	24. ix. 45	—	—	—	—	—	—	—	—	—	—	—	—	0
	A.	Blocks (6), 12 m.	,,	14. viii. 43	9. xii. 43	·	·	·	·	·	·	·	—	—	—	—	—	

× Production of sporophytes during month.
— No production of sporophytes during month.
? Production of sporophytes at the beginning or the end of the month.
* Size of all concrete blocks 0·3 × 0·3 × 0·1 m.; weight of blocks approximately 20 kg.
A. Argyll coast off island of Luing.
M. South Devon coast, Mouthstone Ledges at mouth of River Yealm.
P. South Devon coast, Plymouth Sound.
W. South Devon coast, Wembury, Blackstone Rocks.

External factors, chiefly bathymetric zone and type of habitat, appear to control the fertility and longevity of the gametophyte and consequently the production of the sporophyte. From the observations on normal areas of the shore and on experimental cleared areas (Table I) four groups can be distinguished:

(1) Habitats in which sporophytes are produced during all months of the year.
(2) Habitats in which sporophyte production ceases in the late spring and early summer.
(3) Habitats in which sporophyte production ceases in the winter.
(4) Habitats in which no sporophyte production has been recorded.

Although the sporophytes are produced during these periods it does not necessarily follow that they persist on the shore beyond the sporeling stage.

The first group includes habitats in the intertidal and sublittoral fringe zones that are always covered at low tide, even at extreme low water of spring tides, by up to 0·5 m. of water, that is, intertidal pools. The submerged parts of such objects as floating rafts, buoys, and ropes from just below the surface down to 0·5 m. can also be included in this group. These habitats appear to be the most favourable for the continued production of sporophytes throughout the year. The sporophytes may arise from the persistent fertility of perennial gametophytes or by the development of successive crops of new gametophytes some of which become mature during all months of the year.

The continued production of sporophytes during every month of the year on the floating raft in Plymouth Sound, where the surface water temperature ranges from 7° to 16° C., possibly 17° C., and in the pools on the lower part of the intertidal zone, indicates that actual temperature rise may not be the controlling factor for the fertility of the gametophyte under natural conditions as is suggested by Schreiber (1930).

The results of culture experiments carried out at the Plymouth Laboratory also disagree with Schreiber's results, since gametophytes were fertile from February until May, with the temperature of the cultures rising from 10° to 19° C. When the cultures were discarded in May fertile gametophytes were still present in the cultures.

The second group includes habitats in the intertidal and sublittoral fringe zones that become completely uncovered and dry out during the period of low water of spring tides. The cessation of sporophyte production during May and June in these habitats can be caused by the onset of sterility in the gametophyte or by its complete destruction. Schreiber (1930) found that the gametophytes were killed in a few days if placed near a window in summer light and that at all times the gametophytes were unable to survive drying out, even for a short period. He found that up to a certain extent they were insensitive to a rise in osmotic pressure and that the male gametophytes were more resistant to the

rise in osmotic pressure than were the female gametophytes. So strongly developed was this character that the female gametophytes could be completely obliterated from a culture by slow evaporation so that the surviving plants were all male. In these habitats that dry out during low tide it seems more probable that the lack of sporophyte production during May and June is caused by the destruction of the gametophytes, perhaps only the female, during this period rather than by their sterility. This point, however, needs further investigation.

The third group includes habitats in the sublittoral zone 1–4 m. below E.L.W.S.T. The cessation of sporophyte development, possibly gametophyte development also, in these habitats from November to February, is most probably due to the low light intensities reaching these areas during the winter months. Atkins (1939) has shown, expressing the mean monthly daylight values as a percentage of the total for the year, that at Plymouth the lowest figures occur from November to January and that the six months, April to September, receive three-quarters to four-fifths of the annual daylight, an amount which increases with increasing latitude.

The proportion of light reaching the sublittoral experimental areas, compared with the full daylight reaching the floating raft in Plymouth Sound on which sporophytes develop during all months of the year, can be estimated roughly from the figures given by Atkins (1939, p. 148, Table I). Taking the extinction coefficient as 0·40, an approximate value for blue light in turbid inshore waters, then approximately 45% only of the subsurface light is transmitted down to a depth of 1–2 m., and only 14% or less to a depth of 5 m. depending on the turbidity of the water in which a Secchi disc could be seen at rather more than 4 m.

Sauvageau (1918) and Harries (1932) both agree that germination of the gametophyte can occur in the dark, but that a certain intensity of light is necessary for further growth and development. Harries also states that germlings developed in the dark can remain for some months capable of growth on being illuminated.

A fact suggestive also of the influence of the intensity of light is that young sporophytes are rarely found below a thick covering of the fronds of older plants. On some concrete blocks at a depth of 1 m. below E.L.W.S.T., for example, sporophytes, developed in the summer and autumn of 1942 and the spring of 1943, had formed a thick covering over the blocks during the late spring and summer of 1943. No new population developed during the summer of 1943, but in the spring and summer of 1944 sporophyte development restarted on the blocks after the majority of the 1942 and early 1943 populations had gone.

The fourth group includes habitats in the sublittoral zone 6–12 m. below E.L.W.S.T. and also all habitats in all zones where the bottom is of soft mud. Although so far no development of young plants has been obtained on prepared surfaces at depths from 6 to 12 m., well-developed plants of *L. saccharina* have

been brought up from depths down to 12 m. These plants, however, were all growing on shingle and may have been washed down into deeper water, having started their development in shallower water.

Habitats with a soft muddy substratum or prepared surfaces placed on soft mud appear to be quite useless for the production of sporophytes. This may be due to the continued sedimentation of the mud either cutting off the light, or smothering any possible gametophyte development, or forming a substratum from which the gametophytes are too easily removed.

Sporophyte production on the British coast can, therefore, be said to take place at the higher levels during the winter, early spring, late summer and autumn, and at the lower levels, down to a certain depth, during spring, summer and early autumn (Table I). In certain specialized types of habitats sporophyte production does not occur, and in others can take place throughout the whole year. In general, this species affords yet another example of algal migration up and down the shore first mentioned by Knight & Parke (1931), and since noted by other workers.

LONGEVITY AND RATE OF DEPOPULATION OF THE SPOROPHYTE

Throughout the period of sporophyte production at all levels and in all habitats a proportion, usually high, of the sporelings become detached from the substratum when they reach a length of from 1 to 2 cm. The variation in numbers of sporelings lost during the first month of growth and the longevity of the plants which survive the sporeling stage appear to be dependent on two factors, the time of the year at which germination of the plant occurs and the type of habitat in which it arises.

The data on the longevity and rate of depopulation of this species, taken from the records of populations that developed on experimental areas from 1941 to 1945, is summarized under three headings according to the time of germination of the sporophytes. Table II records the maximum ages, in months, reached by populations growing under different habitat conditions on the experimental areas.

Sporophytes arising in the Winter (November to February)

Winter sporophytes, produced only in the intertidal and sublittoral fringe zones, rarely survive beyond the sporeling stage unless the habitat is one of extreme shelter. The figures show that the loss of winter sporophytes during the first month of growth ranges from a 95% loss in sheltered habitats to a 100% loss in exposed habitats. The complete removal of winter sporophytes during the first month of growth takes place consistently year after year in all habitats with any degree of exposure, irrespective of whether the habitat dries out or remains covered by a shallow depth of water at low tide (Table II, nos. 2–6).

TABLE II. LONGEVITY OF THE SPOROPHYTE OF *LAMINARIA SACCHARINA* IN RELATION TO TIME OF GERMINATION, BATHYMETRIC ZONE AND HABITAT

Type of habitat	Locality	Names given to experimental areas	Nature of substratum	Observations commenced	Observations ceased		Maximum age in months of *L. saccharina* shown against dates of germination											
							Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Floating at surface:																		
Permanent submergence at shallow depth at all times	P.	(1) Floating raft	Tarred wood	14. xi. 41	30. x. 43	1941:	—	—	—	—	—	—	—	—	—	—	—	23+*
						1942:	22+	21+	20+	19+	18+	17+	16+	15+	14+	13+	12+	11+
						1943:	10+	9+	8+	7+	6+	5+	4+	3+	2+	1+	—	—
Lower intertidal to sublittoral fringe zone:																		
Permanent submergence in pools at M.L.W.S.T.	W.	(2) Inlet-cleared area	Rock	3. iv. 42	26. vi. 45	1942:	—	—	—	23	22	21	8	7	6	5	<1	<1
						1943:	<1	<1	<1	26+	25+	20	7	6	5	4	<1	<1
						1944:	<1	<1	16+	15+	14+	8	7	6	5	—	—	—
Periodical emergence at spring tides	W.	(3) Digitata cleared I	Rock	23. x. 41	4. x. 44	1941:	—	—	—	—	—	—	—	—	—	—	<1	<1
						1942:	<1	<1	26	25	—	—	8	7	6	5	<1	<1
						1943:	<1	<1	19+	18+	—	—	7	6	5	4	<1	<1
						1944:	<1	<1	7+	6+	—	—	3+	2+	1+	—	—	—
Do.	W.	(4) Digitata cleared II	Rock	10. xi. 42	4. x. 44	1942:	—	—	—	—	—	—	—	—	—	—	<1	<1
						1943:	<1	<1	<1	18	—	—	7	6	5	4	<1	<1
						1944:	<1	<1	<1	6+	—	—	3+	2+	1+	—	—	—
Do.	A.	(5) Digitata cleared I	Rock	5. xi. 41	5. ix. 44	1941:	—	—	—	—	—	—	—	—	—	—	—	<1
						1942:	<1	<1	18	17	—	—	11	10	9	8	<1	<1
						1943:	<1	<1	8	7	—	—	3	2	—	—	—	—
Do.	A.	(6) Digitata cleared II	Rock	30. v. 42	4. ix. 44	1942:	—	—	—	—	—	—	11	10	9	8	<1	<1
						1943:	<1	<1	12	11	—	—	8	7	6	5	<1	<1
Sublittoral zone:																		
Permanent submergence at 1 m. depth below E.L.W.S.T.	A.	(7) Blocks (3) shallow	Concrete on gravel	20. xi. 41	7. ix. 44	1942:	—	—	—	—	—	—	27+	26+	25+	24+	—	—
						1943:	—	—	19+	18+	—	—	—	—	—	—	—	—
						1944:	—	—	7+	6+	5+	4+	3+	2+	1+	—	—	—

* + sign after a figure denotes that population still represented when observations ceased.

A. Argyll coast off island of Luing.

P. South Devon coast, Plymouth Sound.

W. South Devon coast, Wembury, Blackstone Rocks.

On three experimental areas only did winter sporophytes survive beyond the sporeling stage (Table II, no. 1). These were the 'Lobster Pond' off the west coast of the island of Luing, an artificial pond situated between small islands, the 'floating raft' anchored just inside and protected by the Breakwater in Plymouth Sound, and the sublittoral fringe zone on the north side (protected) of the Plymouth Breakwater.

On substrata, other than rock, for example, gravel mixed with small stones as found in the 'Lobster Pond', the winter sporophytes which survive the sporeling stage disappear from the shore during the first few months of growth. They may be washed down into deeper water where they survive to maturity, but this has not been proved.

Although winter sporophytes growing on the 'floating raft' had to be removed when up to 23 months old, as the raft was required for other purposes, labelled plants on the north side of the Breakwater showed that very small numbers of winter sporophytes survived into the third year of growth. These sporophytes disappeared from the shore during the fourth winter when the plants were approximately 3 years old.

As the development of winter sporophytes has not been recorded for the sublittoral zone, except perhaps during late February, the only type of natural habitat in which winter sporophytes are known to persist to maturity is one with a rocky substratum in the intertidal or sublittoral fringe zones on coasts where there is extreme shelter.

Sporophytes arising in the Spring (March to May)

During the spring months sporophyte production occurs in the sublittoral zone in addition to the intertidal and sublittoral fringe zones, and therefore takes place over a more extended range during the spring than during the winter. Greater numbers of sporelings also are produced during the spring than during the winter in the intertidal and sublittoral fringe zones, except during May in habitats that dry out at low tide. Winter counts of sporelings give up to 2500 developing on 1 m.^{2}, whilst spring counts of the sporelings give up to 5300.

Not only is there a larger production area and a much greater fertility of the gametophytes at all levels during the spring than during the winter, but there is also a higher percentage survival rate of the sporeling stage at all levels in both sheltered and exposed habitats. The higher survival rate of spring sporelings is due, most probably, to the more rapid initial growth of the spring plants. As the initial growth is more rapid, holdfast development is also more rapid and consequently a firm attachment to the substratum is procured more quickly in the spring than in the winter.

In very sheltered habitats in the intertidal and sublittoral fringe zones the rate of depopulation of spring sporophytes is approximately the same as in the sublittoral zone on the less exposed parts of the coast. In these habitats from

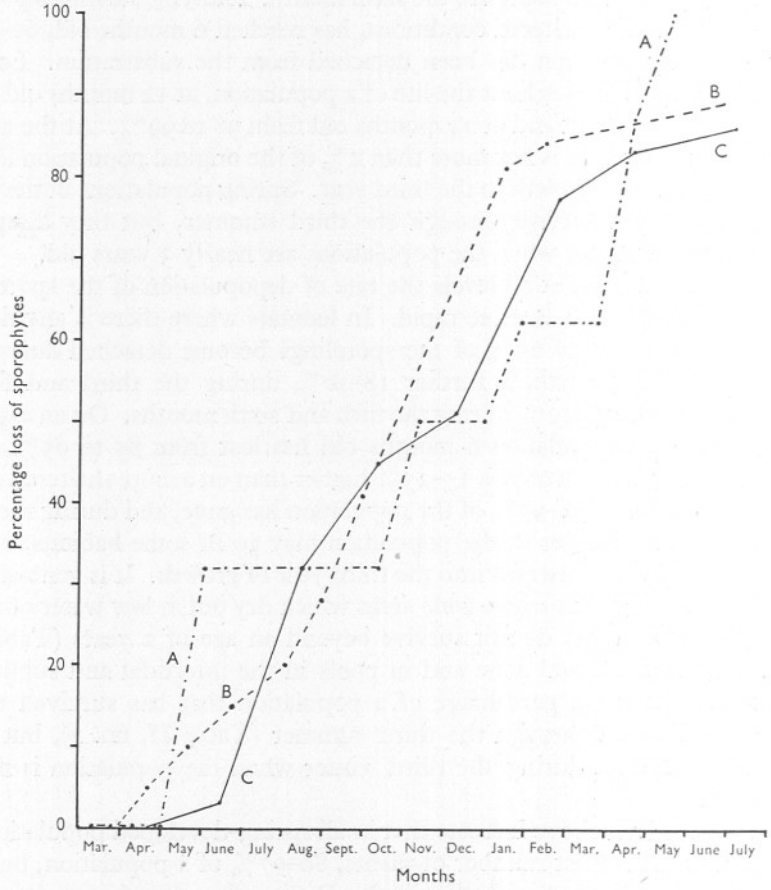
40 to 50% of the sporelings go from the substratum during the first 2 months of growth; a further 15–20% are lost from the second to the fourth month and another 5–10% from the fourth to the sixth month. Thus, by the time a population, growing under sheltered conditions, has reached 6 months old, 60–80% of the original population has been detached from the substratum. Loss in numbers continues throughout the life of a population, at 12 months old from 86 to 91% has been lost and at 24 months old from 98 to 99%. At the end of 2 years, therefore, there is not more than 2% of the original population left on the shore to continue growth in the third year. Spring populations in the third year of growth can survive through the third summer, but they disappear during the third winter when the populations are nearly 3 years old.

On an exposed coast at all levels the rate of depopulation of the sporelings and of the young plants is more rapid. In habitats where there is any degree of exposure, from 60 to 65% of the sporelings become detached during the first 2 months of growth, a further 18–20% during the third and fourth months and another 7–10% during the fifth and sixth months. On an exposed coast, therefore, a population 6 months old has lost from 85 to 95% of its original number, a loss which is 15–25% higher than on a more sheltered coast. By the twelfth month 94–97% of the population has gone, and during the next 12 months the remainder of the population may go in some habitats, but in others up to 0·7% may persist into the third year of growth. It is generally on intertidal and sublittoral fringe zone areas which dry out at low water of mean spring tides that plants do not survive beyond an age of 2 years (Table II, no. 3). In the sublittoral zone and in pools in the intertidal and sublittoral fringe zones the small percentage of a population that has survived up to 2 years, can live on through the third summer (Table II, no. 2), but goes from the substratum during the third winter when the population is nearly 3 years old.

The figures given above indicate that in all spring-developed populations of *L. saccharina* the largest number of plants, 86–97% of a population, become detached during the first year of growth. During the second year, however, the figures for the depopulation-rate of labelled plants shows that the heaviest losses of plants occur at different times of the year at different levels and in different types of habitats (Text-fig. 1). In the intertidal and sublittoral fringe zone areas that dry out at low tide, although there is fairly heavy loss during the autumn and early winter months, the heaviest loss takes place during the spring—in May at the beginning of the second year, and during April and May at the beginning of the third year when all surviving plants succumb.

At the same levels, but in habitats which remain submerged at a shallow depth at low tide, there is some loss during the spring and the summer months; but the heaviest loss of second-year plants occurs during the autumn and early winter months (Text-fig. 1B). In the sublittoral zone, even on sheltered coasts, heavy losses occur at two seasons of the year, during the

summer from June to August and during the winter from December to February (Text-fig. 1 C).



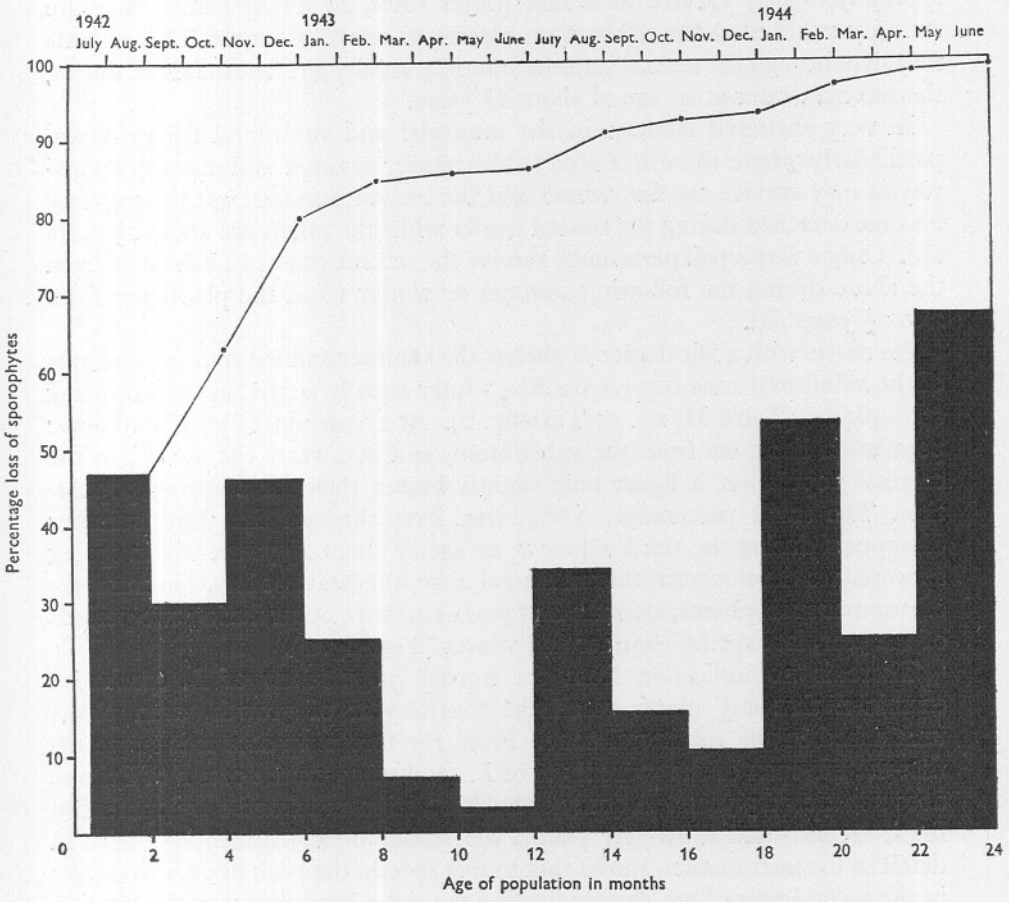
Text-fig. 1. Depopulation in three spring populations of *L. saccharina*, growing in different habitats, from the 13th to 27th month of life. A, exposed shore, intertidal zone, above M.L.W.S.T. B, exposed shore, intertidal zone, at same level as above, but submerged in pools. C, sheltered shore, sublittoral zone, at a depth of 1 m. below E.L.W.S.T.

Spring sporophytes in all habitats, except perhaps in the sublittoral zone on very sheltered coasts, can be said to form, at all times of the year, the bulk of any *L. saccharina* population occurring on the shore, since they are more persistent in nearly all habitats than either the summer or the winter sporelings.

Sporophytes arising in the Summer and Autumn (June to October)

The longevity of sporophytes produced during the summer and autumn is controlled mainly by the nature of the habitat in which development occurs. At all levels, on shores with any degree of exposure, summer and autumn

sporophytes rarely survive beyond the first winter although equally large numbers are produced as during the spring (Table II, nos. 2, 3, 4). Spring sporophytes by October are more robust and more firmly attached to the substratum than are the summer and autumn sporophytes and consequently



Text-fig. 2. Depopulation during the first 2 years of growth in a summer-developed population of *L. saccharina*, growing on a sheltered shore in the sublittoral zone at a depth of 1 m. below E.L.W.S.T. The upper curve gives progressive percentage loss throughout the 2-year period. Solid columns give percentage loss of the population present 2 months earlier.

stand a better chance of survival during the winter months than do the later developed plants.

The very small numbers of summer and autumn sporophytes that may survive the first winter in habitats which dry out at low tide disappear from the shore during the early part of the following summer before maturity has been reached (Table II, nos. 5, 6). The only summer sporophytes that may

survive, in any number, into the second year in exposed habitats are those developed either in the sublittoral zone or on areas which remain covered by a shallow depth of water at low tide (Table II, no. 2). In these habitats, since no cessation of sporophyte production occurs during June, early summer sporophytes may survive their first winter since, as spring plants, they are strongly attached to the substratum before the onset of winter. These plants may live through the second summer but they usually go from the shore during the second winter at an age of about 1½ years.

In very sheltered habitats in the intertidal and sublittoral fringe zones, particularly where there is a rocky substratum, summer and autumn sporophytes may survive the first winter and the second summer, but the majority become detached during the second winter when the plants are about 1½ years old. Only a very small percentage survive the second winter and these go from the shore during the following summer or winter when the plants are from 2 to 2½ years old.

On coasts with a fair degree of shelter the summer and autumn sporophytes of the sublittoral zone survive the first winter equally as well as do the spring sporophytes (Table II, no. 7; Text-fig. 2). At 1 year old 86% of a summer population has gone from the substratum, and at 2 years old 99·2% of the original population, a figure only slightly higher than for a spring population. The small percentage, 0·8%, that lives through the third summer disappears during the third winter at an age of about 2½ years. As in spring sporophytes developed in the sublittoral zone, the heaviest losses in numbers of summer sporophytes, after the first year of growth, occur during two periods of the year, late spring-summer and winter (Text-fig. 2).

There is no indication from the normal populations of *L. saccharina* examined that any plants reach the fourth year of growth, even plants unattached in the sublittoral zone. From the foregoing data it is suggested that the life-span of the sporophyte of *L. saccharina*, on the coasts of Britain, does not exceed 3 years. A study of holdfast, stipe and frond development in first-, second- and third-year plants, the results of which are dealt with in detail in the next section, shows that in this species the peak of growth occurs in the second year of life, thus indicating the short-lived nature of the species.

The information that has been obtained during this work makes it possible to give an indication as to the composition of *L. saccharina* populations in year classes at different levels and in different habitats on the shore during each season of the year. This estimation is given in Table III. The knowledge of the components of a 'normal' population of *L. saccharina* growing in any particular habitat is of importance since from it the approximate extent of the reproductive period of that population can be estimated.

TABLE III. THE COMPOSITION OF *LAMINARIA SACCHARINA* POPULATIONS IN YEAR CLASSES AT DIFFERENT LEVELS AND IN DIFFERENT HABITATS DURING EACH SEASON OF THE YEAR

Season of the year	Winter				Spring				Summer				Autumn			
Time of year populations were produced ...	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
Nature of habitat:																
Exposed coast, intertidal and sublittoral fringe zones; emergence at spring tides	1st†*	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st*	—	1st	1st	1st†
	—	2nd	—	—	—	2nd	—	—	—	2nd	2nd*	—	—	2nd	—	—
	—	—	—	—	—	3rd*	—	—	—	—	—	—	—	—	—	—
Exposed coast, intertidal and sublittoral fringe zones, in pools	1st†*	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st*	—	1st	1st	1st†
	—	2nd	2nd*	—	—	2nd	—	—	—	2nd	2nd	—	—	2nd	2nd	—
	—	3rd*	—	—	—	3rd	—	—	—	3rd	—	—	—	3rd	—	—
Exposed coast, sublittoral zone, 1–4 m. below E.L.W.S.T.	—	1st	1st	1st	—	1st†	1st	1st	—	1st	1st†	1st	—	1st	1st	1st†
	—	2nd	2nd*	2nd*	—	2nd	—	—	—	2nd	2nd	—	—	2nd	2nd	2nd
	—	3rd*	—	—	—	3rd	—	—	—	3rd	—	—	—	3rd	—	—
Sheltered coast, intertidal and sublittoral fringe zones; emergence at spring tides, or in pools	1st†	1st	1st	1st	1st	1st†	1st	1st	1st	1st	1st†	1st	1st	1st	1st	1st†
	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd	2nd
	3rd	3rd*	3rd*	3rd*	3rd	3rd	—	—	3rd	3rd	3rd	—	3rd	3rd	3rd	3rd
	4th*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sheltered coast, sublittoral zone, 1–4 m. below E.L.W.S.T.	—	1st	1st	1 st	—	1st†	1st	1st	—	1st	1st†	1st	—	1st	1st	1st†
	—	2nd	2nd	2nd	—	2nd	2nd	2nd	—	2nd	2nd	2nd	—	2nd	2nd	2nd
	—	3rd*	3rd*	3rd*	—	3rd	—	—	—	3rd	3rd	—	—	3rd	3rd	3rd

† Sporeling stages.

* Maximum age reached by population. For example, winter sporophytes germinate in the 1st winter, second year growth starts in the 2nd winter, third year growth starts in the 3rd winter and the plants become detached during the 4th winter when approximately 3 years old. The winter populations are the only populations to survive a full 3 years; spring sporophytes can survive $2\frac{3}{4}$ years, summer sporophytes $2\frac{1}{2}$ years and autumn sporophytes $2\frac{1}{4}$ years.

GROWTH OF THE SPOROPHYTE

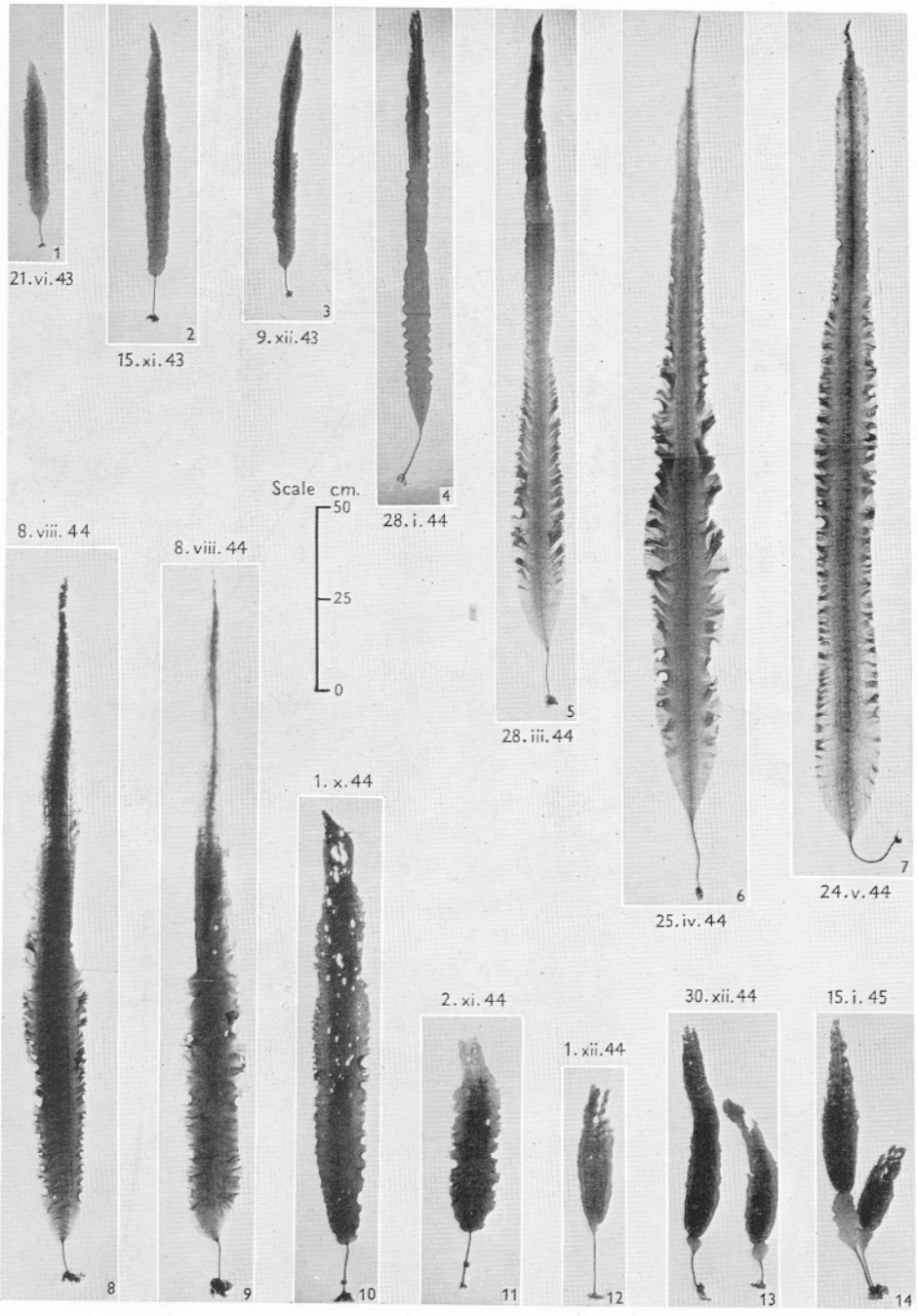
Although the sporophyte of *L. saccharina* shows continuous growth throughout its life, very considerable variation occurs in the rate of the growth in both the frond and the stipe during the different seasons of the year. The change in the rate of growth with the time of the year produces periods of rapid and slow growth which alternate during the life of the sporophyte. As the rate of growth of the sporophyte rises gradually to a maximum and then drops gradually to a minimum during each yearly cycle two growth periods, one 'rapid' and one 'slow', are distinguished in each yearly cycle in the development of this species. The 'period of rapid growth' starts in January and continues until June-July with the most rapid growth taking place from March to June, whilst the 'period of slow growth' is from July to December with the slowest growth occurring between September and December.

The sporelings show variation also in the rate of development with the time of the year at which they arise, developing very much more rapidly during the rapid-growth period of the older plants than during the slow-growth period. For instance, sporophytes developing on experimental areas at Wembury reached 20 cm. in length in 4 weeks when they arose during the months of April and May, but when development started in November the sporelings grew very slowly, reaching a length of only 2 cm. in 4 weeks. Similar results were obtained in cultures set up in the laboratory at Plymouth. Here zygotes of *L. saccharina*, developing during the months of November and December, took 6 weeks to produce sporophytes with a length of from 2 to 3 cm. At this stage complete differentiation into stipe and frond had been attained and the first row of true haptera had been formed and was attached.

PLATE V. *Laminaria saccharina* (L.) Lamour.

Photographs of different-aged plants from a population that arose in April 1943 on a cleared experimental area on the Blackstone Rocks, Wembury, Devon. Fairly exposed habitat in the intertidal zone (0·2 m. above M.L.W.S.T.) with shallow submergence at low water of mean spring tides. $\times\frac{1}{20}$.

Fig. 1. Three-months-old plant—sterile. 21. vi. 1943.
Fig. 2. Seven-months-old plant—immature reproductive tissue. 15. xi. 1943.
Fig. 3. Eight-months-old plant—mature reproductive tissue: first sporulation. 9. xii. 1943.
Fig. 4. Ten-months-old plant—mature reproductive tissue. 28. i. 1944.
Fig. 5. Twelve-months-old plant—liberation of zoospores practically ceased. 28. iii. 1944.
Fig. 6. Thirteen-months-old plant—sterile. 25. iv. 1944.
Fig. 7. Fourteen-months-old plant—sterile. 24. v. 1944.
Fig. 8. Sixteen-months-old plant—immature reproductive tissue. 8. viii. 1944.
Fig. 9. Sixteen-months-old plant—mature reproductive tissue. 8. viii. 1944.
Fig. 10. Eighteen-months-old plant—mature reproductive tissue. 1. x. 1944.
Fig. 11. Nineteen-months-old plant—mature reproductive tissue. 2. xi. 1944.
Fig. 12. Twenty-months-old plant—mature reproductive tissue. 1. xii. 1944.
Fig. 13. Twenty-one-months-old plant—mature reproductive tissue. 30. xii. 1944.
Fig. 14. Twenty-two-months-old plant—mature reproductive tissue. 15. i. 1945.


1
21.vi.43
2
15.xi.43
3
9.xii.43
4
28.i.44
5
28.iii.44
6
25.iv.44
7
24.v.44
Scale cm.
50
25
0
8.viii.44
8
8.viii.44
9
1.x.44
10
2.xi.44
11
1.xii.44
12
30.xii.44
13
15.i.45
14

Figs. 1–14.

In the frond the change in the rate of the growth throughout a yearly cycle is indicated by the change in the shape of the base and also by the variation in the width of the tissue produced during the different seasons (Pls. V–VII, IX–XI). As tissue is cast off from the distal end of the frond normally when it reaches the age of 6 or 7 months (Pls. IX–XI), a population must be examined at intervals throughout a complete year if the change in frond width is to be followed.

The periods of varying rate of growth can be seen reflected most clearly, however, in the perennial part of the sporophyte, in the alternate light and dark 'ring' formation (Pl. XIII) that shows in the stipe and holdfast, the darker 'rings' being formed by the tissue developed during the periods of slower growth.

Growth of the Frond

The growth in length of the frond, the variation in the frond width and the loss of distal (apical) frond tissue have been followed in *L. saccharina* plants (sporophytes), developing under different habitat conditions on the shore, from the earliest visible stages up to the age of approximately 2 years.

Pls. IX–XI have been compiled from the records of plants of known age growing on experimental areas. Pl. IX covers the period from March 1942, when the plants were first visible on the shore, to April 1944, the month in which the last record was taken before the plants disappeared. This diagram illustrates the behaviour of frond tissue on plants, growing intertidally on an exposed shore, in habitats which are uncovered when low water is at the level of mean springs.

For the sake of contrast to the above, plants were studied growing at the same level on the same shore, but remaining permanently submerged in pools. Pl. X illustrates the growth of such plants, covering a period of 2 years and 3 months from April 1943, when the plants germinated.

In Pl. XI growth of the frond of summer-developed plants in the upper part of the sublittoral zone (1 m. below E.L.W.S.T.) is illustrated, and covers also a period of 2 years from July 1942 to July 1944.

In the diagrams on Pls. IX–XI the thick line running through and across the columns joins up the average actual frond length of the population at the times of measurement, the length of the column above this line indicating the average amount of frond length that has been cast off by the population up to that date since the time of germination. The thin line joining up the tops of the columns gives the curve for the overall growth in length of the frond, including the cast-off tissue.

The solid block at the base of each of the columns shows the average length of frond added by the population since the previous measurement, whilst the hatched part of the column, immediately above the thick line denoting frond

length, gives the average amount of frond tissue that has been cast off by the population since the previous measurement.

In the final column of each of the three diagrams are shown: (i) the total average frond length that has been produced by a plant of each of the populations during the complete period of observation, and (ii) the variation in the average width of the frond, at the same scale as frond length, throughout the whole period. On the left side of these final columns the average monthly growth in the length of the frond is marked off, and on the right side of the columns is recorded the approximate period during which each month's frond tissue is cast.

Growth in Length

General Rhythm in Rate of Growth

The general rhythm in the rise and fall in the rate of growth in length of the frond during a yearly cycle in any *L. saccharina* population can be seen from an examination of Pls. IX–XI and Text-fig. 3. These figures show that in general, whatever the age, habitat, latitude or time of germination of the population, frond growth in length is at a more rapid rate from January to June-July than from July-August to December. They show also that during the period of more rapid growth, January to June, the rate of growth gradually increases from January until March, the rate then either still increasing or remaining fairly stable during the period of the most rapid growth from March to May-June.

Towards the end of the period of rapid growth the rate begins to slow down, gradually decreasing from June-July onwards during the period of slower growth, July to December, until the minimum rate is reached during the months of either October or November, after which the rate again begins to rise.

PLATES VI and VII. *Laminaria saccharina* (L.) Lamour.

With the exception of Figs. 15 and 20 the photographs are of different-aged plants from a population that arose in July 1942 on experimental blocks situated off the west coast of the island of Luing, Argyll. Blocks at 1 m. depth below E.L.W.S.T. in a sheltered habitat. The plant illustrated in Fig. 20 is a second-year plant growing in the same habitat but from a different experimental series. 'Four-holed punch' indicates that four holes were punched in the frond of a plant at 2·5, 5·0, 7·5 and 10·0 cm. above the base. $\times \frac{1}{20}$.

PLATE VI

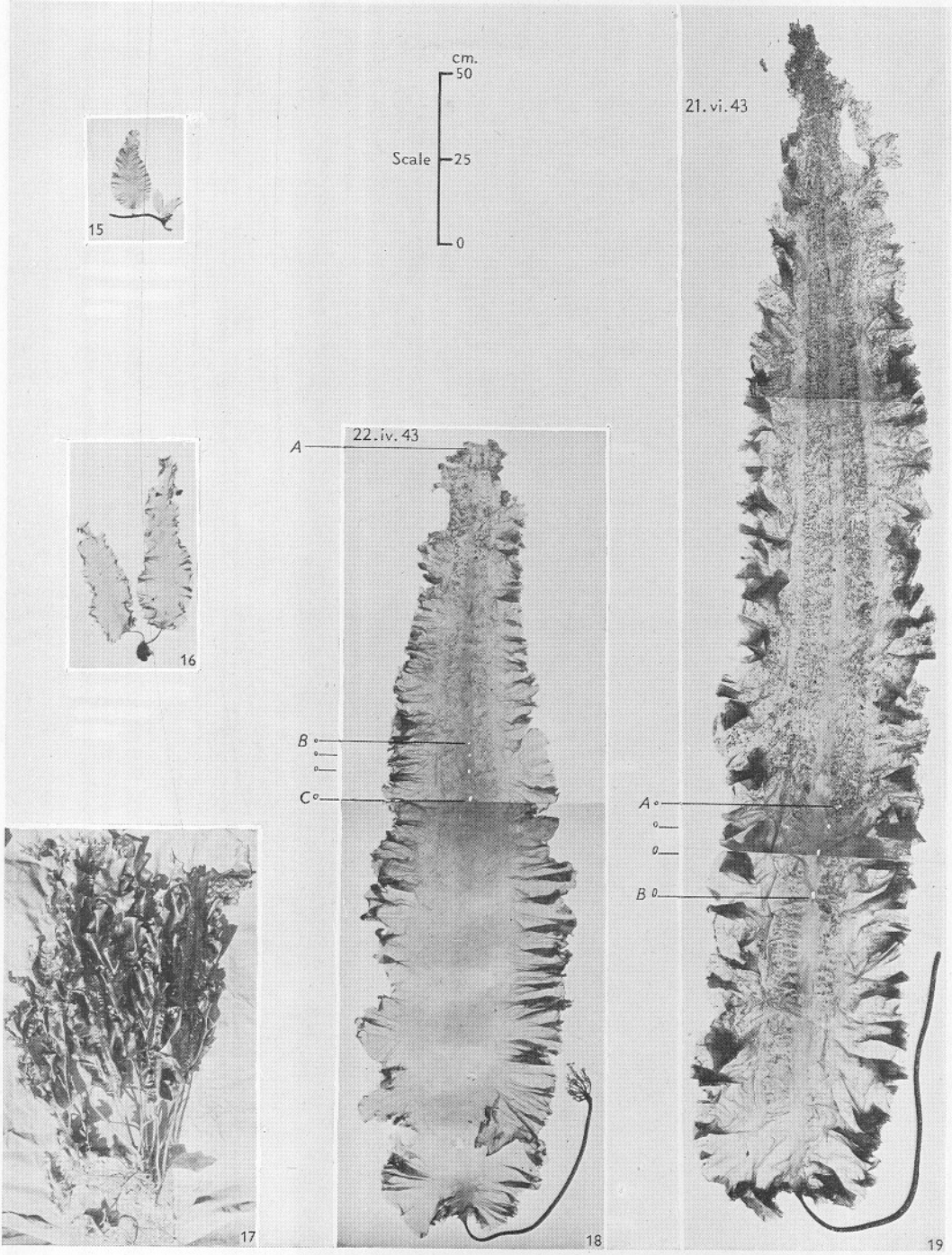
Fig. 15. Plants less than 2 months old growing on the stipe of an older plant.

Fig. 16. Plants 3–4 months old—sterile.

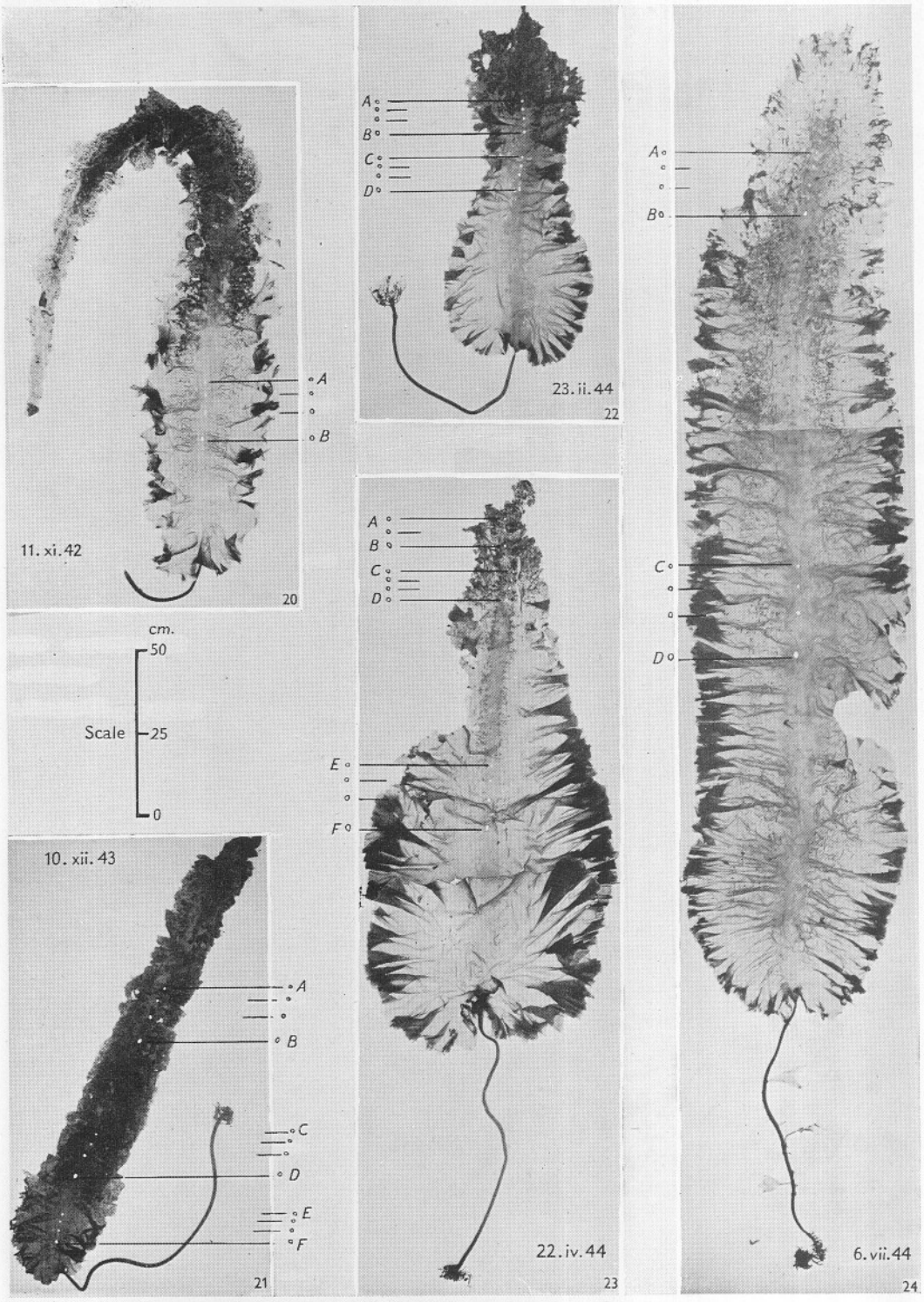
Fig. 17. Plants up to 6 months old growing on one of the concrete blocks—sterile.

Fig. 18. Ten-months-old plant—sterile. 22. iv. 1943. A, single-hole punch 2·5 cm. above the base, 12. xi. 1942; B–C, four-holed punch, 6. ii. 1943.

Fig. 19. Twelve-months-old plant—first development of reproductive tissue (immature). 21. vi. 1943. A–B, four-holed punch, 22. iv. 1943. This plant was one of the largest 1-year-old plants on the experimental blocks; it weighed 1·928 kg. ($4\frac{1}{4}$ lb.).



Figs. 15–19.


A
B
11. xi. 42
20
cm.
50
Scale
25
0
10. xii. 43
A
B
C
D
E
F
21
A
B
C
D
23. ii. 44
22
A
B
C
D
E
F
22. iv. 44
23
A
B
C
D
6. vii. 44
24

Figs. 20–24.

Variation in Rate of Growth

For the variation in the rate of frond growth in length that occurs among the plants of this species, irrespective of the general rhythm in growth-rate that takes place during a yearly cycle, the following factors appear to be responsible: (i) age and season of development of the plant, (ii) habitat, and (iii) geographical position.

In Text-fig. 3, graphs 1–6 illustrate the average daily growth in frond length for six populations of *L. saccharina* growing in different types of habitat on the Devon and Argyll coast, and cover periods of from 7 to 27 months. Graphs 1, 4 and 6 of this figure give the daily growth in frond length of the three populations illustrated in detail in Pls. IX–XI. The figures given in these graphs can be approximate only, since the average daily growth figure for the period between measurements makes no allowance for any alteration in the rate of growth within any one period. These figures are reproduced as they demonstrate to some extent, first, the change in the rate of frond growth in length throughout the year and the rapidity with which it is possible for frond tissue to be produced (nos. 5, 6); secondly, the change in the rate of growth with the increase in the age of the population (nos. 1, 4, 5 and 6) and the difference in rate of growth of populations arising at different times of the year (nos. 5, 6); thirdly, the variation in rate of growth with the type of habitat (nos. 1, 4 and 5); and fourthly, the variation in the growth-rate with change in geographical position (nos. 2, 3).

The influence of the *age of the plant* on the rate of growth in length of the frond can be traced in Pls. IX–XI; Text-fig. 3, nos. 1, 4, 5 and 6. The sequence of this variation in rate of growth with increase in age can be seen more clearly when the rate of growth is traced through the successive growth periods in the life of the plant—first, second and third rapid- and slow-growth periods, rather than when followed through yearly cycles starting with the month of germination of the plant.

When growth is traced in the former way the figures show that the rate of frond development in length during the first rapid-growth period is not so

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PLATE VII

Fig. 20. Sixteen-months-old plant—mature reproductive tissue. 11. xi. 1942. A–B, four-holed punch, 16. ix. 1942.

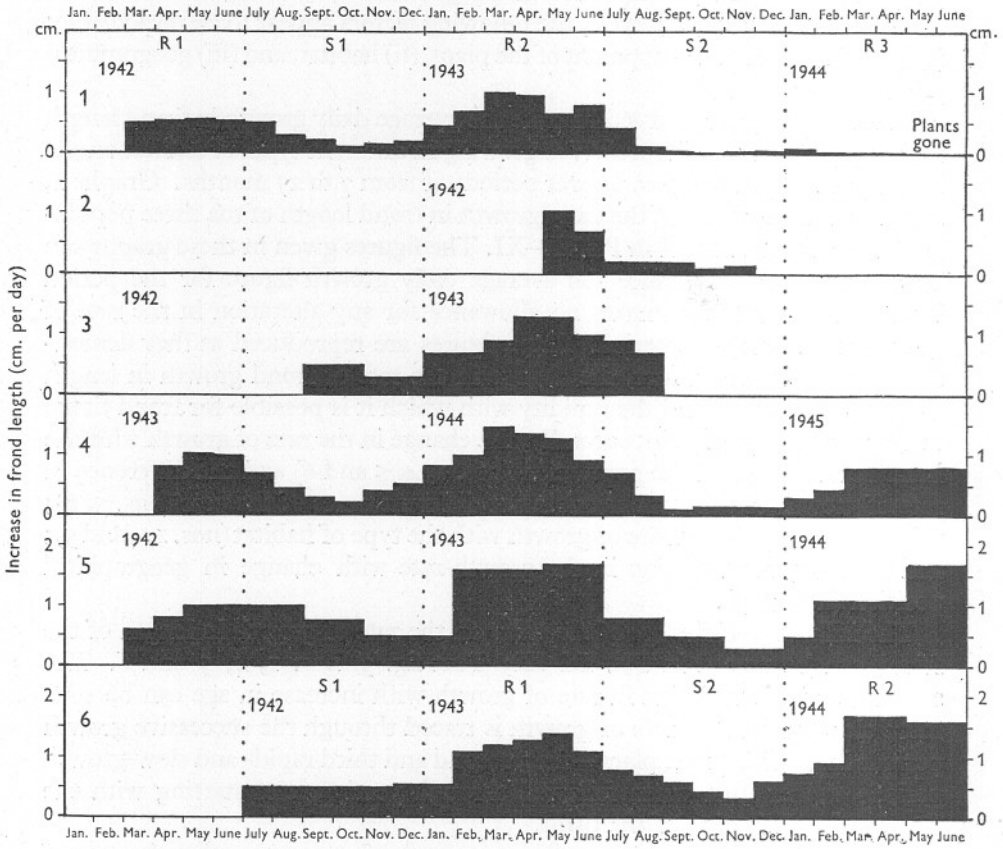
Fig. 21. Eighteen-months-old plant—mature reproductive tissue. 10. xii. 1943. A–B, four-holed punch, 16. vi. 1943; C–D, four-holed punch, 16. viii. 1943; E–F, four-holed punch, 13. x. 1943.

Fig. 22. Twenty-months-old plant—mature reproductive tissue. 23. ii. 1944. A–B, four-holed punch, 13. x. 1943; C–D, four-holed punch, 10. xii. 1943.

Fig. 23. Twenty-two-months-old plant—sterile. 22. iv. 1944. A–B, four-holed punch, 13. x. 1943 (three holes remain); C–D, four-holed punch, 10. xii. 1943; E–F, four-holed punch, 23. ii. 1944.

Fig. 24. Twenty-four-months-old plant—immature reproductive tissue. 6. vii. 1944. A–B, four-holed punch, 23. ii. 1944.; C–D, four-holed punch, 22. iv. 1944.

great as during the second rapid-growth period, and that the rate reached during the third period never surpasses that achieved during the second period.



Text-fig. 3. Daily growth in frond length in six populations of *L. saccharina*, showing the variation in growth-rate with age, season, habitat and locality.

(1) Spring population, March 1942. Devon, exposed shore, intertidal zone, above M.L.W.S.T. (thus periodically uncovered).

(2) Normal population. Devon, very sheltered shore, intertidal zone, above M.L.W.S.T.

(3) Normal population. Argyll, very sheltered shore, intertidal zone, above M.L.W.S.T.

(4) Spring population, April 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools (thus never uncovered).

(5) Spring population, March 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

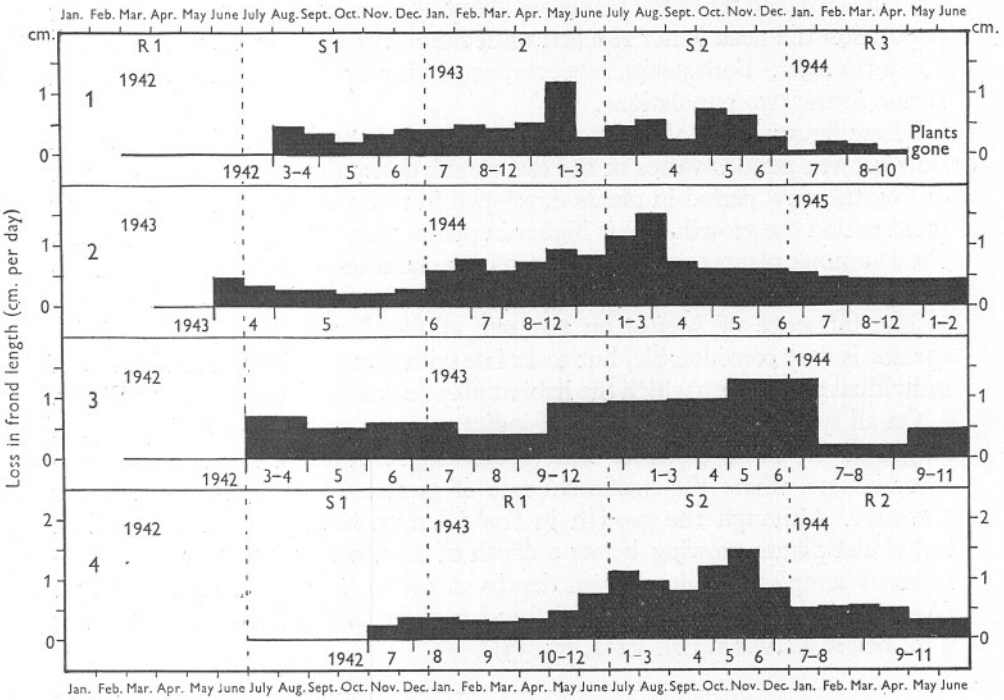
(6) Summer population, July 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

R, rapid-growth period. S, slow-growth period.

The variability in the rate of frond growth during the third rapid-growth period, when compared with the growth during the second rapid-growth

period in the same habitat, is so pronounced among populations growing in different habitats that factors external to the plant appear responsible and will be discussed later (compare Pls. IX, X; Text-fig. 3, nos. 1, 4 and 5).

During the slow-growth periods, however, the rate does not slow down to the same degree, nor does the slowest rate persist for so long a time during the



Text-fig. 4. Daily loss in length of frond in four populations of *L. saccharina*, showing the variation with age, season and habitat.

(1) Spring population, March 1942. Devon, exposed shore, intertidal zone (above M.L.W.S.T.).

(2) Spring population, April 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools.

(3) Spring population, March 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

(4) Summer population, July 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

The numbers below each diagram give the month during which the frond tissue concerned was developed. R, rapid-growth period. S, slow-growth period.

first slow-growth period as during the second, whilst during the third period the growth-rate is so slow that it is practically negligible.

Although the peak in growth-rate may vary with habitat and geographical position, the maximum rate of frond growth in length is reached in all populations during the second rapid-growth period in the life of a plant of this species;

the actual age in months at which the peak occurs being dependent on the time of germination of the plant.

For example, graphs 5 and 6 of Text-fig. 3 show the daily growth-rate of two groups of *L. saccharina* plants growing in the same habitat; in no. 5 development of the plants started in the spring (March), whilst in no. 6 development did not start until the summer (July). In the spring population the peak of growth is reached when the plants are about 15 months old, but in the summer population the peak is not reached until the plants are about 21 months old, 6 months later. Both peaks, however, occur during the second rapid-growth period in the two populations.

These figures show also that the rate of growth during the first rapid- and slow-growth periods varies in the two populations; the growth-rate is higher during the slow period in plants developed in the spring, but during the first rapid period the growth-rate is higher in plants that developed in the summer. Thus summer plants reach approximately the same length as 12- to 13-months-old spring-developed plants when they are from 9 to 10 months old.

The influence of *habitat* on the rate of frond growth in length of this species is very considerable, but to isolate with any certainty the influence of individual factors into which the habitat may be analysed is extremely difficult.

On all types of shore the general indications are that the rate of growth in length of the frond increases with decreasing level down to the upper sublittoral zone, where the maximum rate of growth is reached 1–4 m. below E.L.W.S.T. Although the growth in frond length has not been followed in individual plants growing below a depth of 4 m. below E.L.W.S.T., measurement of samples examined from depths down to 8 m. (Devon) and 12 m. (Argyll) showed that the rate of frond growth in length was less than at 4 m. below E.L.W.S.T. (Pl. VIII, fig. 33).

PLATE VIII. *Laminaria saccharina* (L.) Lamour.

Photographs of plants from different types of habitat. Figs. 25, 27 and 28 are of summer-developed plants growing on the Argyll coast in the intertidal zone in a fairly exposed habitat with emergence at low water of mean spring tides. Figs. 29–31 are of spring-developed plants growing on the Devon coast in the intertidal zone in a very exposed habitat with emergence at low water of mean spring tides. $\times\frac{1}{20}$.

Fig. 25. Six-months-old plant—sterile. 9. ii. 1943.

Fig. 26. Clump of plants up to 9 months old, from the same habitat as the series on Pl. V, showing different stages in frond regeneration and two plants bearing reproductive tissue. 30. xii. 1943.

Fig. 27. Ten-months-old plant—sterile. 20. vi. 1943.

Fig. 28. Eight-months-old plant—sterile. 22. iv. 1943.

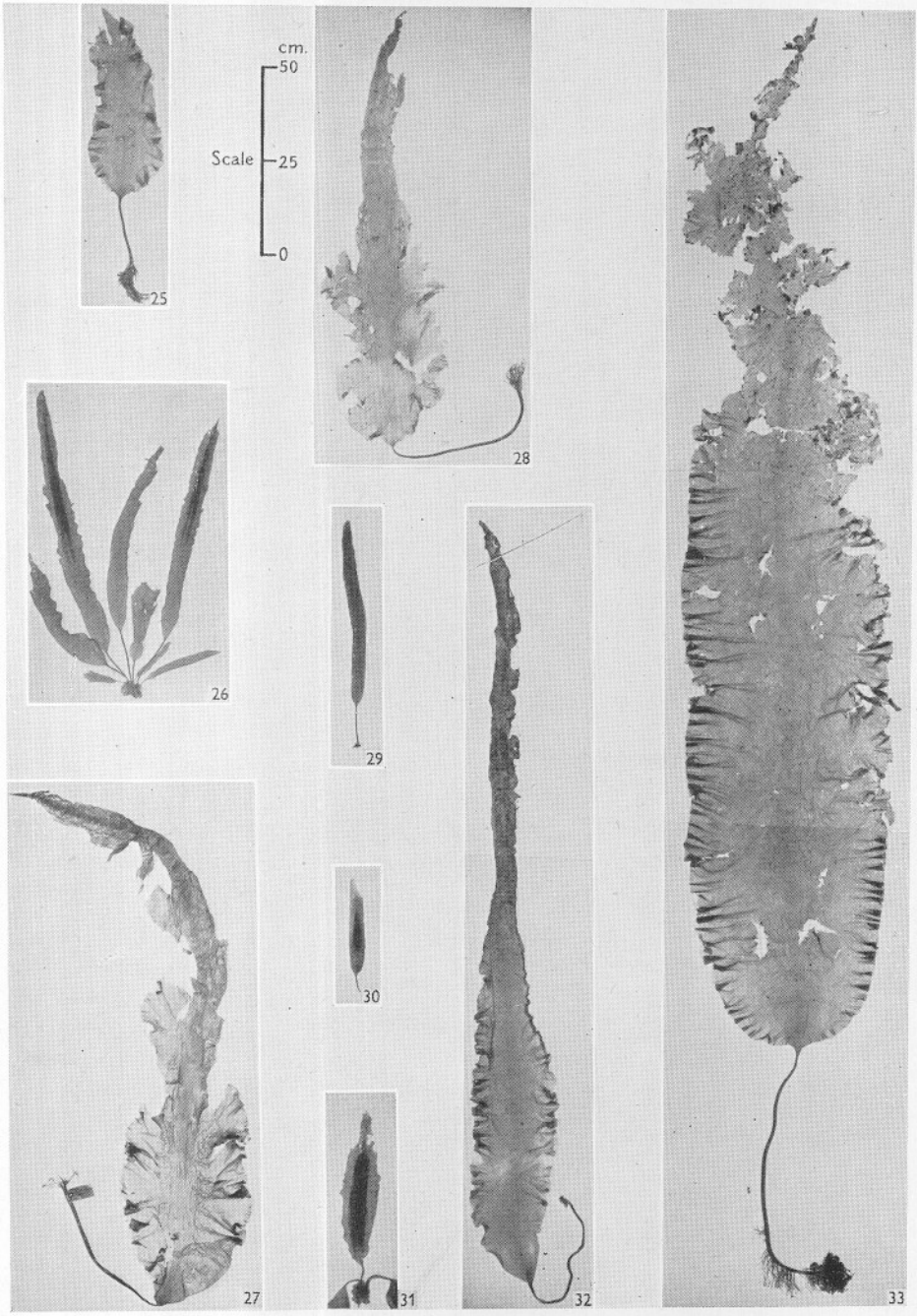
Fig. 29. First-year plant—immature reproductive tissue. 29. xi. 1943.

Fig. 30. First-year plant—mature reproductive tissue. 13. xii. 1943.

Fig. 31. Second-year plant—mature reproductive tissue. 28. xii. 1943.

Fig. 32. Plant approximately 1 year old—form of plant growing on raft in Plymouth Sound. 30. iv. 1943.

Fig. 33. Plant approximately 1 year old—form of plant growing on shingle off the Argyll coast at a depth of 12 m. below E.L.W.S.T. 5. vii. 1944.



Figs 25–33.

The records of the maximum growth figures show that at and above E.L.W.S.T. the daily growth in frond length never reaches a figure of 2 cm. increase a day during the rapid-growth period, whilst in the sublittoral zone a daily increase of up to 2·3 cm. can be obtained.

In addition to the effect of level on the growth in frond length the influence exerted by two other factors must be taken into consideration. The first of these factors is the degree of exposure or shelter of the habitat; the records show that the rate of growth in frond length increases with the degree of shelter of the habitat. The second factor is that of emergence or submergence of the plants during the period of low tide and concerns only habitats in the intertidal and sublittoral fringe zones. In these zones plants growing on the same shore and at the same level show a higher growth-rate if they remain continuously submerged (pool type), even under a very shallow covering of water, than do the plants which completely emerge during the period of low water (Pls. IX, X; Text-fig. 3, nos. 1, 4).

The variability in growth-rate in frond length during the third period of rapid growth, mentioned previously, is almost certainly connected with the depth of immersion of the plants and in consequence also with the factor of level on the shore. If the rates of growth during the second and third rapid-growth periods in the same populations are compared (e.g. in Text-fig. 3, nos. 1, 4 and 5), and if this is done for different habitats, the following points can be noted. On exposed coasts populations of plants growing in the intertidal zone above M.L.W.S.T. fail to survive the third period of rapid growth (Text-fig. 3, no. 1), showing only slight frond growth from the end of the second period of rapid growth until they disappear during the third period of rapid growth. The amount of frond length added in this type of habitat during the third rapid-growth period is approximately 4% only of the length of tissue added during the second period of rapid growth. Populations growing at the same level on the same shore but in pools, even in shallow pools of 30–50 cm. depth during the period of low water, survive the third period of rapid growth and show fair growth (Text-fig. 3, no. 4) during that period; the frond length added, however, during the third period is only 50–60% of that which is added during the second rapid-growth period. Finally, the populations growing in the upper part of the sublittoral zone (1–4 m. below E.L.W.S.T.) not only survive the third rapid-growth period but show a higher rate of growth during this period than do the two previous types mentioned, producing approximately 85% of the length developed during the second period (Text-fig. 3, no. 5). The difference in the frond growth-rate in these three populations during the third period of rapid growth is no doubt connected with the variation in the metabolism of the three populations, since Black (1948) has shown that the chemical composition of plants of the same *Laminaria* species varies at different depths of immersion.

To assess the *influence of geographical distribution* or of latitude on the growth

of this species records of growth from many more stations would be required before any clear indication could be obtained. The figures available, however, for the growth of this species on the coasts of Devon (50° 18′ 20″ N., 4° 06′ 15″ W.) and Argyll (56° 14′ 22″ N., 5° 39′ 40″ W.) suggest, that over this portion of the species' range, the difference in the growth of plants in the two localities might be correlated with the difference in latitude; probably also with differences in the nature of the inshore water at the two stations.

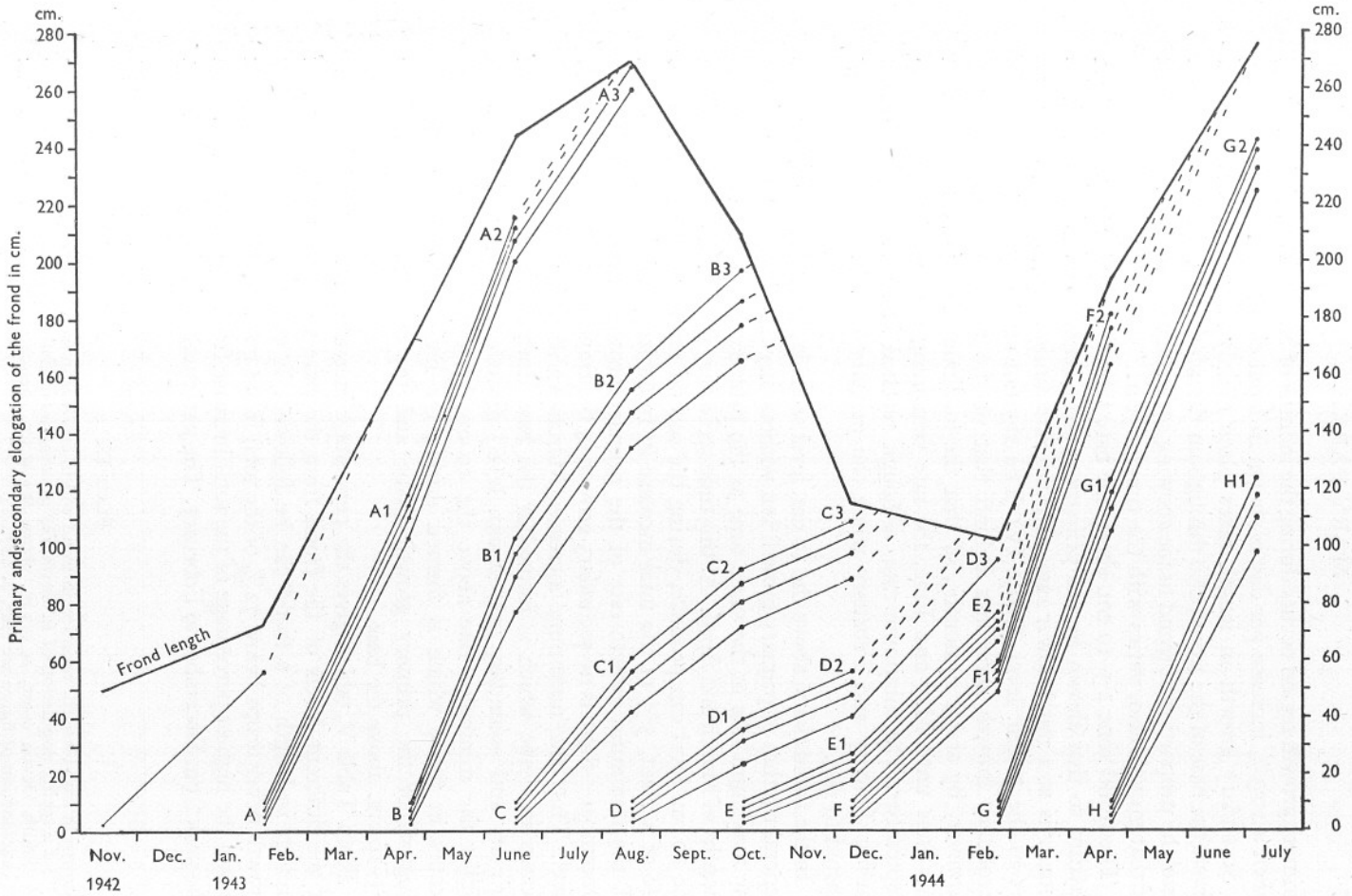
The differences noted are that, with an increase of approximately 6° in the latitude, there is a higher rate of frond growth throughout the yearly cycle at the more northern station; there also the time when the minimum and maximum rate of frond growth in length is reached is at least 1 month later than at the more southern station. An examination of the mucilage canals, in the same position on the frond in plants of the same age from the two stations (since Guignard (1892) has indicated these may vary in plants of different ages and in different parts of a single frond), shows that they are larger in the frond tissue of plants at the northern station than at the southern station. So also is the cell size of the frond tissue.

Primary and Secondary Growth in Length

So far the figures for frond elongation have been given as total increase in length for the whole frond and therefore do not show the differential growth-rate or elongation of the frond tissue at successive levels up the frond.

In this species, as in all Laminariales, the main growth region for increase in length is situated in the transition zone between the stipe and the frond, and so any tissue which forms below a level of 2·5 cm. above the base of the frond will be classed as *primary growth*, that is, new tissue formation, since below the 2·5 cm. level the differentiation of frond tissues is not complete, neither is the mucilage canal system developed. Above the 2·5 cm. level any increase in length of the tissues will be classed as *secondary growth*, this term including both increase in length by cell division and elongation by enlargement of the cells of the tissues already developed. Table IV and Text-fig. 5 give the primary and secondary elongation of frond tissue that took place in one plant from the age of 4 to 24 months, and illustrates the general method of frond growth in this species. The figures for elongation are obtained from the measurements of the distances between series of holes in the frond, punched at approximately 2-monthly intervals at 2·5, 5·0, 7·5 and 10·0 cm. up from the base (Pls. VI, VII).

Primary growth throughout the yearly cycles follows the general rhythm of periods of rapid and slow growth described earlier, the peak in primary growth being reached during the months of March and April, when a frond in the first and second rapid-growth periods can show a 54% and a 69% increase respectively per day in basal elongation. The minimum rate of growth for the



Text-fig. 5. Primary and secondary elongation of the frond in a plant of *L. saccharina* from the 4th to the 24th month of growth, illustrated by means of holes punched in the frond at 2·5, 5·0, 7·5 and 10·0 cm. above the base. Plant germinated July 1942 in the sublittoral zone on the Argyll coast at a depth of 1 m. below E.L.W.S.T.

primary growth region occurs during the months of November and December, when a 10·3% increase per day is shown in basal elongation.

Secondary growth in length takes place mainly in the zone 2·5–10 cm. above the base of the frond, also throughout the whole year. Above the 10 cm. level the proportion of frond tissue showing secondary growth, and the amount of that growth also, varies with the time of year.

The frond zone 2·5–10 cm. above the base follows a similar type of growth rhythm to that shown by the primary growth zone, but the growth in the former is at a much lower rate, with the rate diminishing upwards from the 2·5 to the 10 cm. level (Table IV). The rhythm of the growth-rate in this secondary growth zone lags behind that of the primary-growth rhythm, however, by about 2 months, so that the maximum rate is not reached in this zone until May and June, the rate remaining still high until August-September. The minimum rate, although reached in December, continues during January and February when the primary growth-rate has already started to rise.

In the frond tissue above the 10 cm. level secondary growth also follows the general rhythm of primary growth but without any time lag, and thus reaches the maximum rate at the same time as the primary growth zone during the months of March and April. At this time secondary growth in the tissue above the 10 cm. level can produce, during the second rapid-growth period in the life of a plant, 5% of the total increase in frond length. During the period of the minimum growth-rate of the primary growth tissue—November to December—there is no secondary growth in the frond tissue above the 10 cm. level. Thus the maximum increase (March-April) above the 10 cm. level occurs in tissue which is formed at the base during the minimum rate of primary and secondary (2·5–10 cm. level) growth (October to December), whilst the minimum rate above the 10 cm. level (October to December) occurs in tissue which is formed during the high growth-rates (June to August) of the primary growth tissue and the secondary growth tissue 2·5–10 cm. above the base.

From Table V, which gives the percentage increase in length of the tissue at the different levels of the frond from the base upwards, the method of growth in length of a frond can be followed. It can be seen that primary growth never drops below 72% of the total frond growth in length and that it shows the highest percentage of the total increase from October to April with the peak from December to February. The percentage of primary growth then

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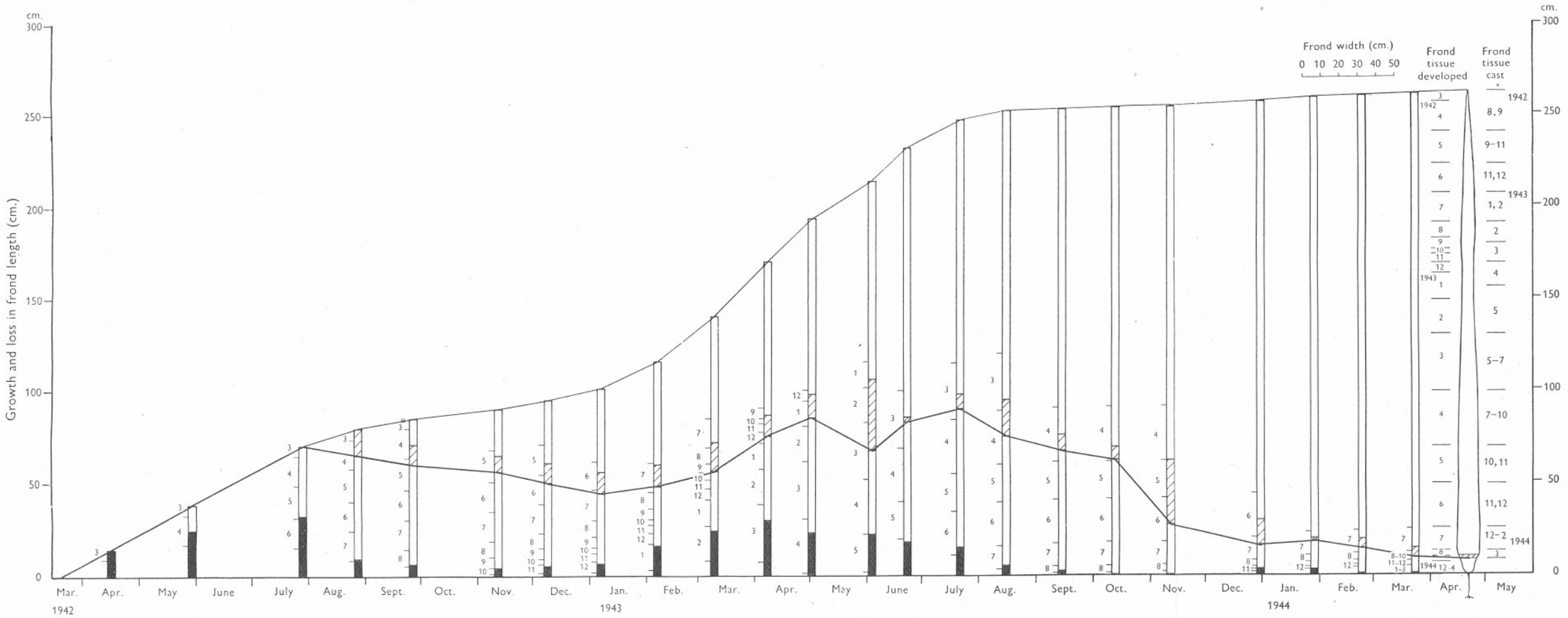
PLATE IX

Growth in frond length, variation in frond width, and loss in frond length throughout the life of a spring population of *L. saccharina* growing intertidally on an exposed shore, on the South Devon coast, at 0·2 m. above M.L.W.S.T. (hence periodically uncovered). For explanation of figure see text, p. 667.


cm.
300
250
200
150
100
50
0
Growth and loss in frond length (cm.)
Frond width (cm.)
0 10 20 30 40 50
Frond tissue developed
Frond tissue cast
Mar. Apr. May June July Aug. Sept. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May June July Aug. Sept. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May
1942
1943
1944

falls from April to October as the percentage of secondary growth in the 2·5–10 cm. zone above the base rises; the highest percentage increase in this tissue being recorded from August to October when the lowest percentage for primary growth is recorded. In the frond tissue above the 10 cm. level the highest percentage increase is from February to April in the tissue 3–4 months old with a decrease from April to June as in the primary tissue. In this tissue,

TABLE V. RELATIVE INCREASE IN FROND LENGTH AT DIFFERENT FROND LEVELS IN A PLANT OF *LAMINARIA SACCHARINA* FROM THE SEVENTH TO THE TWENTY-FOURTH MONTH OF GROWTH

Percentage of total increase

Growth periods ...	6. ii. 43–22. iv. 43		22. iv. 43–16. vi. 43		16. vi. 43–16. viii. 43		16. viii. 43–13. x. 43	
Secondary growth above the 10 cm. level in tissue:								
5–6 months old	—		—		0·4		0·0	
3–4 months old	—		0·4	0·4	1·2	1·6	1·4	1·4
Secondary growth:								
7·5–10·0 cm.	0·7		3·0		4·7		3·5	
5·0–7·5 cm.	1·6	7·0	5·9	19·7	5·9	22·3	6·5	26·8
2·5–5·0 cm.	4·7		10·8		11·7		16·8	
Primary growth:								
Base–2·5 cm.		93·0		79·9		76·1		71·8

Growth periods ...	13. x. 43–10. xii. 43		10. xii. 43–23. ii. 44		23. ii. 44–22. iv. 44		22. iv. 44–6. vii. 44	
Secondary growth above the 10 cm. level in tissue:								
5–6 months old	0·0		0·0		—		—	
3–4 months old	0·0	0·0	1·4	1·4	5·2	5·2	0·3	0·3
Secondary growth:								
7·5–10·0 cm.	1·7		0·6		1·2		3·3	
5·0–7·5 cm.	3·0	10·8	1·1	4·7	2·5	8·7	4·9	16·5
2·5–5·0 cm.	6·1		3·0		5·0		8·3	
Primary growth:								
Base–2·5 cm.		89·2		93·9		86·1		83·2

however, the percentage increase then rises again from June to September before growth ceases during the months from October to December.

The frond growth illustrated above is of a plant growing on the Argyll coast; in plants growing on the Devon coast, however, the peaks of primary growth and secondary growth above the 10 cm. level are reached during February and March, and that of secondary growth at the 2·5–10 cm. level during April and May, the growth peaks, therefore, occurring a month earlier than on the Argyll coast.

Regeneration of the Frond

From the results of the experiments in which *L. saccharina* fronds were cut to a length of 5, 10 and 20 cm., and also by following the growth of labelled

plants of known age from which the greater part of the frond had been torn off naturally, it has been found that complete regeneration of the frond does not occur in *L. saccharina* plants over 1 year old. Plants in the second and third year of growth may persist on the shore for a number of months after the fronds have been torn or cut if approximately 20 cm. of frond remains; they may also show a slight growth in length of the frond during that period, but they do not appear to survive through the winter months following the cutting or tearing of the frond.

During the first year of growth the younger the plant the more complete is the regeneration of the frond after cutting. Fronds of plants up to 3 months old can be cut to 10 cm. from the base at any time of the year and the fronds will regenerate in a few months to the size of the uncut fronds. This is probably due to the fact that in the young plants practically the whole of the growth in length is primary or basal growth. In plants between the age of 3 and 12 months, if tearing or cutting occurs during the rapid-growth period of this species (Pl. VIII, fig. 26) complete regeneration of the frond takes place in 6 months if from 15 to 20 cm. of frond is left on the plant. If less than 15 cm. of frond is left, or if the plants are cut during the period of slower growth, some regeneration does occur but the fronds always remain smaller than the uncut fronds of plants of the same age. When the whole frond is removed from a plant of any age no regeneration occurs, the stipe rots away gradually, and the holdfast eventually becomes detached from the substratum.

Experiments on the regenerative powers of *L. saccharina* carried out in 1920 on the French coast at Roscoff and at Iles Saint Quay by Freundler and Ménager (1921) gave results similar to those described above for second- and third-year plants. They state, however, that too young or too old plants were removed and not used in the experiments.

Fallis (1916), working from 15 June to 6 August 1915 on plants of the Laminariaceae, including *L. saccharina*, attached artificially to a floating raft in Friday Harbour, Washington, states that the cutting of the tip of the blade (frond) does not materially effect the growth so long as the basal 5–50 cm. of frond is left, and that larger plants grow faster than the smaller. The age of the 'larger' and 'smaller' plants, however, is not indicated.

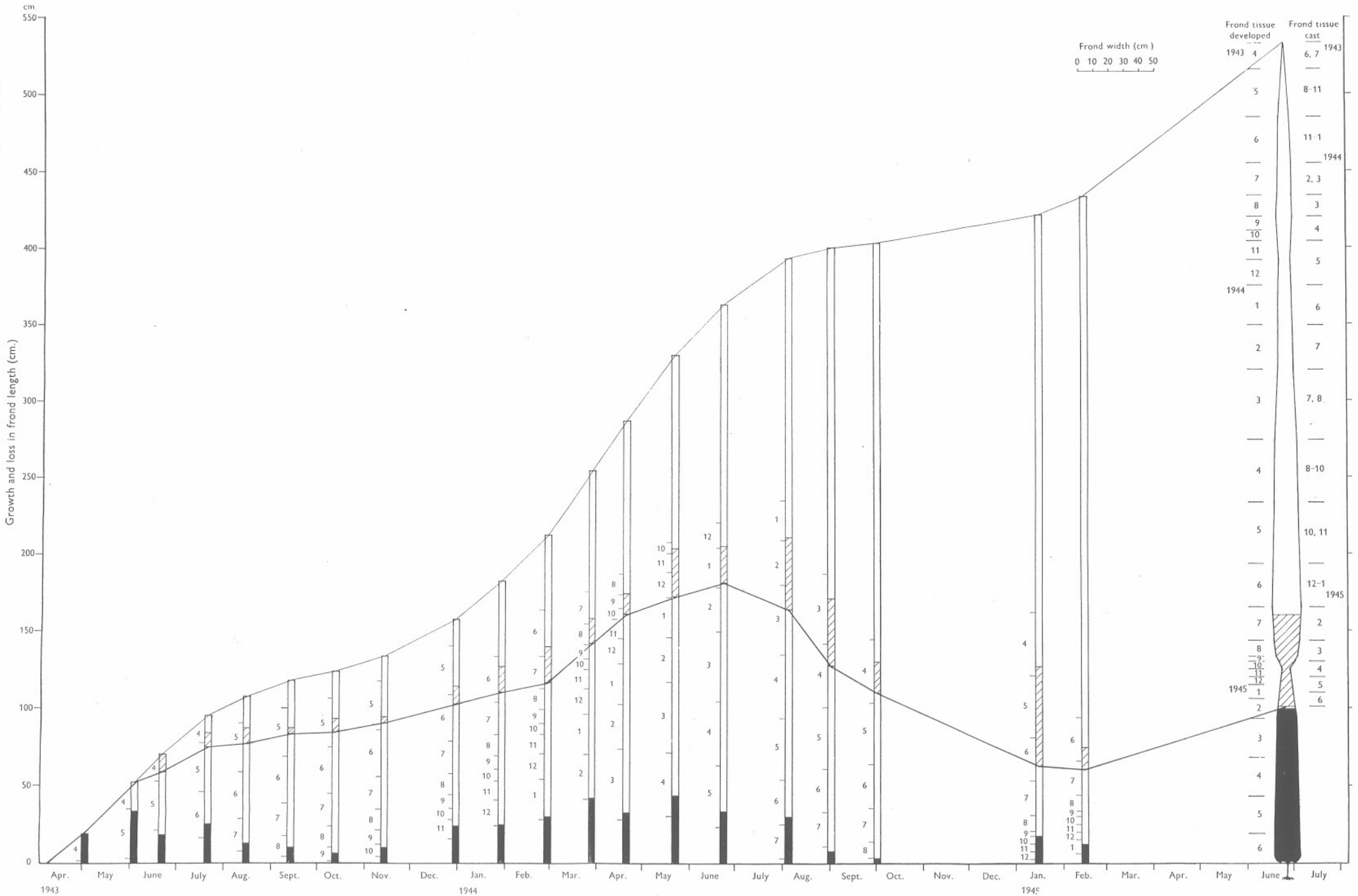
Growth in Width

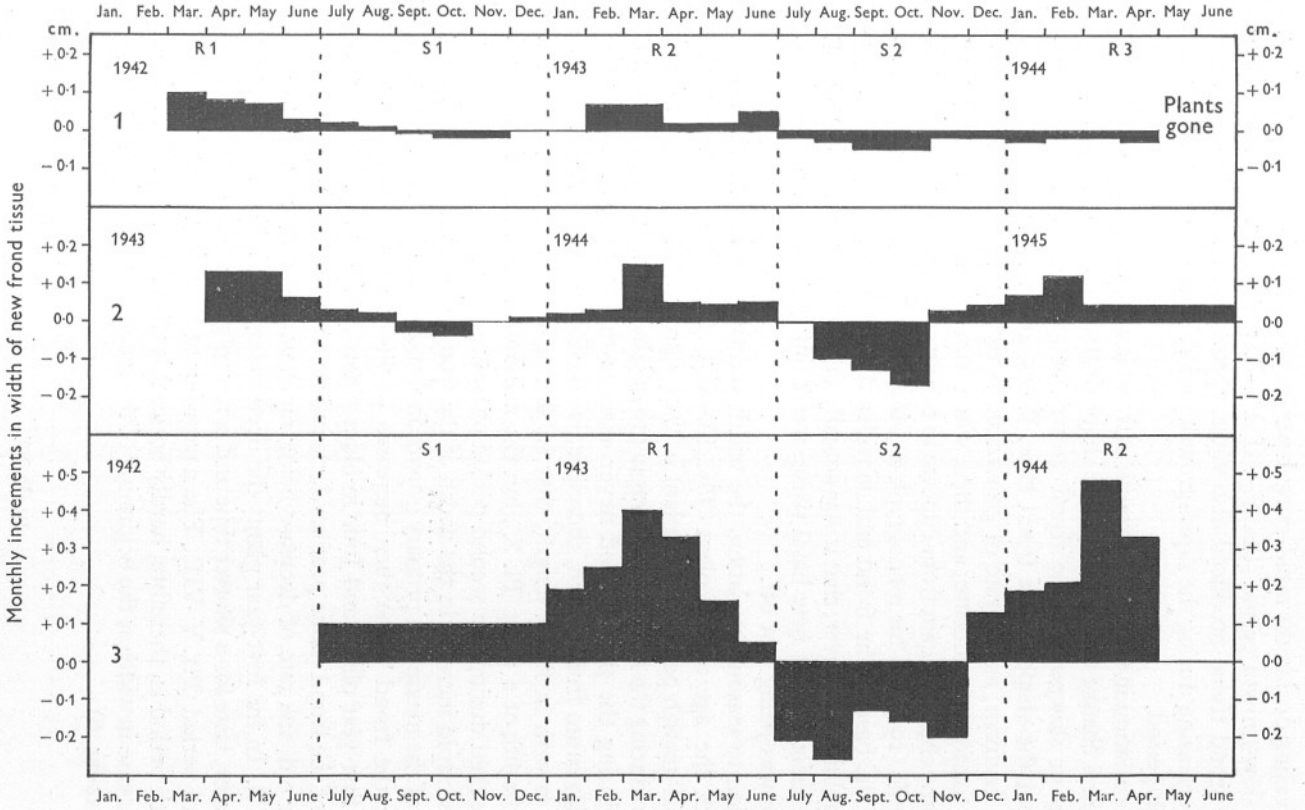
Variation in Width of Frond throughout Life of Plant

The width of the tissue developed by the fronds of plants of any age and in any habitat varies throughout a yearly cycle, as does the growth in frond

PLATE X

Growth in frond length, variation in frond width, and loss in frond length throughout the first 27 months of life of a spring population of *L. saccharina* growing intertidally on the same shore as in Pl. IX and at the same level, but remaining permanently submerged in pools. For explanation of figure see text, p. 667.


cm
Growth and loss in frond length (cm.)
Frond width (cm.)
0 10 20 30 40 50
Frond tissue developed
Frond tissue cast
Apr. May June July Aug. Sept. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May June July Aug. Sept. Oct. Nov. Dec. Jan. Feb. Mar. Apr. May June July
1943
1944
1945



Text-fig. 6. Monthly increments in width of new frond tissue in three populations of *L. saccharina*, showing the variation with age, season and habitat. The figures, expressed in cm. per day, represent the difference (positive or negative) from the width of tissue produced during the previous month.

(1) Spring population, March 1942. Devon, exposed shore, intertidal zone, above M.L.W.S.T.
(2) Spring population, April 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools.
(3) Summer population, July 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

R, rapid-growth period. S, slow-growth period.

length, increasing during the rapid-growth period of the species and decreasing during the slow-growth period (Pls. V–VII, IX–XI; Text-fig. 6). The thickness of the frond tissue produced also varies throughout a yearly cycle, the thickness decreasing during the rapid-growth period and increasing during the slow-growth period.

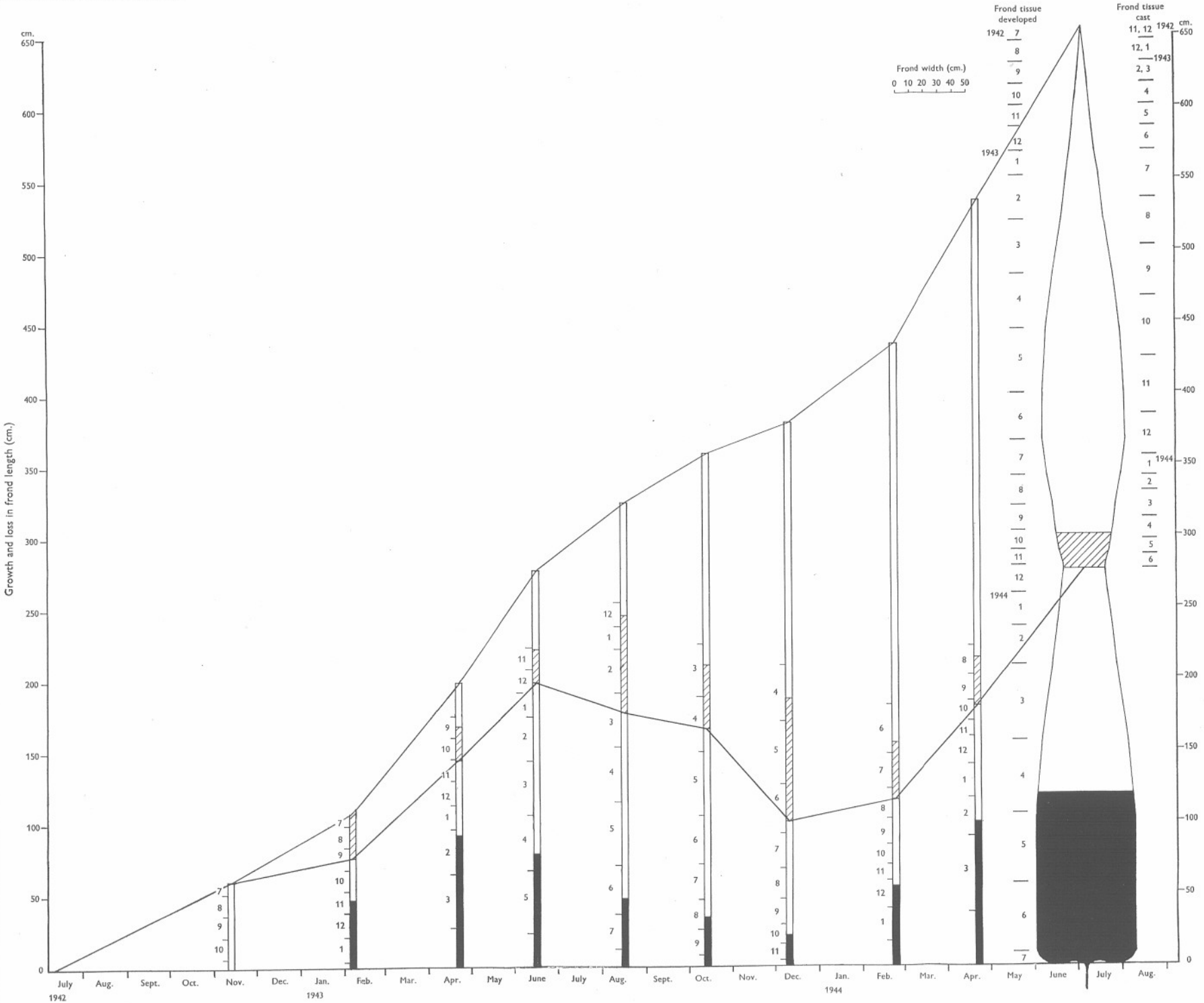
With the variation in the rate of growth in frond length and width throughout a yearly cycle a change takes place in the shape of the base of the frond so that the rapidity or slowness of the frond growth at any time can be assessed roughly from the shape of the frond base. When growth is extremely rapid the base is fusiform; as the rate of growth slows down the shape of the base alters from fusiform to cuneate; and then, when frond growth is at a very slow rate, the shape changes again from cuneate to nearly semicircular or subcordate (Pl. V). Yendo (1919), in his monograph on *Alaria*, also remarks on the change in shape of the base of the frond and considered it a remarkable process. He was of the opinion, however, that it was actually the same frond tissue changing shape, not realizing that new basal tissue was being produced whilst the old distal tissue was being cast off.

In addition to seasonal variation, the width and thickness of the frond also change with the age of the plant (Pls. IX–XI). Frond width during the second rapid-growth period of the plant is always greater and the frond tissue thicker than during the first period of rapid growth, but the width and thickness produced during the third period never exceeds that developed during the second. Maximum frond width, therefore, is reached at the same time as the maximum growth in frond length, that is, during the second rapid-growth period in the life of a plant (Pl. X), but the maximum thickness of the frond tissue is reached during the second period of slow growth.

The most rapid increase in the width of the frond tissue takes place during the period of the maximum primary growth in frond length between February and April; the frond tissue then increases in width at a slower rate until August in first-year plants and June in older plants (Text-fig. 6). Decrease in the width of the frond tissue produced, therefore, starts earlier, July, in plants over 1 year old, the rate of decrease being rapid until October or November (Pls. V–VII). In the first-year plants the decrease in frond width starts about 2 months later, lasts for a shorter time and is not so great as during the second slow-growth period (Pls. V–VII). The narrowing of the frond during the first slow-growth period is, therefore, hardly noticeable when the new frond tissue starts to increase in width at the beginning of the second period of rapid growth (Pl. V; Text-fig. 6).

PLATE XI

Growth in frond length, variation in frond width and loss in frond length throughout the first 24 months of life of a summer population of *L. saccharina* growing in the sublittoral zone on the Argyll coast in a sheltered habitat at a depth of 1 m. below E.L.W.S.T. For explanation of figure see text, p. 667.


Growth and loss in frond length (cm.)
cm.
650
600
550
500
450
400
350
300
250
200
150
100
50
0
Frond width (cm.)
0 10 20 30 40 50
Frond tissue developed
Frond tissue cast
July 1942
Aug.
Sept.
Oct.
Nov.
Dec.
Jan. 1943
Feb.
Mar.
Apr.
May
June
July
Aug.
Sept.
Oct.
Nov.
Dec.
Jan. 1944
Feb.
Mar.
Apr.
May
June
July
Aug.

In second-year plants, however, the constriction that appears in the frond due to the slow growth in length and great reduction in the width of the tissue produced during the second period of slow growth gives the impression, when the next rapid-growth period starts, of the so-called 'new frond' formation (Pls. V, VII, X and XI). If older plants are removed or become detached at any time of the year, the younger plants beneath, after a short period, give the same impression of 'new frond' formation as do the second-year plants, owing to the more rapid growth in length and width of the new frond tissue that has developed since the removal of the older plants.

Variation in Width of Frond with External Factors

In addition to the change in frond width with age of plant and season, variation also occurs in the width of the frond tissue with difference in bathymetric zone, habitat and geographical position. The statements made earlier in connexion with the variation in the rate of frond growth in length with changes in these factors hold good also for width variation, since with an increase in the rate of frond growth in length there is, in general, a corresponding increase in frond width, and with a decrease in length-rate, a decrease in frond width.

The width of the frond increases therefore, first, with fall in level down to the upper sublittoral zone where the maximum width is reached; secondly, with the increase in the degree of shelter of the habitat; and thirdly, from the southern to the northern station. The frond is also wider in intertidal plants that remain submerged, as compared with plants which are uncovered at low tides (Pls. V–XI; Text-fig. 6). Farlow (1882) also notes that in going northward on the east coast of North America the fronds of the plants of this species become broader.

For populations growing in the intertidal zone the figures show that during the second period of rapid growth there is, in addition to the maximum increase during February and March, a secondary rise in the rate of width increase during the month of June, the rate of increase having slowed down from March to May (Text-fig. 6). This secondary rise is more pronounced in populations with emergence at low tide, since the rate of width increase slows down more from April to May; it is accompanied in these populations by a corresponding rise in the rate of frond growth in length (Text-fig. 3). Populations that remain submerged during low water in the intertidal zone also show a slight rise in the rate of width increase during June (Text-fig. 6), but they show a decrease in the rate of frond growth in length from the previous month (Text-fig. 3). In the sublittoral zone no secondary rise in the rate of frond growth in length or width has been recorded.

Tikhovskaya (1940) has shown for *Laminaria saccharina* plants on the Russian coast that the coefficient assimilation/respiration reaches its maximum from February to May when photosynthesis is strongest; the coefficient

decreases with diminishing energy of photosynthesis and increasing energy of respiration during the summer months, but in the autumn (October) a slight rise in the energy of photosynthesis is recorded. From his work he concludes that the temperature and light optimum of this species are low.

It can be seen from the foregoing facts that to give figures for the frond width of a *L. saccharina* population in any one habitat would be of little value, since during the time of maximum width production a variation in populations in different habitats and localities of from 9·5 to 45 cm. has been obtained on the Devon coast, and from 13 to 103 cm. on the Argyll coast.

Loss in Length

In this species loss of frond tissue from the distal end starts when a plant is a few months old and continues throughout the life of a plant (Pls. IX–XI; Text-fig. 4). The rate of frond loss from the apex in plants over 6 months old is such that the age of the oldest frond tissue varies normally between 5 and 7 months (Pls. X, XI), but in populations growing in exposed habitats in the intertidal and sublittoral fringe zones the average age of the apical frond tissue can drop to less than 4 months (Pl. IX). Frond tissue between 7 and 8 months old can survive on plants for short periods (Pls. IX, X), but in none of the populations examined has 9-months-old tissue been recorded (Text-figs. 8, 9).

Plants growing in the sublittoral zone show a more regular casting of apical frond tissue, according to the month the tissue was produced, than do plants growing in the intertidal zone (Text-figs. 3, 4). In the former zone frond tissue developed from January to June is cast from July-August to December, and that developed from July to December between January and July (Pl. XI). Since it is the frond tissue developed during the rapid-growth period of the frond that is cast from July-August to December in this zone, there is, therefore, a much heavier loss of frond tissue, both in length and weight during that period than during the period from January to June (Text-fig. 4, nos. 3, 4), and consequently the maximum frond length and weight for the year is reached between the months of June and July. There is a more definite tendency in plants in the intertidal and sublittoral fringe zones for the average age of the oldest frond tissue to vary with the season of the year, and to be slightly higher from October to March than from April to September; this retention of older frond tissue from October to March may be connected with the slowing down in the growth-rate and therefore the shorter frond length produced during the period (Pls. IX, X).

In intertidal populations also the rate of casting of frond tissue varies with the degree of exposure of the habitat. In extreme shelter the time of casting of the different months' frond tissue agrees with that found in the sublittoral zone. As the exposure of the habitat increases, the tissue produced during the months of slower growth is cast more rapidly (Pl. X; Text-fig. 4, no. 2), but the tissue developed from February to July is still cast between July and

February. With further increase in the exposure of the habitat the tissue produced in the early part of the rapid-growth period is also cast earlier until eventually, in exposed habitats, tissue developed from January to June (rapid growth) is cast from April-May to November-December, and that developed from July to December (slow growth) is cast between December and April (Pl. IX; Text-fig. 4, no. 1).

Frond loss in length from July to December is therefore still higher than from January to June in a habitat with medium exposure (Text-fig. 4, no. 2), but with greater exposure the amount of frond length lost from January to July is very little different from that lost between July and December (Text-fig. 4, no. 1). The maximum frond length and weight for the year in the intertidal and sublittoral fringe zones is reached at about the same time as in the sublittoral zone, or a little earlier, even when the frond loss is more evenly distributed throughout the year.

In all habitats plants in the first year of growth show some variation in the rate of frond loss due to the time of year at which they arise. On plants developed during the winter and spring sufficiently old frond tissue has been retained at the apex by the following September to November for the plants to follow the rhythm of frond loss of the older plants. In plants arising in the early part of the year the rate of growth during the slow-growth period is more rapid than in plants arising during the summer and autumn (Text-fig. 3, nos. 5, 6). Casting of apical frond tissue is more rapid, therefore, during the following spring and summer in plants developed during the summer and autumn than in plants developed during the previous winter and spring (Text-fig. 4, nos. 3, 4). This variation in the rate of casting of individual months' frond tissue in the first year of growth, due to the time of germination of a plant, has been shown to alter the age and the time of the year at which maturity is first reached in plants of this species. Plants over 12 months old, whatever their time of germination, follow the general rate of frond loss from the apex fairly consistently according to the habitat in which they are growing.

In this species also, whatever the time of germination, age or habitat of a plant, frond tissue produced from April-May to August-September is cast from the fronds during approximately the same period each year between October and March-April (Text-fig. 4). The variation, with time of germination of the plant and with habitat, in the time of casting of frond tissue developed between September and March-April appears to have an important bearing on the reproductive cycle of the sporophyte.

Growth of the Stipe and Holdfast

Before the sporeling of *L. saccharina* differentiates into stipe and frond it is attached by colourless rhizoids to the substratum. As differentiation proceeds an attachment disk develops at the base of the young stipe by cell multiplication. The first true haptera of the holdfast originate as outgrowths from this

attachment disk, but later-formed haptera develop above the original haptera as outgrowths from the cortical tissue of the stipe.

The following zones can be recognized in a transverse section of a young stipe: a central medulla, surrounded by an inner and outer cortex, and on the outside of the cortex several layers of small cells, the outermost layer being an actively dividing meristoderm. A mucilage layer covers the meristoderm. Details of the structure of the stipe and of the development from the sporeling stage can be obtained from Drew (1910), Killian (1911) and Fritsch (1945).

Many workers, in particular Foslie (1884), Setchell (1900), Killian (1911), and Flerov & Karsakoff (1932), have drawn attention to the variation that occurs in stipe length and in the arrangement of the haptera of the holdfast in plants of the same species of *Laminaria* with variation in habitat and substratum, and have concluded that neither stipe length nor holdfast arrangement can be taken as criteria for specific distinction.

There are also many references in the literature (see Fritsch, 1945) to the periodic formation of new haptera series and to the ringed appearance of the stipe in the perennial Laminariales. The 'rings' in the stipes of the *Laminaria* species have not been studied except by Schultz-Schultzenstein (1853) and by Printz (1926) for *L. digitata* Lamour. Le Jolis (1855) does, however, correlate the 'ring' formation in the stipe of *L. cloustoni* with the annual increase in thickness which, he says, corresponds with a new whorl of haptera that is produced at the same time as a new frond. The growth of the stipe and the relation of the 'rings' in the stipe to both stipe and frond growth have not so far been followed in any species of *Laminaria*.

In the present work the growth in length of the stipe, the increase in stipe diameter and the development of the haptera forming the holdfast have been followed in all the plants of the different *L. saccharina* populations that have been studied for the growth of the frond.

The diagrammatic longitudinal sections of the stipe and holdfast on Pl. XII, illustrate the growth of both the stipe and holdfast up to the age of approximately 2 years in two populations of *L. saccharina*, an intertidal population growing on the Devon coast (frond growth in Pls. V and X) and a sublittoral population growing on the Argyll coast (frond growth in Pls. VI, VII and XI). In these figures the central medullary zone of the stipe is indicated by two lines; the dotted areas inside the medulla represent air pockets. The stippled areas indicate the tissue of the outer cortex of the stipe that is responsible for the darker 'rings' that show in a transverse section of the stipe. The outside lines represent the surface layers of small cells including, in the younger tissue, the outermost meristoderm layer.

General Rhythm in Rate of Growth

The growth of the stipe is similar to that of the frond in that it shows considerable variation in the rate of the growth during the different seasons of

the year. The rhythm in the rise and fall in the rate of stipe and holdfast growth during a yearly cycle follows, fairly closely, the rhythm of the primary growth in frond length.

The figures on Pl. XII show that stipe growth in length and thickness is more rapid from January to June than from July to December with the maximum growth-rate between January and April and the minimum rate between September and November.

The figures show also that the formation of a new haptera series at the base of the stipe starts after the period of minimum growth, at the same time as the rise in the rate of stipe growth in length at the apex, the full haptera series completing its development by the end of the period of rapid growth. Normally, haptera series are not developed during the slow-growth period of the plant except, of course, in sporelings arising during that period, but after holdfast tissue has been eaten or damaged small secondary haptera may develop from the injured surface.

Variation in Rate of Growth

The same factors that appear responsible for the variation in frond growth seem to be responsible for the variation in the rate of stipe and holdfast growth that occurs among plants of this species, irrespective of the general rhythm in growth-rate that takes place during a yearly cycle. These factors are age and season of development of the plant, bathymetric zone, habitat and geographical position. An additional factor, the substratum, also influences the form and arrangement of the haptera of the holdfast.

Effect of Age

The influence of the age of the plant on the rate of stipe growth and the general sequence in stipe and holdfast development can be followed from the figures on Pl. XII.

After the young sporeling has differentiated into stipe and frond the primary growth in stipe length is from the apex and takes place by the cutting off of cells downwards by the formative or transition region between stipe and frond. A certain amount of secondary increase in stipe length by cell division and cell stretching occurs in the stipe tissue below the transition zone but at a diminishing rate downwards. The length of stipe tissue showing secondary increase depends on the rate of the stipe growth in length.

Increase in the diameter of the young stipe, holdfast region and haptera is due to the activity of the meristoderm or surface layer that cuts off cells inwards, thus increasing the thickness of the cortical tissue.

From July onwards, as the rate of growth of the stipe in length slows down during the period of slow growth, so also does the rate of increase in thickness, since the activity of the surface meristoderm also slows down, producing fewer cortical cells than during the period of rapid growth. The cortical cells

produced during the period of slow growth do not reach the size of the cells formed during the rapid-growth period. The contents of these cells also appear denser, in some habitats darker brown. The denser and darker appearance may be due to the greater accumulation in the cells of physodes impregnated with fucosan, since the classical reaction of tannins was obtained with vanelin chlorohydrate. Except in the newly formed apical tissue in which the meristoderm retains its activity, there is a gradual decrease in the cell size of the cortical tissue produced until the activity of the meristoderm ceases in September or October, towards the end of the first period of minimum stipe growth.

Colour change in the surface of the stipe, holdfast region and haptera is an external indication of the change in the rate of stipe growth. When the growth-rate is rapid the surface tissue is light-coloured, but as the rate slows down the tissue darkens gradually, until at the end of the period of minimum growth, when the activity of the meristoderm ceases, the tissue is comparatively dark in colour.

After the minimum rate of stipe growth has been reached in the first slow-growth period there is, except in the newly formed apical stipe tissue, beneath the surface layers of the stipe, holdfast region and haptera a narrow layer of

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PLATE XII

Growth of the stipe and holdfast in two populations of *L. saccharina*. A, growth throughout first 27 months of life of a spring population in the intertidal zone (0·2 m. above M.L.W.S.T.) on the south Devon coast, in an exposed habitat, submerged at a shallow depth at low water of mean spring tides. B, growth throughout first 24 months of life of a summer population, growing in the sublittoral zone on the Argyll coast, in a sheltered habitat at a depth of 1 m. below E.L.W.S.T. For explanation see text, p. 684.

Notes

A, 1, first series haptera still forming, lower haptera attached.
2, first series haptera formed, majority attached.
3, first series haptera attached and darkening.
4, first series haptera dark.
5, beginning of second series of haptera.
6, first haptera of second series forming.
7, first haptera of second series formed, majority not attached.
8, first haptera of second series attached, further haptera forming above.
9, all haptera of second series formed, majority attached, pale in colour.
10, all haptera of second series attached and darkening.
11, 12, second series haptera dark.
13, beginning of third series of haptera.
14, haptera of third series forming.
15, third series haptera formed but not attached.
16, third series haptera attached.

B, 1, first series haptera formed, majority attached, pale colour.
2, beginning of second series of haptera, first series darkened.
3, first haptera of second series formed, some attached, further haptera forming above.
4, first haptera of second series attached, further haptera forming above.
5, all haptera of second series formed, majority attached, pale in colour.
6, all haptera of second series attached and darkening.
7, 8, second series haptera dark.
9, beginning of third series of haptera.
10, haptera of third series forming.
11, third series of haptera formed, majority attached, pale in colour

small-celled cortical tissue, the smallest cells being immediately inside the innermost cells of the surface layers. This cortical layer appears denser and more compact because of the smaller cell size of the tissue, and with further stipe growth in thickness will present the appearance of a darker 'ring' in a transverse section of a stipe (Pl. XIII, figs. 35, 36). This denser tissue will, in future, be referred to as 'compact' tissue or layer.

The stipes of plants that arise during the winter, spring and early summer show, after the first period of slow growth, a more definite compact layer than do the stipes of plants developed during the late summer and early autumn.

The first external indication of the start of the rise in rate of stipe and holdfast growth after the first minimum-growth period is the lightening in colour of both the apical part of the stipe below the transition zone and the base of the stipe immediately above the first haptera series. This colour change takes place from late October to early November.

At this time a layer of cells immediately outside the compact tissue starts to function as a secondary meristem. By the activity of this meristem new cortical cells, showing a radial arrangement, are produced on the outside of the compact layer. The secondary meristem first shows activity at the base of the stipe immediately above the first haptera series, and as its activity increases the original surface layers are cast off leaving the newly formed, lighter-coloured tissue at the surface. The change in colour at the base of the stipe indicates the activity of this secondary meristem and also the start of the formation of a new haptera series. At the apex the colour change is due to the more rapid rate in the growth in stipe length from the transition zone, and also to the increase in activity of the meristoderm that has remained functional in the apical part of the stipe.

By the end of December there is a further addition to the stipe length at the apex, but only a slight increase in the thickness of the new stipe tissue, whilst at the base of the stipe the first haptera of the second series can be observed as small protuberances. The activity of the secondary meristem has also spread upwards and downwards, so that a very narrow layer of new cortical tissue is present on the outside of the compact tissue part way up its length and below the new haptera down to the level of the first haptera series; the new growth frequently shows also on the outside of the proximal part of the uppermost haptera of the first series.

During January the activity of the secondary meristem continues to spread upwards on the outside of the compact tissue and the rate of stipe growth in length and thickness increases so that by February a layer of new cortical tissue is present on the outside of the whole length of the compact layer and there is an appreciable increase in the thickness of the young tissue of the stipe. At this time also the first haptera of the second series are fully grown, although the majority are not yet attached to the substratum and further haptera of the second series may be developing above those already formed.

From late February to April there is a very rapid increase in the rate of stipe growth (Pl. XII); the increase is shown in the new length of stipe added, in the increase in the thickness of all the young stipe tissue produced since the beginning of the rapid-growth period and also in the increase in thickness of the secondary cortical layer outside the layer of compact tissue (Pl. XIII, fig. 37). At this stage transverse sections of the stipe show, throughout the length of the compact layer, the new secondary cortical tissue as a lighter 'ring' or zone on the outside of the darker 'ring' of the compact layer (Pl. XIII, figs. 35, 36), whereas sections of the younger stipe tissue above the level of the compact layer show no 'ring' formation in the cortical tissue (Pl. XIII, fig. 34).

In the holdfast region the first-formed haptera of the second series are attached and further haptera are forming above them. The increased activity of the secondary meristem in the holdfast region below the level of the second haptera series is shown by the increase in width of the layer of secondary light-coloured cortical tissue on the outside of the compact layer of part of the holdfast region and on the outside of the proximal parts of the upper haptera of the first series. At this stage transverse sections of the uppermost haptera of the first series, taken near the point of origin from the stipe, show 'ring' formation (Pl. XIII, fig. 45).

PLATE XIII. *Laminaria saccharina* (L.) Lamour.

Photographs of sections of the stipe and holdfast. Figs. 34 and 35 are sections of the stipe of a plant from the same habitat as the plants illustrated on Pl. V. Figs. 36–45 are sections of the stipes of plants from the same blocks as the plants illustrated on Pls. VI and VII. Natural size.

Fig. 34. T.S. of stipe of 12-months-old plant taken from the stipe length produced during the second period of rapid growth. 28. iii. 1944.

Fig. 35. T.S. of stipe of 12-months-old plant taken from half-way up the length of the first compact layer. 28. iii. 1944.

Fig. 36. T.S. of stipe of 10-months-old plant taken from half-way up the length of the first compact layer. 22. iv. 1943.

Fig. 37. L.S. of base of the stipe and the holdfast of a 10-months-old plant. 22. iv. 1943.

Fig. 38. T.S. of stipe of 18-months-old plant taken from near the apex. 10. xii. 1943. See text, p. 691, for explanation of Figs. 38–41.

Fig. 39. T.S. of stipe of 18-months-old plant taken from the middle of the stipe length produced during the first rapid-growth period—medulla broken down. 10. xii. 1943.

Fig. 40. T.S. of stipe of 18-months-old plant taken from near the top of the length of the first compact layer. 10. xii. 1943.

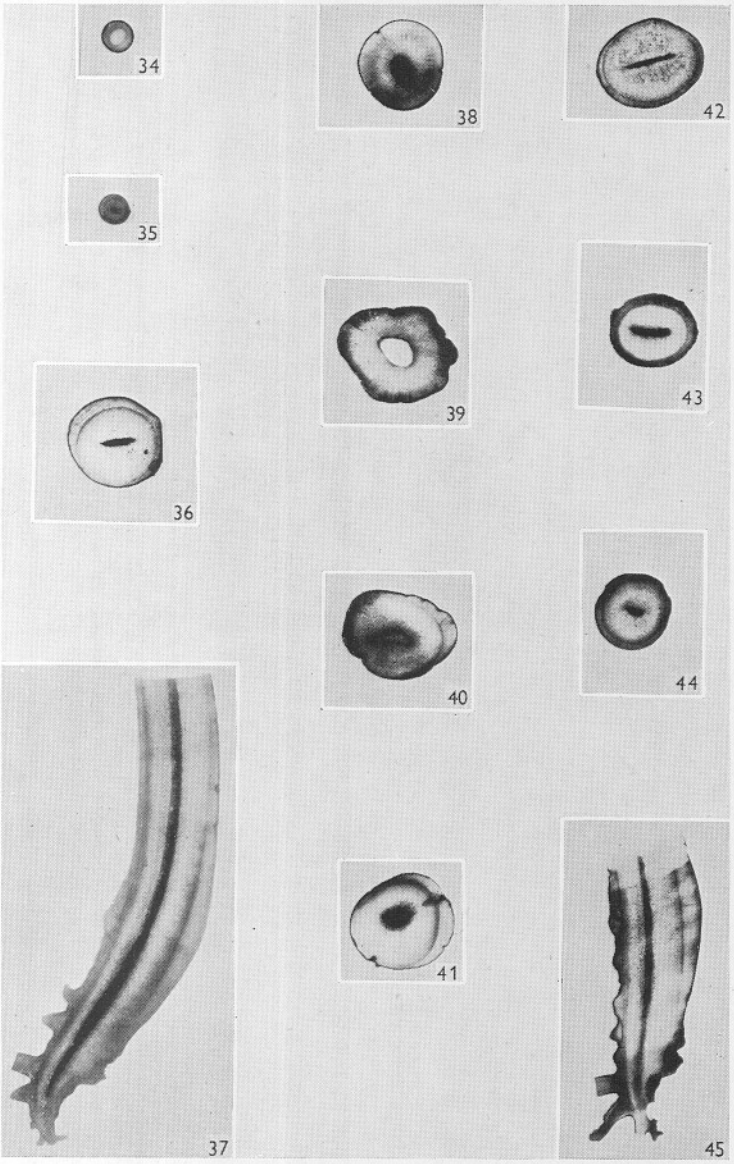
Fig. 41. T.S. of stipe of 18-months-old plant taken from half-way up the length of the first compact layer. 10. xii. 1943.

Fig. 42. T.S. of stipe of 24-months-old plant taken near the top of the stipe length added during the first rapid-growth period. 6. vii. 1944.

Fig. 43. T.S. of stipe of 18-months-old plant at the end of the second slow-growth period. Section taken near top of first compact layer. 10. xii. 1943.

Fig. 44. T.S. of stipe of 18-months-old plant at the end of the second slow-growth period. Section taken half-way up length of first compact layer. 10. xii. 1943.

Fig. 45. L.S. of stipe and holdfast of 18-months-old plant at the end of the second slow-growth period showing the compact layer formed in the haptera during the first slow-growth period. 10. xii. 1943.



Figs. 34–45.

Growth in length and thickness of the stipe continues during May and June, but at a slower rate than during March and April. By the end of June all the haptera of the second series are formed and the majority are attached to the substratum. The haptera of the second series are larger than those of the first series. Externally the stipe and second series of haptera are still light in colour showing that the surface meristoderm of the younger stipe tissue and the secondary meristem of the older stipe tissue are still producing rapidly growing tissue.

As the growth-rate slows down from July onwards, in the second slow-growth period of a plant, a second compact layer is formed on the outside of the stipe, holdfast region and haptera (Pl. XIII, figs. 43–45). The minimum growth-rate is reached between September and October, but in the second slow-growth period the rate of growth does not start to rise again until the middle or end of December, approximately 1 month later than in the first period of slow growth.

During the rapid-growth period following the second period of slow growth in the life of a plant (second or third depending on time of germination of the plant), although a cell layer on the outside of the second compact layer of the stipe again functions as a secondary meristem, it is not so active as the secondary meristem of the previous rapid-growth period. In this rapid-growth period new light-coloured tissue is formed only on the outside of the second compact layer at and near the base of the stipe above the second series of haptera (Pl. XII). The third haptera series develops from this tissue, but the haptera are fewer in number and of a smaller size than those developed during the previous rapid-growth period.

From just above the base of the stipe up to the level of the top of the first compact layer there is very little activity of the secondary meristem, and therefore during this rapid-growth period there is only a slight increase in thickness of this region of the stipe. The tissue formed by the secondary meristem in this region of the stipe is small-celled and in most plants cannot be distinguished from the tissue of the second compact layer, since all the cells show a radial arrangement. The surface of this part of the stipe, therefore, remains dark in colour.

In the region of the stipe in which the meristoderm ceased to function at the end of the second slow-growth period, that is, the stipe length from the level of the top of the first compact layer to the level of the top of the second compact layer, the new secondary meristem is more active than in the region of the first compact layer. Although the secondary cortical tissue produced by this secondary meristem on the outside of the second compact layer is rather small-celled tissue and therefore appears fairly dense, it can be distinguished from the tissue of the second compact layer by the radial arrangement of the cells (Pl. XIII, fig. 42). The original surface layers, including the meristoderm, are cast from this region of the stipe, and therefore externally this region can be

distinguished from the older stipe length by the lighter colour of the surface tissues. The colour of this region is not so light, however, as the new stipe length that has developed during this rapid-growth period. Externally three colour zones can, therefore, be distinguished in the stipe at the end of the rapid-growth period following the second period of slow growth.

During the third slow-growth period the rate of growth in both stipe length and thickness is extremely slow, so slow in some plants that it is hardly discernible. The third compact layer that forms on the outside of the stipe and on the third series of haptera is therefore very narrow, and in many plants can be recognized only at the base and apex of the stipe.

The method of stipe growth in this species described above and figured on Pl. XII shows that, whatever the habitat, the approximate age of a *L. saccharina* plant can be assessed from an examination of the holdfast region (thick longitudinal section), since at this level the number of lighter and darker growth zones indicates the number of rapid- and slow-growth periods through which a plant has survived. The approximate length of stipe tissue formed during the first, second and third rapid- and slow-growth periods can also be obtained from a longitudinal section of the stipe. In the present work no evidence has been obtained from stipe and holdfast examinations to show that plants of this species persist on the British coast beyond the third period of slow growth.

The following points emerge from the observations on the growth of the stipe and holdfast in different-aged plants of this species. In plants arising early in the year the stipe length produced during the second period of rapid and slow growth is often equal to and seldom much less than that produced during the first period, but the length of stipe produced during the third period is always shorter than that produced during either of the two previous rapid- and slow-growth periods. The diameter of the stipe tissue produced during the second rapid- and slow-growth period is, however, greater than that produced during either the first or the third period of rapid and slow growth. Haptera development and secondary increase in thickness of the stipe also reach their maximum during the second period of rapid growth.

In plants arising later in the year, that is, during the slow-growth period of the species, the stipe length produced during the first slow- and rapid-growth period is always far greater than that produced during the second period. These plants go from the shore before the third period of rapid growth. The diameter of the stipe tissue produced during the first rapid-growth period is equal to if not greater than that produced during the second period. Haptera development and secondary increase in stipe thickness reach their maximum during the first period of rapid growth; thus the time of the maximum differs from that found in plants arising during the rapid-growth period of the species.

The stipes of the summer- and autumn-developed plants grow so rapidly in length and thickness during the first rapid-growth period that the development of the central medullary tissue does not keep pace with that of the cortical

tissue and the medulla therefore becomes filled with air pockets (Pl. XII, B). In some plants the medulla breaks down completely in the rapidly growing part of the stipe and this part of the stipe becomes hollow; it also remains hollow throughout the life of the plant.

Pl. XIII, figs. 38–41, show transverse sections of the stipe of a summer-developed plant at the end of the second period of slow growth. From the base upwards the first section (fig. 41) is taken from halfway up the length of the first compact layer and the second section (fig. 40) from near the top of the first compact layer. The third section (fig. 39) is taken from the middle of the stipe length produced during the first rapid-growth period. This part of the stipe is hollow because of the complete breakdown of the medullary tissue. The fourth section (fig. 38) is taken from near the top of the stipe and is through the young stipe tissue in which the meristoderm has not ceased to function. The zone of less dense tissue on the outside indicates the beginning of the increase in activity of the meristoderm.

These summer-developed plants in which the apical part of the stipe becomes hollow agree with the description given by Børgesen (1903) for the species *Laminaria faeroensis*.

The sequence of the variation in the rate of growth of the stipe in plants arising during the rapid-growth period agrees fairly closely with the sequence that occurs in the rate of growth of the frond with change in age of the plant. Although the length of stipe tissue produced during the first rapid-growth period may be greater than the length produced during the second rapid-growth period, the actual amount of stipe tissue added, that is, in length, thickness, secondary thickness and haptera, is greater during the second rapid-growth period than during the first. As in the frond growth, the rate of stipe and holdfast growth during the third rapid-growth period varies considerably in populations growing in different habitats, but it is always less than the rate of growth of the stipe and holdfast during the second rapid-growth period. During the slow-growth periods the sequence in the rate of stipe growth is also in accord with that found in the frond except that the minimum rate is reached slightly earlier than in the frond.

For plants arising during the slow-growth period it has been shown that the growth-rate of the frond is higher during the first rapid-growth period than in plants arising during the early part of the year. The rate of stipe growth is also higher during the first rapid-growth period in plants arising during the slow-growth period, but unlike the rate of growth of the frond which increases during the second rapid-growth period, the rate of stipe growth is not so great during the second as during the first period of rapid growth.

Effect of Habitat

Habitat influences the rate of growth of the stipe and holdfast as it does the rate of growth of the frond (Pls. V–VIII). As in the frond the general

indications are that the rate of stipe growth increases with the degree of shelter of the habitat, with submergence of the plants as against emergence at low water, and with fall in shore-level down to the upper sublittoral zone. The maximum rate of stipe growth is reached 1–4 m. below extreme low water of spring tides.

At and above the level of E.L.W.S.T. the growth in length of the stipe never reaches a 0·3 cm. increase a day during the rapid-growth period, whereas in the sublittoral zone the daily increase in stipe length can reach a figure of 0·5 cm. The measurements of stipes of plants of this species growing on the Devon and Argyll coast show that the range of stipe size is very great. On exposed shores in the intertidal zone in habitats that dry out at low water the stipe of a plant at the end of the second slow-growth period may be less than 10 cm. long with a diameter of 0·5 cm., while plants of the same age growing in the sublittoral zone on sheltered coasts may have a stipe length of up to 130 cm. with a diameter of 1·9 cm.

The tissue of the slow-growing stipes, particularly that formed during the slow-growth periods, is much darker in colour than the tissue of the more rapidly growing stipes. This colour variation of the stipe tissue in plants growing in different habitats may be due, partly to the smaller cell size of the tissue in slow-growing stipes, and partly to variation in chemical composition of the stipe tissue of plants growing at different levels on the shore. Black (1948) working on *Laminaria* spp., Russell-Wells (1932) and Haas & Hill (1933) working on *Laminaria* and other genera have shown that there is a variation in the chemical composition with the degree of emergence and the depth of immersion of the plants.

The variability in frond development during the third period of rapid growth in populations of this species growing in different habitats has been connected with depth of submergence of the plants. Stipe and holdfast development during the third period of rapid growth also shows variability with difference in depth of submergence of the plants. In populations growing in the intertidal zone in habitats that dry out at low water of mean spring tides growth of the stipe and holdfast practically ceases early in the second period of slow growth. The third haptera series, therefore, is not produced, and on exposed coasts the plants fail to survive the third period of rapid growth.

In populations growing at the same level in the intertidal zone but in pools there is usually a slight increase in stipe length during the third period of rapid growth and a third haptera series is also formed, but the haptera are small and very few in number. In populations growing in the upper part of the sublittoral zone, however, there is, during the third period of rapid growth, an appreciable increase in stipe length and a fuller development of the third haptera series.

In this species the form of the holdfast depends on the nature of the substratum on which the plant is growing. The variation in form that can occur

with variation in the character of the ground has been dealt with in detail by Flerov & Karsakoff (1932). In general, the two extremes of form occur on rock and on soft silty ground. On rock the holdfast is compact with the haptera thick and only slightly branched (Pls. V; VIII, figs. 26, 29), while on soft silty ground the holdfast is much less compact and the haptera are thinner, longer and very copiously branched (Pl. VIII, fig. 33). All gradations between the two extreme forms can be obtained on different types of ground.

Geographical Variation

The figures for the growth of the stipe and holdfast of this species on the coasts of Devon and Argyll suggest that the difference in the growth of the stipe and holdfast in the two localities might also be correlated with difference in latitude. There is a higher rate of growth at the more northern station, and only at this station is the stipe growth so rapid that the medulla breaks down completely, leaving the stipe hollow. At this station also the maximum rate of stipe growth is reached in April and the minimum rate in October, while at the more southern station the maximum rate is reached in March and the minimum rate in September, approximately one month earlier than at the more northern station.

The results of the work on the growth of the sporophyte of *L. saccharina* on the Devon and Argyll coasts have shown that there is, within the plant itself, some dominant factor controlling the rhythm of its development, but that there are also factors external to the plant that may modify, very considerably, the morphological and anatomical character of the species.

Information from localities round the greater part of the British coast is still needed before a full knowledge of the variation in form of this species with change in its geographical position on the British coast can be assessed.

Records of the growth and behaviour of the species throughout its total range are also necessary before the full influence of latitude, direct or indirect, on the behaviour of the species can be understood, since, according to Wimpenny (1941), one algal group, the Dinophyceae, shows an increase in size with increase in latitude, whilst in another group, the Bacillariophyceae, the marine pelagic forms decrease in size with increase in latitude.

REPRODUCTION IN THE SPOROPHYTE

In the literature very little information is available on the reproductive period of the sporophyte of *L. saccharina* on different parts of the British coast. It is recorded by Rees (1928) for the Aberystwyth and Gower coast as occurring from October to early April; these records are for plants growing in the intertidal zones in habitats that dry out during low water of spring tides. During

the period 1923–27 he found no plants fruiting from late April to September; the main fruiting was from November to the end of February, the peak being reached during either January or February. Harries (1932) states that during 1929–30 reproduction in *L. saccharina* at Aberystwyth started early in November and ended early in March (Text-fig. 7, no. 2*b*), but in a less exposed region, St Davids, reproduction started a month earlier than at Aberystwyth. Knight & Parke (1931) record the production of reproductive tissue during all seasons of the year on plants growing on the coast of the Isle of Man.

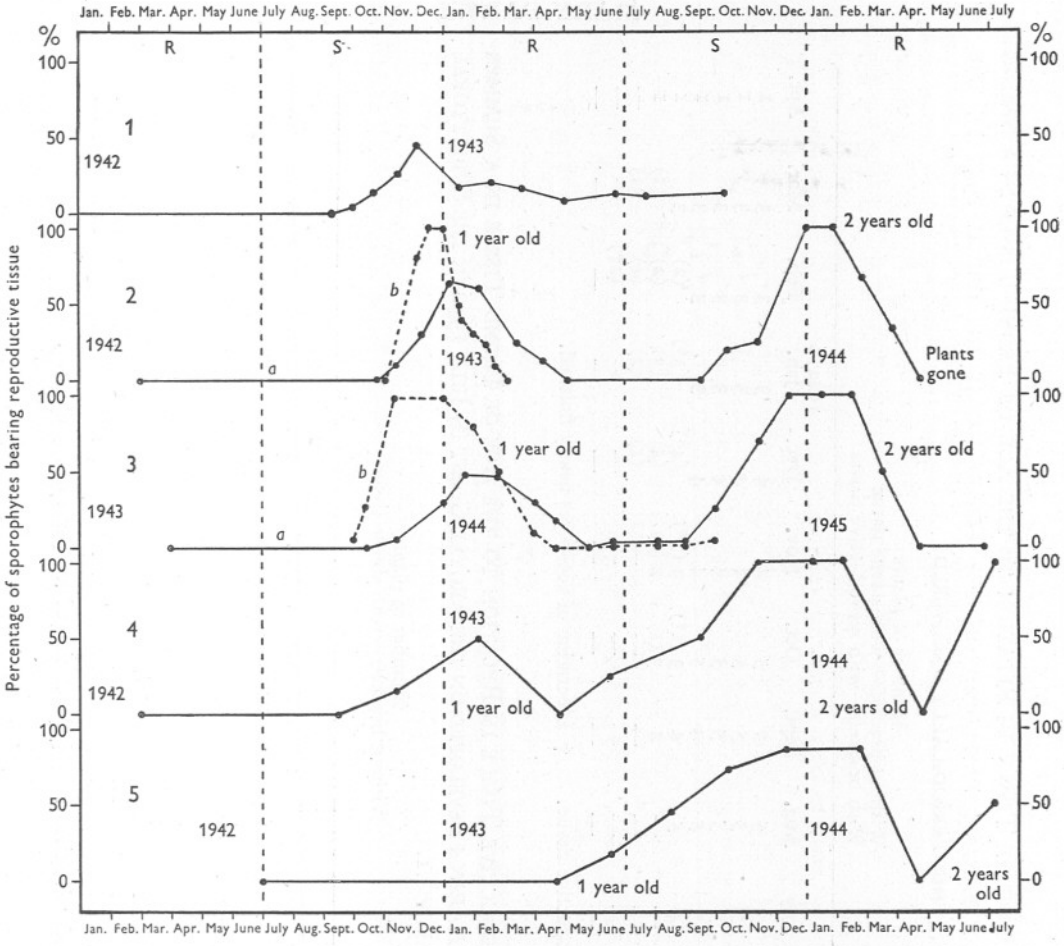
On the French coast Sauvageau (1918) found reproductive tissue on adult plants at all times of the year, whilst Børgesen (1903), during the period from May to November, found fructifying specimens in the Faeröes only during the months of June and July. On the Norwegian coast, in the Trondheim Fjord, Printz (1926) found reproducing plants in the middle of May and at the end of September and concludes that the sporogenous tissue becomes detached gradually from the frond during the autumn, whereas further north, on the East-Finmarken coast, according to Foslie (1890), reproduction occurs in the winter or early in the spring. For the Arctic, Kjellman (1883) states that on the coast of the Polar Sea sublittoral varieties only bear zoosporangia during July, August and early September, the varieties at and near low-water mark being sterile during this period. According to Kireeva & Schapova (1933, 1938) reproduction of this species on the Murman coast starts in July, reaches a maximum early in August and finishes at the end of August.

The present work has shown that on the coast of Devon and Argyll plants of this species can be found bearing reproductive tissue during all months of the year; in all populations, however, the percentage of reproducing plants is highest between the months of October and March (Text-fig. 7).

Contrary to the findings of Kireeva & Schapova (1933, 1938), who state that *L. saccharina* does not reach maturity on the Murman coast until the third year of growth, this work has shown that on the British coast reproductive tissue first develops on the fronds when the plants are from 8 to 12 months old (Pl. V, figs. 2, 3; Pl. VIII, fig. 26). Plants that develop during the early part of the year can start to bear reproductive tissue when they are 8–9 months old, but plants developed later in the year do not form reproductive tissue until they are nearly 1 year old. The plants, therefore, that start life during the rapid-growth period of the species reach maturity approximately 4 months earlier than do plants that start life during the period of slow growth.

Development of Reproductive Tissue

For reproductive tissue to develop on a frond of a *L. saccharina* plant the distal tissue present on the frond must be in at least the sixth month of growth. Once reproductive tissue is present on frond tissue in the sixth month of growth, it can arise also on frond tissue in the fifth month of growth. If how-



Text-fig. 7. Periodicity of reproduction in different populations of *L. saccharina*, showing the variation with age, time of germination, habitat and locality. The graphs start at the month when the plants germinated (except graphs 1, 2*b* and 3*b*).

(1) Population on floating raft. Plymouth Sound, Devon, sheltered habitat, shallow submergence permanent. First sporophytes germinated December 1941–January 1942 and new sporophytes added each succeeding month; all sporophytes, including sporelings, counted in samples examined for percentage reproduction in population.

(2*a*) Spring population, 1942. Devon, exposed shore, intertidal zone, above M.L.W.S.T. (thus periodically uncovered).

(2*b*) Normal population. Aberystwyth, 1929–30. Figures given by Harries (1932).

(3*a*) Spring population, 1943. Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools (thus never uncovered).

(3*b*) Normal population, 1943–44 (chiefly plants in second and third year of growth—very few first-year plants). Devon, exposed shore, intertidal zone (above M.L.W.S.T.), in pools.

(4) Spring population, 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

(5) Summer population, 1942. Argyll, sheltered shore, sublittoral zone, at depth of 1 m. below E.L.W.S.T.

R, rapid-growth period. S, slow-growth period.

TABLE VI. THE PRODUCTION OF REPRODUCTIVE TISSUE IN RELATION TO THE AGE OF FROND TISSUE IN A SPRING POPULATION OF *LAMINARIA SACCHARINA* DEVELOPED ON THE DEVON COAST IN MARCH 1942 IN THE INTERTIDAL ZONE, ABOVE M.L.W.S.T. (THUS PERIODICALLY UNCOVERED)

Number of plants
Without brackets—with sterile tissue
With brackets—with reproductive tissue

Age of frond tissue in months	1943 Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	1944 Jan.	Feb.	Mar.	Apr.
1	8	5	5	5	5	5	5	4	4	3	3	3	1
2	8	5	5	5	5	5	5	4	4	3	3	3	1
3	7	5	5	5	5	5	5	4	4	3	3	3	1
4	7	2	5	5	5	4	5	4	4	3	3	3	1
5	1	—	1	4	5	4	3 (1*)	3 (1*)	(4*)	(3*)	(2)	3	1
6	(1)	—	—	—	—	4	3 (1)	2 (1)	(4)	(3)	(2)	(1)	1
7	—	—	—	—	—	—	—	—	(1)	(2)	(2)	(1)	—
8	—	—	—	—	—	—	—	—	—	—	(2†)	—	—
9	—	—	—	—	—	—	—	—	—	—	—	—	—

* Immature reproductive tissue. † Liberation of zoospores nearly finished.

TABLE VII. THE PRODUCTION OF REPRODUCTIVE TISSUE IN RELATION TO THE AGE OF FROND TISSUE IN A SUMMER POPULATION OF *LAMINARIA SACCHARINA* DEVELOPED ON THE ARGYLL COAST IN JULY 1942 IN THE SUBLITTORAL ZONE AT A DEPTH OF 1 m. BELOW E.L.W.S.T.

Number of plants
Without brackets—with sterile tissue
With brackets—with reproductive tissue

Age of frond tissue in months	1942 Nov.	1943 Feb.	Apr.	June	Aug.	Oct.	Dec.	1944 Feb.	Apr.	June
1	25	20	20	20	11	11	10	7	5	4
2	25	20	20	20	11	11	10	7	5	4
3	25	20	20	20	11	11	10	7	5	4
4	25	20	20	20	11	11	10	7	5	4
5	25	20	14	20	5 (5*)	3 (7*)	(9*)	(6*)	5	4
6	—	8	12	12 (4*)	3 (5)	3 (5)	(9)	(6)	5	1 (3*)
7	—	—	—	(4)	(2)	(7)	(8)	(5)	(3†)	(3)
8	—	—	—	—	—	(2†)	(2†)	—	—	—
9	—	—	—	—	—	—	—	—	—	—

* Immature reproductive tissue. † Liberation of zoospores nearly finished.

ever it arises on frond tissue in the fifth month of growth it does not usually mature until the beginning of the next month (Tables VI–VIII; Text-figs. 8, 9). The evidence available indicates that reproductive tissue is produced only on frond tissue that is approaching or has reached final expansion. Since considerable expansion occurs during the spring months in frond tissue in the fifth and sixth month of growth, during the period of maximum increase in frond length above the 10 cm. level, production of reproductive tissue during this period is at a minimum.

It takes from 14 to 21 days for reproductive tissue to develop and reach maturity in this species. There is no perceptible variation in the time taken for reproductive tissue to develop with differences in the age and habitat of

TABLE VIII. THE PRODUCTION OF REPRODUCTIVE TISSUE IN RELATION TO THE AGE OF FROND TISSUE IN A SPRING POPULATION OF *LAMINARIA SACCHARINA* DEVELOPED ON THE DEVON COAST IN APRIL 1943 IN THE INTERTIDAL ZONE (ABOVE M.L.W.S.T.) IN POOLS

Number of plants
Without brackets—with sterile tissue
With brackets—with reproductive tissue

Age of frond tissue in months	1944 June	July	Aug.	Sept.	1945 Jan.	Feb.	June
1	34	32	29	24	5	4	3
2	33	30	26	24	5	4	3
3	32	26	23	19	5	4	3
4	27	24	22	19	5	4	3
5	23	24	21	13 (6*)	(5*)	(4*)	3
6	3 (1)	3 (3)	1 (1)	8 (6)	(5)	(4)	—
7	—	—	—	(2)	(3)	(3)	—
8	—	—	—	—	(2†)	(1†)	—
9	—	—	—	—	—	—	—

* Immature reproductive tissue. † Liberation of zoospores nearly finished.

the plant, or with the season of the year. Once reproductive tissue has reached maturity it can continue to liberate zoospores for 2–3 months if the frond tissue bearing it is retained by the plant.

When reproductive tissue first reaches maturity it bears approximately 1,000,000 ripe sporangia per cm.^{2} of frond surface. Sporangium initial cells and immature sporangia are not included in the above figure. A fortnight to a month after the first liberation of zoospores, the number of ripe sporangia is about 500,000 per cm.^{2} of frond surface. During the second and third months after the first liberation of zoospores there is a further drop in the number of ripe sporangia present on the reproductive tissue, although new sporangium initial cells continue to develop and mature, frequently inside the walls of sporangia from which the zoospores have been liberated. Kireeva & Schapova (1938) give 562,500 as the number of sporangia per cm.^{2} of frond surface on plants of this species growing on the Murman coast.

The number of zoospores produced by one sporangium is 32; this figure agrees with that given by Schreiber (1931) for plants growing at Heligoland, but not with that given by Kireeva & Schapova (1938) who state that the sporangia developed on plants on the Murman coast produce 64 zoospores.

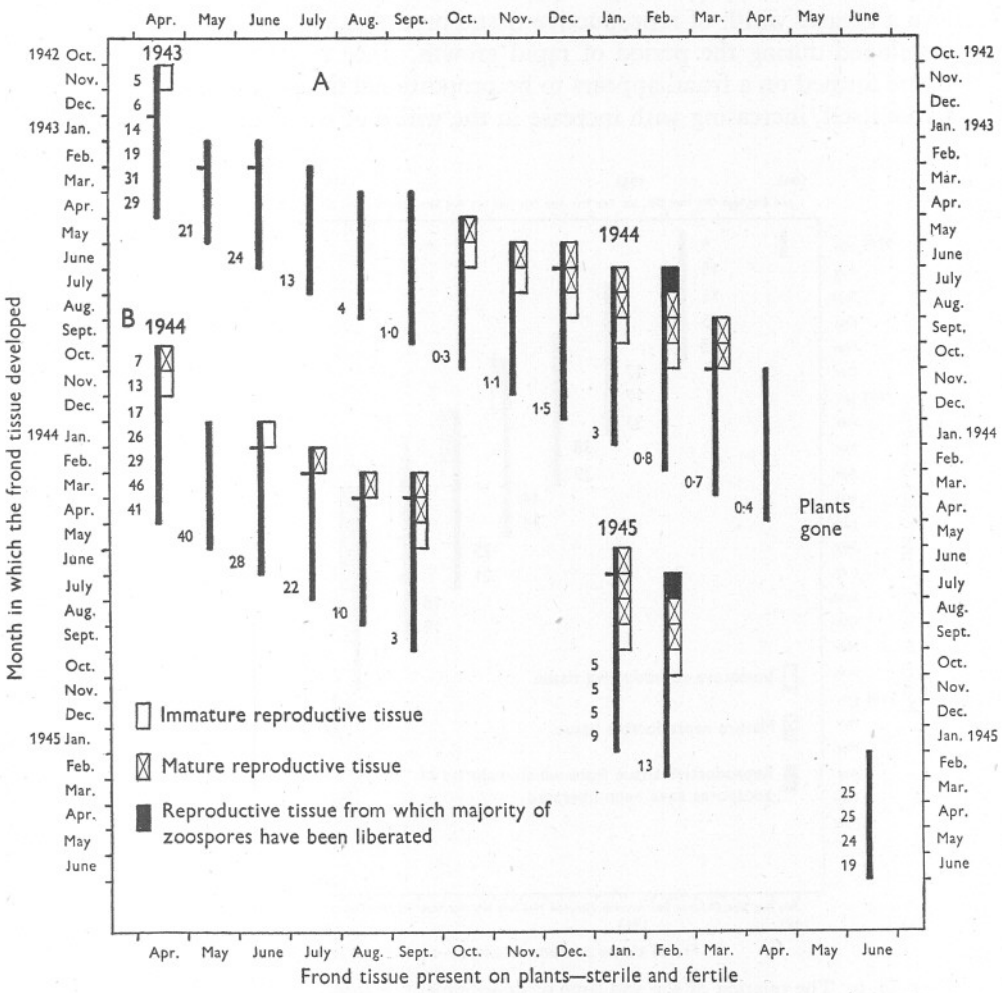
Drew (1910), working at the Plymouth Laboratory, obtained 2,000,000 gametophytes from 1 sq. in. of reproductive area of the frond, whilst from Kireeva's and Schapova's (1938) figures it can be estimated that 36,000,000 zoospores are produced per cm.^{2} of frond surface of plants on the Murman coast. The above figures, however, are the numbers of zoospores, or the gametophytes developed from the zoospores, produced by the reproductive tissue on the frond at one time.

If reproductive tissue is retained for a sufficiently long period on the frond, it develops successive crops of sporangia. It has been estimated that if reproductive tissue can persist on the frond for 3 months after it first reaches maturity, 1 cm.^{2} of frond surface bearing reproductive tissue can produce up to 2,000,000 sporangia. This means that if reproductive tissue is retained on a plant until the frond tissue bearing it is in the eighth month of growth, 1 cm.^{2} of frond surface can liberate 64,000,000 zoospores over a period of 3 months. It is, however, only for a short period during the year that frond tissue in the eighth month of growth is retained by plants of this species (Tables VI–VIII). In the intertidal and sublittoral fringe zones frond tissue in the seventh month of growth also does not persist on the plants for more than 6 months of the year, frequently for a much shorter period (Tables VI, VIII; Text-fig. 8).

There is, therefore, a certain wastage of potential reproductive products in plants of this species, particularly in plants growing in the intertidal and sublittoral fringe zones. The wastage, however, is not more than about 25% of the total number of zoospores that could have been produced if the frond tissue had survived beyond the age of 6 months, since the number of sporangia developed diminish rapidly with each successive crop that is produced. On any frond tissue 50% of the total number of zoospores that can be produced during 3 months are released when the tissue first reaches maturity in the sixth month of growth and another 25% by the end of the sixth month or early in the seventh month, leaving only 25% of the total number that can be produced by the tissue for release during the seventh and eighth months of frond growth.

As frond tissue formed during any month of the year has to reach a certain age and certain stage in development before it can bear reproductive tissue, the frond tissue produced during any one month of the year by all plants of this species will bear reproductive tissue at approximately the same time of the year if it persists on the plants (Text-figs. 8, 9). At any time of the year, therefore, the proportion of the frond length bearing reproductive tissue in plants of this species is obviously dependent on the rate of growth in length of the particular frond, the rate of casting of its distal frond tissue, and the

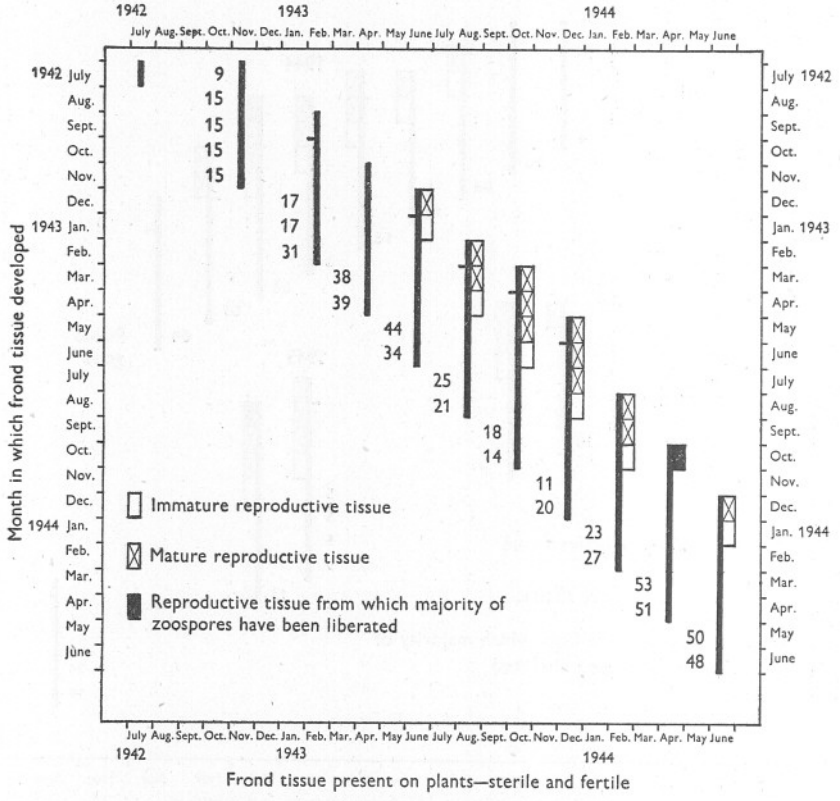
particular month's or months' frond tissue that is bearing the reproductive tissue (see Text-figs. 8, 9 with figures for frond length in cm. at side of



Text-fig. 8. The relation of age and time of development of frond tissue to the production of reproductive tissue on the fronds of two intertidal spring populations of *L. saccharina*. The black column represents frond tissue present on plants; the maximum amount is given by the full length of the line, the average amount marked on the *left* by a short protruding line. Those parts of the frond which have reproductive tissue are clearly marked by the rectangles projecting on the *right* side of the column. Figures at the side of the columns indicate the length of frond tissue (in cm.) developed during that month. Devon, exposed shore, intertidal zone; A, above M.L.W.S.T. (from 14th to 25th month of life); B, at same level in pools (from 13th to 27th month of life).

columns). Throughout a yearly cycle, the frond tissue formed during the period of rapid growth will produce a greater proportion of reproductive tissue, and

therefore a greater number of zoospores, than the frond tissue formed during the period of slow growth, providing these tissues persist on the plant until they reach maturity (Text-figs. 8, 9). There is not only a greater length but also a greater width of reproductive tissue produced on frond tissue that has developed during the period of rapid growth, since the width of sporangial tissue formed on a frond appears to be proportional to the width of the frond tissue itself, increasing with increase in the width of the frond.



Text-fig. 9. The relation of age and time of development of frond tissue to the production of reproductive tissue on the fronds in a sublittoral summer population of *L. saccharina*, growing on the Argyll coast in a sheltered habitat at a depth of 1 m. below E.L.W.S.T. Explanation as in Text-fig. 8.

In any habitat, therefore, the maximum production of reproductive tissue takes place in a second-year plant since the peak of frond growth in length and width is reached during the second year of growth. There is also variation in the amount of reproductive tissue produced by plants growing in different habitats and at different latitudes, the area of reproductive tissue produced by the plants increasing with decrease in level on the shore, with increase in the

shelter of the habitat, and with increase in the latitude. Considerable variation is, therefore, to be found in the shape, area and position of the reproductive tissue that develops on the fronds of plants of this species (Pls. V–VIII).

Periodicity of Reproduction

As the age of the distal frond tissue on a first-year plant is controlled more by the time of development of the plant and the resulting initial rate of growth during the first 6 months than by factors external to the plant, the time of the year that reproductive tissue first develops on a plant is controlled also by the time of the year the plant starts to develop.

In a plant over 12 months old, however, the age of the distal frond tissue depends on the degree of exposure or protection afforded to the plant by the habitat in which it develops. The period during which a plant can produce reproductive tissue depends, therefore, on the nature of the habitat in which the plant is growing; the reproductive period is extended in sheltered habitats and curtailed in exposed habitats.

Throughout a yearly cycle, therefore, the duration of the reproductive period in any population of *L. saccharina*, and the percentage of that population bearing reproductive tissue during the reproductive period, depend on two factors, the type of habitat in which the population is growing and the numbers of the different season and year groups making up the population.

As frond tissue developed from April-May to August-September is cast in all plants of this species between the months from October to March-April, and as the age of the oldest frond tissue in all plants is higher from October to March than from April to September, the maximum production of reproductive tissue will take place in all populations, whatever the type of habitat, from October to March on the frond tissue developed from approximately April to September (Text-fig. 7). It is, therefore, the extension of the reproductive period of a population beyond October to March that is controlled by the two factors, the habitat and the components of a population.

Earlier in this paper, production, longevity and depopulation-rate of the sporophytes were related to bathymetric zone and degree of exposure of the habitat, therefore the components of any population, at any season, depend also on the habitat factor. The nature of the habitat of a population is therefore the controlling factor for the production, or lack of production, of reproductive tissue on the plants during the period from April to September.

The nature and locality of the shore examined by different workers is no doubt responsible for the apparent discrepancy given in the literature in the records of the time of reproduction of this species.

On the British coast, throughout a yearly cycle, the reproductive period of this species is shortest (October to early April) in populations growing on exposed shores in intertidal habitats that dry out at low water of mean spring tides (Text-fig. 7, nos. 2*a*, *b*).

In these habitats, the persistence of just the spring sporophytes (Table III) that first reach maturity during the autumn and winter following their germination (Text-fig. 7, no. 2*a*) and the rapid casting of the frond tissue from April to September in the second-year spring plants (Pl. IX; Text-fig. 8A), so that frond tissue sufficiently old to bear reproductive tissue is not retained by the plants (Table VI; Text-fig. 8A), account for the short duration of the reproductive period.

On exposed shores, but in the populations in the pools and in the sublittoral zone, although the main reproductive period is still October to early April (Text-fig. 7, no. 3*a*, *b*), it is more extended (June to April), as a very small percentage of the populations in these habitats bears reproductive tissue from June to September (Text-figs. 7, no. 3*a*, *b*; 8B). The extension of the reproductive period of the populations growing in these habitats is due partly to the persistence of small numbers of early summer sporophytes in the pools and of small numbers of summer and autumn sporophytes in the sublittoral zone (Table III) that first reach maturity during the summer and autumn following their germination; it is due equally to the retention of frond tissue in at least the sixth month of growth by a small percentage of the second-year spring plants (Table VIII; Text-fig. 8B).

In this species the reproductive period is longest in populations growing on sheltered parts of the coast in both intertidal and sublittoral-zone habitats. Here it extends usually from the middle or end of May until the beginning or middle of April (Text-figs. 7, nos. 4, 5; 9), but sometimes plants can be found bearing reproductive tissue during late April and early May (Text-fig. 7, no. 1). The percentage of plants bearing reproductive tissue is also much higher in these habitats from June to September than on exposed shores, although the period of maximum reproduction still occurs at the same time (Text-fig. 7, nos. 1, 4 and 5).

The slower rate of casting of the distal frond tissue in the older plants in these habitats is partly responsible for the increase in the percentage reproduction during the summer and autumn months (Text-fig. 7, nos. 1, 4); equally important, however, is the persistence of large numbers of summer and autumn sporophytes that start to bear reproductive tissue during the summer and autumn following their germination (Table VII; Text-figs. 7, no. 5; 9), when they are approximately 1 year old.

In most populations of this species growing on the British coast reproductive tissue is not developed by the plants during late April and early May. Two factors are responsible for the absence of reproductive tissue during this period. In some populations, particularly in those growing on exposed shores, the distal frond tissue persisting on the plants during that period is not normally more than 5 months old and consequently it does not develop reproductive tissue (Text-figs. 7, nos. 2, 3; 8A, B). In other populations, usually those growing on sheltered parts of the coast, although distal frond

tissue in the sixth month of growth may be present on the plants during that period, it is still expanding (secondary growth above the 10 cm. level) and therefore does not form reproductive tissue (Text-figs. 7, nos. 4, 5; 9).

The few plants of this species which do bear reproductive tissue during late April and early May have either retained distal frond tissue in the seventh month of growth, or have distal frond tissue in the sixth month of growth that has reached its full expansion and can therefore produce reproductive tissue.

As the peak of secondary growth above the 10 cm. level occurs a month earlier on the Devon coast (February, March) than on the Argyll coast (March, April), there is a higher percentage of plants bearing reproductive tissue during late April and early May on the Devon coast, in habitats in which the plants can retain sufficiently old frond tissue to reach maturity (Text-fig. 7, cf. no. 1 with nos. 4 and 5).

From the above information on the reproductive cycles of populations of this species growing in different habitats it should be possible to estimate the approximate duration of the reproductive period in any population of *L. saccharina* growing on the British coast.

The data that have been accumulated during this work seem to indicate that the development of reproductive tissue in plants of this species is controlled by some factor or factors within the frond tissue of the plant, not by factors external to the plant. Van Overbeck (1940) extracted an auxin from a member of the Laminariales, *Macrocystis pyrifera*, and produced evidence to show that in this species the auxin was a growth hormone. It would be of interest if chemical changes, or an alteration in a hormonal balance, could be traced within the frond tissue of *L. saccharina* over a period of 6 months from the time of formation of the tissue until the tissue approaches maturity in the sixth month of growth.

WEIGHT OF THE SPOROPHYTE

In the literature there is very little information on the quantities of the different *Laminaria* species growing on the coastline of any country. From a Russian survey in July 1931 (Meyer, 1933) the stock of the Laminariales in the White Sea was estimated at 1,500,000 metric tons.

At the same time Kireeva & Schapova (1933) showed that, on the Murman coast in Kolsky Fjord and off Kildin Island, the average weight of a *L. saccharina* plant and of a *L. saccharina* population varied in different regions, the plant from 140 to 470 g. and the population from 4·7 to 5·7 kg./m.^{2}

Tikhovskaya (1940), working on the seasonal variations in the productivity and photosynthesis of *L. saccharina*, calculated that the biomass of *L. saccharina* in the Dalne-Zelenety Bay of the Barents Sea amounts to 4000 metric tons/km.^{2} He found that in August the average weight of a *L. saccharina* plant was 613 g. and that the weight of the *L. saccharina* population varied from 2 to 8 kg./m.^{2},

the weight of the population decreasing gradually towards the shore line from the level of 0·2 m. (height of water level above 0 depth). He also states that with decrease in level below 0·2 m. the plant size increased while the number decreased. The quantity of another species, *L. japonica* Aresch., growing on the coast of the Japanese Sea near Cape Povorotny is given by Gail (1935) as 4000 metric tons/km.^{2}

In the last few years only has any estimation of the quantities of the Laminariales on the British coast been attempted. In 1942 Chapman (1944) made a rapid survey for the Ministry of Supply of the quantities of the Laminariales growing round the coasts of England and Scotland. At the present time a detailed survey of the *Laminaria* resources of the Scottish coast is being made by the Scottish Seaweed Research Association. The results already published (Walker, 1947) show that the average growth of the Laminariales on the sublittoral areas so far surveyed around Orkney (Scapa Flow and Bay of Firth) amounts to just under 4000 metric tons/km.^{2} as against the estimated figure of 1400 metric tons/km.^{2} for plant production in the English Channel down to 70 m. (Atkins, 1923).

Maximum Weight

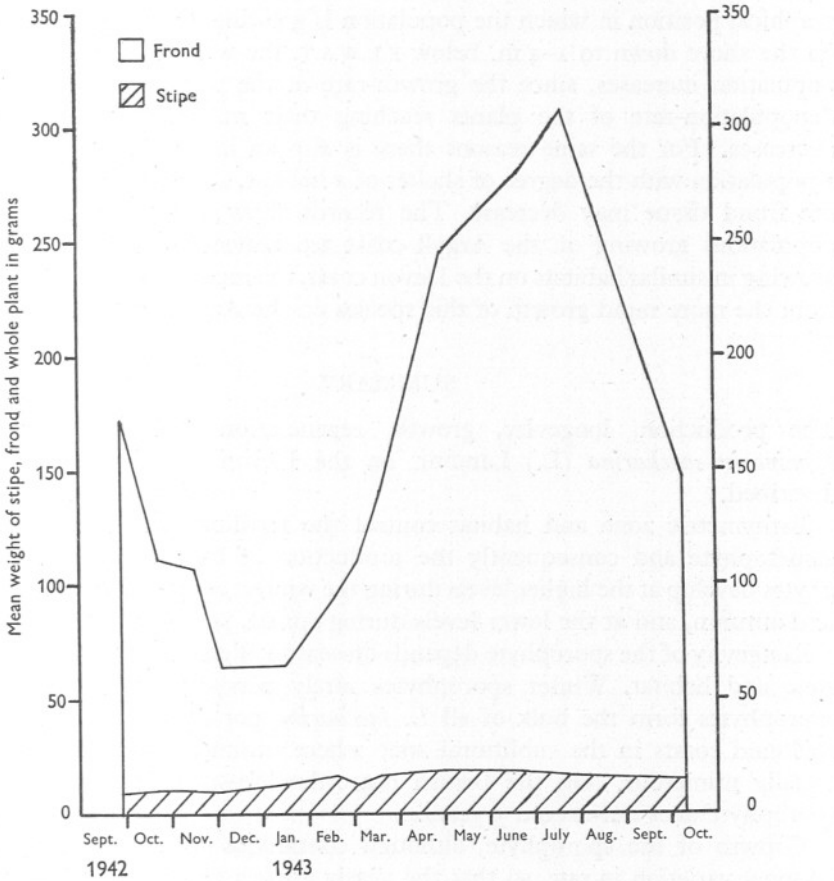
A plant of *L. saccharina* growing on the British coast reaches its maximum weight at the end of the second period of rapid growth when the frond tissue of the plant shows the greatest length and width. Winter- and spring-developed plants are eight to fourteen times heavier at the end of the second period of rapid growth than at the end of the first period of rapid growth; plants developed later in the year, however, do not show such a great difference in weight at the end of the two growth periods owing to the greater growth-rate during the first period of rapid growth. Depending on the bathymetric zone, habitat and geographical position in which the species is growing, the maximum weight of a plant can vary from 0·12 to 2·5 kg.

According to Yendo (1919) and Gail (1935) *L. japonica* and three other Japanese species also reach their maximum weight during the months of May and June in the second year of growth. They state, however, that these species perish after the second sporulation. Their life cycles are therefore similar to that of the *L. saccharina* plants growing in the intertidal zone on exposed parts of the British coast in habitats that dry out at low water of mean spring tides.

Seasonal Variation in Weight

On the British coast there is a seasonal variation in the weight of any *L. saccharina* plant (Text-fig. 10) whatever the age, bathymetric zone, habitat or latitude as there is in the frond size of the plant (Pls. V–VII, IX–XI). This seasonal variation in the weight of the sporophyte is also recorded by the

Russian workers for the White Sea and the Barents Sea. Kireeva & Schapova (1933, 1938) and Tikhovskaya (1940) show that on the Russian coast *L. saccharina* reaches its maximum weight in August and its minimum weight in March. On the British coast, however, *L. saccharina* reaches its maximum



Text-fig. 10. Seasonal variation in the weight of *L. saccharina* plants growing on a raft in Plymouth Sound.

weight in June or July and its minimum weight in December or January (Text-fig. 10), that is, 1–2 months earlier than on the Russian coast. On the British coast the maximum weight is four to six times greater than the minimum weight, whilst on the Russian coast the maximum weight is recorded as seven times greater than the minimum weight (Kireeva & Schapova, 1938).

Variation in Weight with Bathymetric Zone, Habitat and Geographical Position

From the earlier sections of this paper it can be seen that the weight of any *L. saccharina* population depends on the bathymetric zone, habitat and geographical position in which the population is growing. With decrease in level on the shore down to 1–4 m. below E.L.W.S.T. the weight of a *L. saccharina* population increases, since the growth-rate of the plants increases and the depopulation-rate of the plants reaching their maximum weight usually decreases. For the same reasons there is also an increase in the weight of a population with the degree of shelter of a habitat, although the thickness of the frond tissue may decrease. The records show also that *L. saccharina* populations growing on the Argyll coast are heavier than the populations growing in similar habitats on the Devon coast, the increase in weight resulting from the more rapid growth of this species on the Argyll coast.

SUMMARY

The production, longevity, growth, regeneration and reproduction of *Laminaria saccharina* (L.) Lamour. on the Devon and Argyll coasts are described.

Bathymetric zone and habitat control the fertility and longevity of the gametophyte and consequently the production of the sporophyte. Sporophytes develop at the higher levels during the winter, early spring, late summer and autumn, and at the lower levels during spring, summer and autumn.

Longevity of the sporophyte depends on season of germination, bathymetric zone and habitat. Winter sporophytes rarely persist to maturity. Spring sporophytes form the bulk of all *L. saccharina* populations except on very sheltered coasts in the sublittoral zone where summer sporophytes may be equally numerous. On the British coast the life-span of a *L. saccharina* sporophyte does not exceed 3 years.

Growth of the sporophyte, although continuous throughout life, shows seasonal variation in rate, so that the yearly growth can be divided into two periods, one of more rapid growth (January to June) and one of slower growth (July to December). Seasonal change in rate of frond growth is indicated by change in shape of the base and also by the variation in the width of the tissue produced. The rate of growth of the tissue at successive levels up the frond also shows a seasonal variation. Seasonal change in rate of stipe growth is indicated by alternate zones or 'rings' of lighter and darker tissue, the darker being formed during the periods of slow growth. The approximate age of the sporophyte can be assessed from an examination of the holdfast.

The growth-rate changes with the increase in the age of the sporophyte, the maximum rate being reached during the second period of rapid growth. The

rate of growth also varies with change in bathymetric zone, habitat and latitude.

Distal frond tissue is cast continuously throughout the life of a sporophyte, the rate of casting varying with the time of germination and with the habitat. The normal age of the oldest frond tissue is from 5 to 7 months; 9-months-old frond tissue has not been recorded.

Complete regeneration of the frond after cutting occurs only in sporophytes up to the age of 1 year. No regeneration occurs when the whole frond is removed.

Sporophytes first reach maturity when they are from 8 to 12 months old.

For reproductive tissue to develop on a plant the distal tissue present on the frond must be in at least the sixth month of growth. Once reproductive tissue is present on frond tissue in the sixth month of growth, it can arise on frond tissue in the fifth month of growth but not on younger frond tissue.

The percentage of reproducing plants and the duration of the reproductive period in a population depend on the numbers of different season and year groups making up the population and on the habitat in which it is growing.

The maximum weight of the sporophyte is reached at the end of the second period of rapid growth. The sporophyte shows a seasonal variation in weight and also a variation in weight with change in bathymetric zone, habitat and geographical position.

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LUMBRICILLUS REYNOLDSONI N.SP., AN ENCHYTRAEID FROM THE BEACHES OF NORTH WALES

By Helge O. Backlund

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(Plate XIV and Text-figs. 1–4)

Dr T. B. Reynoldson of the Department of Zoology, University College of North Wales, Bangor, found some large enchytraeids on the shores of the Menai Straits. He suspected that it was an undescribed, or at least a rare and interesting species, and kindly sent six specimens to me for further study. I find that the specimens are indeed to be ascribed to a new species, which is here named *Lumbricillus reynoldsoni*, in recognition of the finder's prominent work on the ecology of *Lumbricillus lineatus* Mull. and *Enchytraeus albidus* Henle.

Dr Reynoldson gives the following description of the habitat. 'The worm was found in considerable numbers among decaying seaweed and the underlying gravel at the extreme high tide level along with *Enchytraeus albidus* Henle in the Bangor area of the Menai Straits at the locality known as Gorad-y-Gyt. It occurs all the year round here, and cocoons have been collected during March and April. So far these worms have not been taken from other shores in North Wales although search has been made during general collecting trips.'

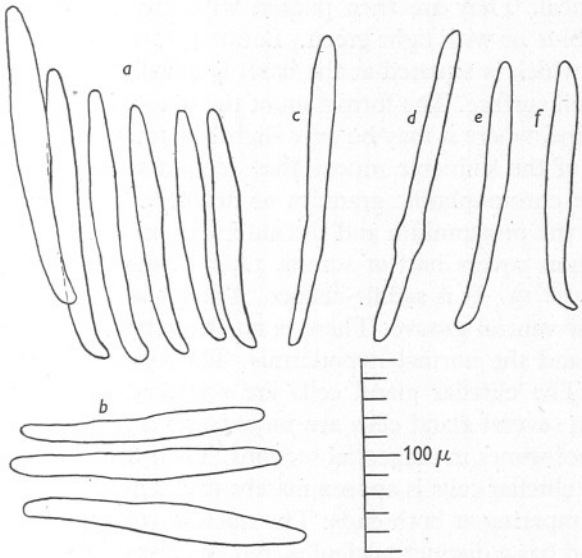
The specimens were excellently preserved. Dr Reynoldson had narcotized them with chloroform vapour and fixed them in Bouin's solution. Three specimens were examined in sections stained with Masson's and Mallory's stain respectively, one specimen was heated in lactic acid.

The length of the mature worm is 40 mm., the width 1·2 mm. The number of somites is about 65. The worm is opaque and light pink from the coloured blood. The segmental grooves are obsolete, while the clitellum is not prominent. The worm tapers at the hinder extremity. The prostomium is small and rounded. The head-pore is situated between pro- and peristomium. The mouth-grooves are shallow on the prostomium, deeper on the peristomium.

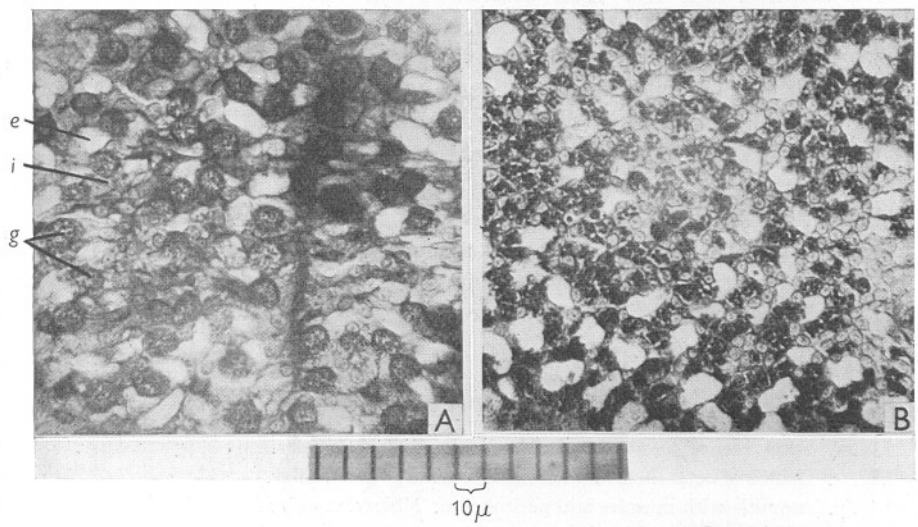
The setae (Text-fig. 1) are almost straight, particularly in the anteclitellar somites. The recently formed setae in the last somites are slightly smaller than the older ones. In the first 25–30 somites there are 5–*6*–7 lateral and 6–*8*–9 ventral setae, then the number decreases to 3–4 lateral and 3–4 ventral setae.

The cuticle is very thin for such a large species, only 1–1·2μ thick.

In the hypodermis there are no regular rows of enlarged gland cells. Instead, the whole hypodermis is scattered with small gland cells (Text-fig. 2A and Plate XIV, fig. 6). In their most active stage these cells are swollen and



Text-fig. 1. Setae (*a*) from somite 25, (*b*) from somite 60, (*c–f*) from various somites.



Text-fig. 2. A. Tangential section through hypodermis of anteclitellar somites; *e*, emptied gland cell; *i*, group of interstitial cells; *g*, active gland cells. The dark stripe is part of a muscle band. Masson stain. Red filter. B. Tangential section through clitellar hypodermis. Stain, filter and magnification as in A. The active gland cells are narrow, columnar. The mucous droplets much larger than in common gland cells.

almost spherical. They are then packed with mucous droplets which stain with aniline blue or with light green. Because of the pressure within the cell the nucleus, which is situated at the base, is usually seen protruding beyond the general cell surface. The formation of the mucus begins in cells of regular columnar shape, where it may be only slightly stainable. When the gland cells are emptied of the stainable mucus they remain swollen and are filled with small, diffuse chromophobic granules or droplets. The gland cells are most numerous in the prostomium and the anterior somites.

The clitellum covers half of somite 11, the whole of 12, and almost the whole of somite 13. It is saddle-shaped. The gland-free surface is, however, only a narrow ventral groove. There is no sharp border between the clitellar hypodermis and the normal hypodermis. The latter changes gradually into the former. The clitellar gland cells are scattered quite irregularly (Text-fig. 2B), often several gland cells are united into a group. These cells appear as irregular polygones in tangential sections. Their diameter is 5–9μ only. The height of the clitellar cells is approximately 50μ. Thus the gland cells are high and narrow, tapering at both ends. The nucleus is always at the narrow base of the cell and has a distinct nucleolus, but the rest of the chromatic matter is less distinct than in the interstitial cells. Instead, the nucleoplasm stains with iron trioxyhaematin. The mucous droplets are large, with a diameter of 1μ. They stain very brightly with light green, less so with aniline blue. The droplets are sharply defined, since the rest of the plasma remains unstained. The emptied cells lose their connexion with the basement membrane and become subspherical. They are situated just under the cuticle. These cells are not really quite empty, since they contain some unstainable, slightly granular matter. Their nuclei have no nucleolus and are little stained. In the narrow interstitial cells the nuclei may be situated at any level, but are usually concentrated near the basement membrane.

The muscle layers are thick. The circular muscles are well-defined bands which protrude into the hypodermis, giving the latter a wavy inner surface. The longitudinal muscles are of an extreme lumbricilline type, long and pointed. In transverse sections the longitudinal muscle bands are almost feathery and show a superficial similarity to those of *Lumbricus*.

EXPLANATION OF PLATE XIV

Fig. 1. Ectal duct of spermatheca with gland cells and muscles. Masson; red filter.

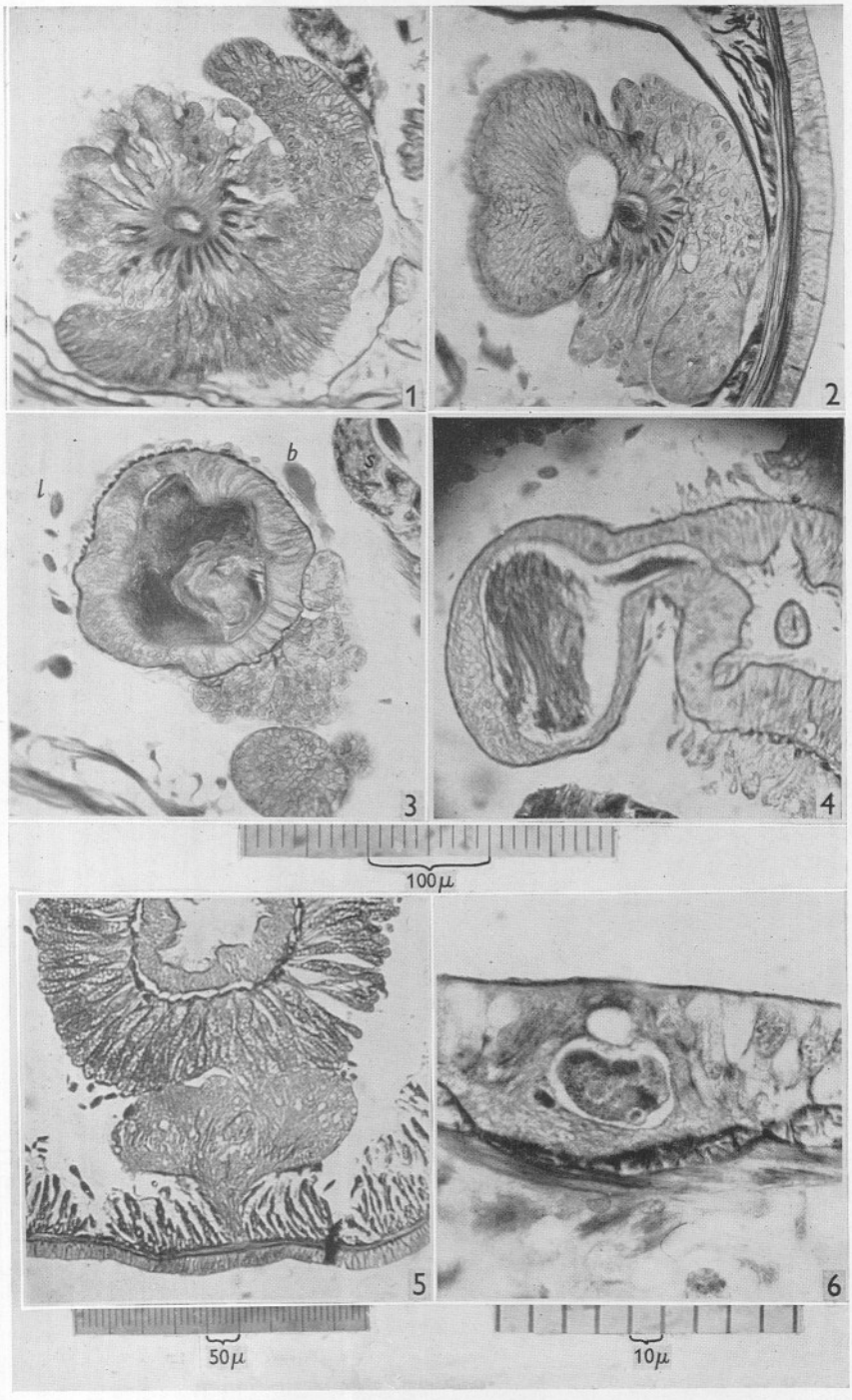
Fig. 2. Orifice of ectal duct into ampulla. Mallory; green filter.

Fig. 3. Ampulla with muscles and peritoneum. *b* blood vessel, *l* lymphocytes, *s* septal gland. Masson; red filter.

Fig. 4. Ampulla, ental duct and oesophagus. In the oesophagus a section through *Anoplophrya* sp. Mallory; green filter.

Fig. 5. Copulatory gland from somite 14. Mallory; green filter.

Fig. 6. Hypodermis with sporozoite in enlarged cell. Masson; red filter.


1
2
b
l
s
3
4
100μ
5
6
50μ
10μ

The peritoneum is highly developed. In many places it consists of several layers of loosely connected, slightly stainable cells and is rather reminiscent of some kind of parenchyma.

The lymphocytes are typical for the genus *Lumbricillus*. The numerous granulocytes are spindle-shaped or ellipsoidal with more or less pointed ends. One end often tapers into a delicate protoplasmic thread, which sometimes is attached to the peritoneum. The cells are filled with minute granules, which stain dark blue-violet in Mallory's, green in Masson's stain. In the spherical nuclei no nucleoli were observed. Aggregations of 5–10 rather small amoebocytes with inclusions of varying size are rather numerous.

There are no peptonephridia or other appendages or widenings of the intestine. The mouth-ridge is large and sharp, the bulbous pharynx is comparatively low. The intestinal epithelium shows several differentiations, but these are too insignificant to have any taxonomic value.

Septal glands occur in segments 4/5 to 6/7; that in 5/6 is the largest. Only the first two pairs fuse in the dorsal line. On the ducts from the glands in 5/6 and 6/7 there are proliferations of glandular tissue, but no real secondary glands.

Chloragogen cells begin in somite 4, but are again missing where the septal glands are at their largest. The chloragogen layer is dense, consisting of long, club-shaped sac-cells, which are only attached to the basement membrane by a narrow stalk (Pl. XIV, fig. 5). Naturally their length varies and reaches 200μ. The maximum width (at the tip) is 20μ. The long stalks contain but few chloragogen granules: most of these are concentrated in the sac-like body of the cell. The granules are small, not exceeding 1μ. They are arranged in a network around and between vacuoles of varying size, up to 12μ in diameter. Probably these vacuoles were filled with fat in the living specimens. The chloragogen granules retain their own yellow-brown colour and stain additionally with iron trioxyhaematin, the surrounding plasma stains slightly with light green. With Mallory's stain the chloragogen material in the body of the cells becomes bright red from acid fuchsin, whereas the small chloragogen granules in the cell stalks are yellow—probably their own natural colour. In the twelfth somite the chloragogen cells are missing; the intestine is covered only with a loose peritoneum of the same kind as on the body walls. Transitional stages between chloragogen cells and peritoneal cells occur.

The brain is 250μ long, 115μ high, and 185μ broad. Its anterior end is convex, the posterior end concave. The first ventral ganglion is large and protrudes in front of the brain connectives.

The first nephridium is situated in segment 6/7. The anteseptalium is small, consisting of the funnel only. The postseptalium is continuous with the terminal ectal duct.

The dorsal blood vessel originates in 14/15. It is enlarged in 14 and 13 and contains here nuclei belonging to a syncytium which is little stainable.

The testes are large, and much lobed. The sperm funnel is slightly bent. It is 750μ long and 280μ wide. The duct is central, 30μ wide. The collar is large but not so wide as the body of the funnel, 200μ only. It is not reflected. The distal end of the sperm funnel is square. The sperm duct is narrow. It is loosely and irregularly coiled and does not extend farther caudad than the penial bulb.

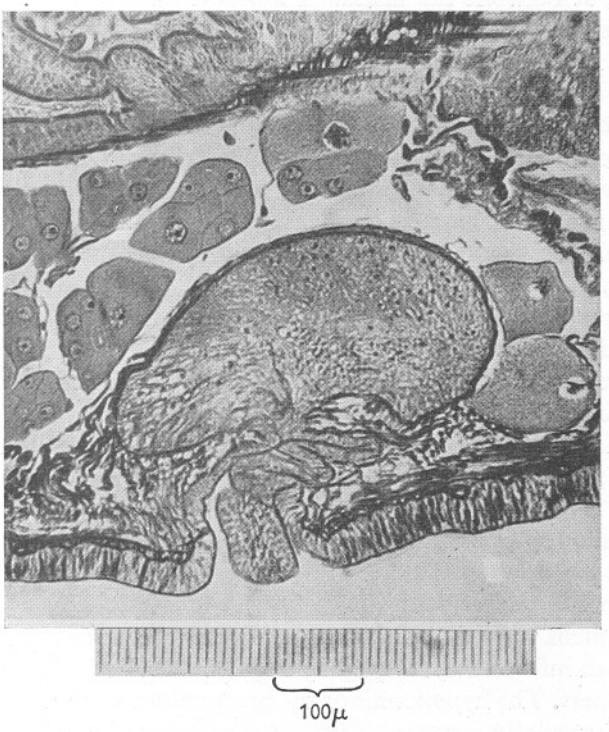
The penial bulb (Text-fig. 3) is strictly lumbricilline, large and covered with a thick muscular coating. It contains a large number of glandular cells in several layers. The penial invagination is very deep and much puckered. The oocytes are confined to somite 12.

The spermatheca (Text-fig. 4; Pl. XIV, figs. 1–4) consists of ectal duct, ampulla, and ental duct. The ectal duct is 140μ long and slightly bent. The lumen is approximately 18μ wide and is bounded by a cuticle which is thicker than the cuticle of the body surface. The walls of the duct consist of long and narrow gland cells. The length of the gland cells may be more than 150μ. In the proximal part, around the duct, there are naturally no intercellular spaces between these gland cells. But distally the cells are united into lobes of some 10–15 cells, the lobes being free from each other. The longest cells are club-shaped, with a narrow proximal neck. Not all gland cells reach the lumen of the duct, some are restricted to the distal parts of the lobes. However, these cells also have narrow extensions, forming ductules, to the cuticle of the duct. These ductules are exceedingly narrow and are visible only as darkly stained, wavy striations (like the ductules in the penial bulb). All nuclei are situated in the distal parts of the cells. The cells stain very lightly while the secreted granules are very small and scarce.

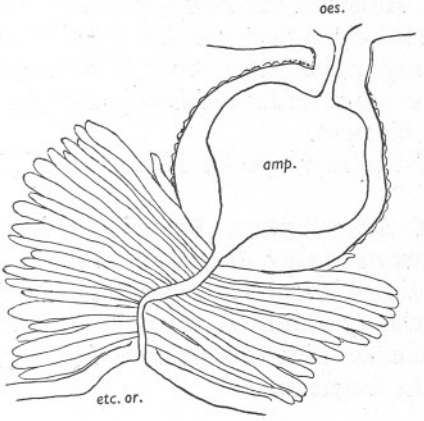
The subspherical ampulla is sharply defined from both the ectal and the ental duct. The length of the ampulla is approximately 290μ, the width 240μ. The walls are 30μ thick in the proximal, 12μ in the distal parts of the ampulla. Thus the lumen is pear-shaped. The cells are non-glandular, columnar in the proximal, cubic in the distal parts. Near the entrance of the ectal duct the inner surface is covered by a thick cuticle, but in the distal parts the inner surface of the ampulla is quite uncovered.

The ental duct is short, only 55μ long and there is a quite wide communication between ampulla and oesophagus. The lumen of the duct is 26μ wide, the total width is 50–55μ. The walls of the ental duct are similar to those in the distal part of the ampulla. In the innermost part of the ental duct the epithelium is ciliated as in the oesophagus.

The spermatheca has a rather interesting and complicated muscle-coating. At the ectal orifice muscles from the circular muscle layer are bent inwards. These muscles follow the ectal duct longitudinally. The muscle bands are broad in the radial direction, flat in the tangential. Thus, in perpendicular sections, the muscles appear as beams radiating from the lumen. The muscles are situated neither on the surface of the gland, nor in the innermost parts near



Text-fig. 3. Sagittal section showing penial bulb with deep invagination and oocytes. Intestine in the upper left corner. Mallory stain. Green filter.



Text-fig. 4. Outline of spermatheca. Schematic drawing with camera lucida.

the cuticle, but between the glandular lobes at the middle of their length. Often the thin parts of the muscles follow the walls of the gland cells closely. Therefore it may be hard to distinguish them from cellular surface-fibrillae. The muscles are continuous with the strong muscles which cover the ampulla. Here these muscles have again the same appearance as the sub-hypodermal circular muscles; they are, however, naturally weaker. On the ental duct the muscles become still weaker, similar to, and continuous with the muscles on the oesophagus. The peritoneal covering is very thin and probably incomplete on the glands of the ectal duct, but quite thick on the ampulla (Pl. XIV, fig. 3).

The elaborate muscle-coating of the spermatheca is a result of the structure of the ectal duct. Naturally, a duct with only glandular instead of epithelial walls must be supported by fibres when it is as large as in *L. reynoldsoni*. Since the fibres of connective tissue do not occur in enchytraeids the spermatheca is strengthened by muscles. I do not think that the muscles function in the emptying of the gland, but probably they do function when sperm is being ejected.

Large copulatory glands exist in somites 14 and 15 (Pl. XIV, fig. 5). The anterior and posterior ends are entirely free, but the median part surrounds the whole ventral nerve cord.

The specimens subjected to me were heavily parasitized. The intestine contained both infusorians, *Anoplophrya* sp. (Pl. XIV, fig. 4), and sporozoans in great numbers. The hypodermis of the prostomium and the first 35 somites held many, irregularly scattered, intracellular sporozoites (Pl. XIV, fig. 6).

Systematic position. Although this new species has almost straight setae it should without doubt belong to the genus *Lumbricillus*.[1] Its main character is the absence of peptonephridia. On account of the lobed testes the species should be placed in the subgenus *Lumbricillus* (= *Pachydrilus*). This subgenus inhabits mainly shore biotopes.

The full name of the new species is thus *Lumbricillus* (*Lumbricillus*) *reynoldsoni*.

The taxonomy of the subgenus *Lumbricillus* is rather complicated. *L. reynoldsoni* is, however, easily distinguished from all earlier described species. It is outstandingly large and the combination of characters of setae, spermatheca and copulatory glands do not occur elsewhere. This species has many characters in common with *L. pagenstecheri* (Ratz.), but the differences are easily seen from the diagnosis.

[1] On the authority of Dr Černosvitov I have earlier (Swedish Enchytraeida I and II, *Lunds Univ. Arsskrift* N.F. XLII, 13 and XLIII, 8) used the generic name *Pachydrilus*. On the suggestion of Dr Reynoldson I have looked through the older literature but could not find out why Černosvitov used the more recent name *Pachydrilus* Claparède 1889 instead of *Lumbricillus* Orsted 1861. Probably Černosvitov in his turn has followed his eminent compatriot Vejdovsky.

Diagnosis. Length 40 mm. Somites about 65. Blood pink. Clitellum saddle-shaped, not prominent, with small, irregularly scattered gland cells. Setae almost straight, L 5–7, V 6–9. Posterior end of brain concave. Nephridia with anteseptalium consisting of funnel only, with terminal ectal duct. Origin of dorsal blood vessel in 14/15. Penial bulb lumbricilline, with deeply puckered invagination. Spermatheca with subspherical ampulla sharply defined from both ectal and ental ducts. Ectal duct consists of large gland cells. Copulatory glands in 14 and 15 surround ventral nerve cord.

The type specimen (longitudinally sectioned) is in the author's collection at the Zoological Institution of Lund.

ON THE SEASONAL ABUNDANCE OF YOUNG FISH. IX. THE YEAR 1947

By P. G. Corbin, B.A.

Zoologist at the Plymouth Laboratory

(Text-figs. 1–3)

The 1947 records of the seasonal abundance of the pelagic young stages of teleosteans in the plankton of Plymouth off-shore waters are a continuation of the series of observations made by Mr F. S. Russell (1930–47). The form of the previous reports is retained. The dates on which collections were made are given in Table I, and the monthly average catches of young fish in Table II. The fortnightly averages of all young fish less clupeids are shown in Fig. 1, together with the corresponding curve for the period 1930–34.

1947 was the first year since the war in which collections were made throughout the twelve months. It is relevant, therefore, to relate the 1947 records to the interrupted observations of the years 1939 and 1946. Describing the conditions of 1939, Russell (1940) states that '...the year 1939 has been the worst yet recorded and sets a new low limit to the production of fish'. As a result of the break in observations due to the war, he says '...we may never know what point the trough of the decline may reach'. Reporting on the 1946 records after the resumption of observations, he writes 'The 1946 collections were started too late to include the main period of abundance of young fish resulting from the spring spawners, but they afford evidence that as regards the summer spawners at any rate there is no significant change from the conditions existing in 1939. We cannot say what the conditions have been during the intervening years, but analyses of phosphorus content of the water during each winter in the period 1939–46 tend to show that conditions have remained much the same as they are at present, and that it is unlikely that there has been any large incursion of rich water characterized by *Sagitta elegans* which supports a large population of young fish.' (Russell, 1947.)

In 1947, the total of all species of young fish was the lowest recorded since the observations started. All summer spawners were extremely scarce. Spring spawners were present in only slightly greater numbers, occurring mainly in two very small peaks in the second half of February and the second half of May. *Gadus luscus* and *Chirolophis galerita* contributed chiefly to the February peak, while the May peak was largely due to *Gadus merlangus* and *Callionymus* spp. It is of interest to record the occurrence of small numbers of young plaice, *Pleuronectes platessa*, in February. The young stages of this species were first taken in the Plymouth collections, also in small numbers, in

TABLE I. DATES ON WHICH COLLECTIONS WERE MADE, 1947

All 2 miles east of Eddystone, unless otherwise stated

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
29	2	6	3	23	2	7	11	1	6	13	3
..	10	12	8	27	16	14	18	10	13	19	10*
..	17	17	17	29	24	22	25	29	21	25	19
..	27	..	25	..	..	28	..	..	27	..	22
..	..	..	..	..	..	..	..	..	..	..	29

* Station E 1.

TABLE II. MONTHLY AVERAGE CATCHES OF POST-LARVAE PER HALF-HOUR

Oblique hauls with 2 m. ring-trawl, 1947

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Σ
Total young fish	..	42	76	27	65	35	19	46	27	62	7	5	411
Ditto, less Clupeids	..	24	8	7	54	25	7	15	6	1	1	+	148
All Clupeid spp.	..	18	67	20	11	10	12	32	21	60	7	5	263
Clupea harengus	..	..	..	..	..	..	..	..	..	..	..	..	..
Gadus pollachius	..	..	..	1	+	..	..	..	..	..	..	..	1
Gadus merlangus	..	..	..	1	22	6	1	..	..	..	..	..	30
Gadus minutus	..	..	2	1	2	..	..	..	..	..	..	..	5
Gadus luscus	..	9	1	..	..	..	..	..	..	..	1	+	11
Gadus callarius	..	..	..	..	..	..	..	..	..	..	..	.	..
Onos spp.	..	..	..	+	3	13	1	..	..	..	..	..	17
Molva molva	..	..	..	..	+	..	..	..	..	..	..	..	+
Merluccius merluccius	..	+	..	..	..	..	..	..	..	..	..	..	+
Raniceps raninus	..	..	..	..	..	..	..	+	..	..	..	..	+
Capros aper	..	..	..	..	..	..	..	..	..	..	..	..	..
Zeus faber	..	..	..	..	..	..	..	..	..	..	..	..	..
Arnoglossus spp.	..	..	..	..	..	..	..	1	1	+	..	..	2
Rhombus spp.	..	..	..	..	..	..	..	+	+	..	..	..	+
Scophthalmus norvegicus	..	..	..	..	5	..	..	..	..	..	..	..	5
Zeugopterus punctatus	..	..	..	..	2	..	..	..	..	..	..	..	2
Zeugopterus unimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Pleuronectes platessa	..	2	..	..	..	..	..	..	..	..	..	..	2
Pleuronectes limanda	..	..	..	..	4	1	..	..	..	..	..	..	5
Pleuronectes flesus	..	..	..	1	..	..	..	..	..	..	..	..	1
Pleuronectes microcephalus	..	..	..	..	1	..	..	..	..	..	..	..	1
Solea vulgaris	..	..	..	+	+	..	..	..	..	..	..	..	+
Solea variegata	..	..	..	..	1	..	..	..	..	..	..	..	1
Solea lascaris	..	..	..	..	..	..	..	+	..	..	..	..	+
Solea lutea	..	..	..	..	..	..	..	..	..	..	..	..	..
Serranus cabrilla	..	..	..	..	..	..	..	..	..	..	..	..	..
Caranx trachurus	..	..	..	..	..	..	..	1	2	..	..	..	3
Mullus surmuletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Morone labrax	..	..	..	..	..	..	..	..	..	..	..	..	..
Ammodytes spp.	..	+	+	1	..	+	..	+	..	..	..	..	2
Ammodytes lanceolatus	..	+	..	..	2	2	+	..	..	..	..	..	4
Cepola rubescens	..	..	..	..	..	..	..	..	1	..	..	..	1
Callionymus spp.	..	..	..	..	11	3	1	4	1	+	..	..	20
Labrus bergylta	..	..	..	..	..	..	+	..	..	..	..	..	+
Labrus mixtus	..	..	..	..	..	..	..	..	..	..	..	..	..
Ctenolabrus rupestris	..	..	..	..	..	..	1	2	+	..	..	..	3
Crenilabrus melops	..	..	..	..	..	..	..	..	..	..	..	..	..
Centrolabrus exoletus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachinus vipera	..	..	..	..	..	..	..	+	..	+	..	..	+
Scomber scombrus	..	..	..	..	..	..	..	3	+	..	..	..	3
Gobius spp.	..	..	..	..	..	..	..	..	..	..	..	..	..
Lebetus scorpioides	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius ocellaris	..	..	..	..	..	..	..	..	..	..	..	..	..
Blennius pholis	..	..	..	..	..	..	+	+	+	..	..	..	1
Blennius gattorugine	..	..	..	..	..	..	2	2	1	..	..	..	5
Chirolophis galerita	..	12	4	..	..	..	..	..	..	..	..	..	16
Agonus cataphractus	..	..	..	..	..	..	..	..	..	..	..	..	..
Trigla spp.	..	..	..	..	..	..	..	+	..	+	..	..	+
Cottus spp.	..	..	..	1	..	..	..	..	..	..	..	..	1
Liparis montagui	..	..	..	..	+	..	..	..	..	..	..	..	+
Lepadogaster bimaculatus	..	..	..	..	..	..	..	..	..	..	..	..	..
Lophius piscatorius	..	..	..	..	..	..	..	..	..	..	..	..	..
Pipe fish	..	..	..	..	..	..	..	..	..	..	..	..	..

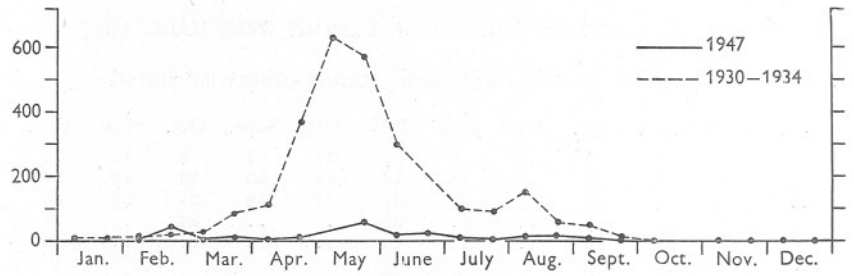


Fig. 1. Curves showing the average catches in half-hour oblique hauls with the 2 m. stramin ring-trawl for each fortnight for all young fish, excluding clupeids, in 1947 (————), and the same average over the period 1930–34 inclusive (– – – –).

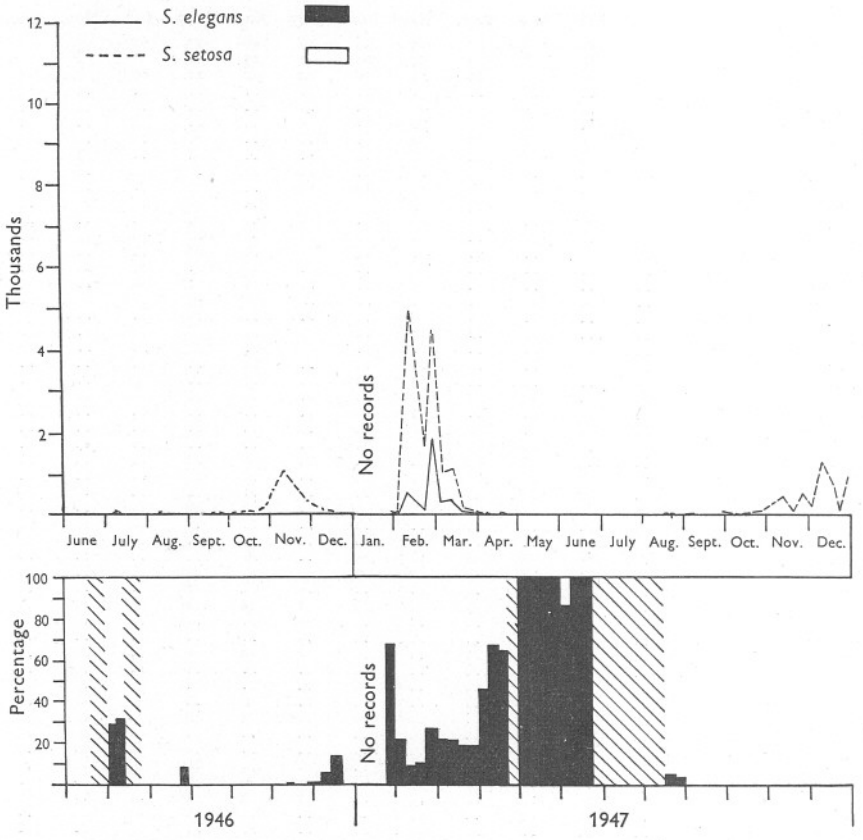


Fig. 2. Above, curves showing the actual abundance of *Sagitta elegans* (————) and *S. setosa* (– – – –) in half-hour oblique hauls with the 2 m. stramin ring-trawl during the period June 1946 to December 1947. Below, the percentage composition of the *Sagitta* populations during the same period: *S. elegans*, black; *S. setosa*, white; no *Sagitta*, hatched. (Continued from Russell, 1947, p. 607, fig. 2.)

February and March, 1939 (Russell, 1940). Since then this low incidence has evidently been maintained in the area. None was, however, recorded in 1946, as collecting was not resumed until June, well after the end of the spawning season of the plaice. The 1947 total (1403) of all species of young fish for the whole year was only 16% greater than the 1946 total (1203) for the seven months period, June to December. It is only too evident that the decline in production of young fish continues without sign of recovery

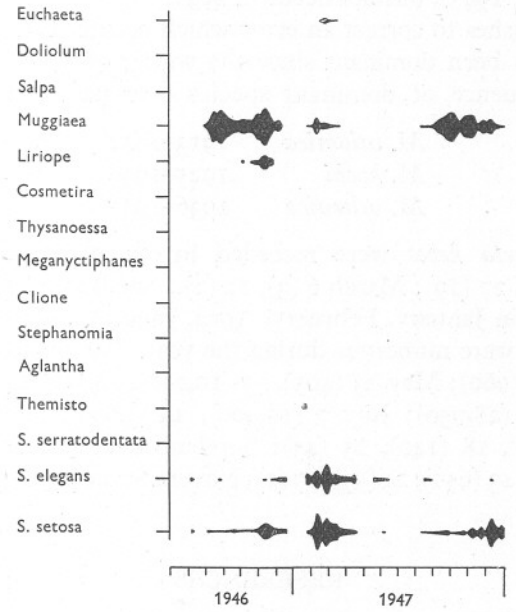


Fig. 3. Diagram showing the occurrence of the various plankton indicators in the collections off Plymouth during the period June 1946 to December 1947. The *Muggiaea* were all *M. atlantica* with the exception of a very few *M. kochi*, generally less than 1%, which occurred during August and September, 1946. (Continued from Russell, 1947, p. 607, fig. 3.)

thus fully bearing out the observations of the incomplete year of 1946 and the deductions from the 1939–46 winter phosphate data.

Plankton indicator species (Figs. 2, 3) showed no great change from the conditions of 1946 when there was a notable scarcity of plankton organisms. *Sagitta setosa*, although never numerous and almost completely absent during May–July, generally predominated over *S. elegans*. The high proportion of *S. elegans* in May and June (lower part of Fig. 2) was not in fact due to large catches of this species (upper part of Fig. 2); the maximum haul during this period contained only 17 specimens of *S. elegans*. In April the numbers of both species of *Sagitta* were similarly very low.

Dr L. H. N. Cooper has kindly provided the information that phosphate values remained poor throughout the year. Towards the end of February, however, there was evidence of some richer water in the neighbourhood; the values at Eddystone were noticeably higher than those at E 1, 10 miles farther out, and the plankton catch was also richer.

Muggiaea atlantica was present in considerable though not exceptional numbers from January to March, and again from August to December; it was absent from April to July. *M. kochi*, which was present in small numbers in 1946 (Russell, 1947), did not occur in 1947.

Mr Russell wishes to correct an error which occurred in this latter paper; *M. atlantica* has been dominant since the winter of 1936, and not 1926 as given. The sequence of dominant species over past years is here summarized:

M. atlantica	1913–1924
M. kochi	1925–1936
M. atlantica	1936–1947

A few *Euchaeta hebes* were recorded in the early part of the year: February 17 (2), 27 (19); March 6 (3), 12 (1). Small numbers of Euphausian larvae occurred in January, February, April, June, August and November.

Pilchard eggs were numerous during the year. The following catches were made: April 25 (960); May 23 (405), 27 (10,200), 29 (12,700); June 2 (6450), 16 (14,650), 24 (28,950); July 7 (15,000), 14 (4600), 22 (4750), 28 (43); August 11 (580), 18 (140), 25 (45); September 1 (41), 10 (680), 29 (65); October 6 (172), 13 (650), 21 (53), 27 (2); November 13 (1), 25 (4); December 10 (5), 22 (4).

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THE RELATION OF THE SUBSTRATUM TO THE METAMORPHOSIS OF *OPHELIA* LARVAE

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(Plates XV–XVII)

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Introduction

It has previously been shown for the pelagic larvae of more than one species of polychaete (Wilson, 1932, 1937; Day & Wilson, 1934) that there is a period of time varying from a few days to several weeks during which the fully developed larva will metamorphose whenever it comes into contact with a substratum suitable for adult life. During this period the larva is able to test the varying types of bottom over which the currents carry it and to select and metamorphose in the particular kind of mud, sand or gravel that forms the normal habitat of the species. The natural processes of development thus do not force metamorphosis to take place at some definite critical stage in the growth of the larva. It is the external environment, or some feature of it, which stimulates the larva to change from an active free-swimming organism to a sluggish semi-sedentary worm buried in the bottom.

The power of selection is likely to be most strongly developed in species restricted to particular kinds of bottom soil. It would obviously not be so important to a species capable of inhabiting a wide range of bottoms, but would be an invaluable factor in aiding the survival of those confined to one special kind of sand or mud. *Ophelia bicornis* Savigny is such a species; it appears to be confined to loose, clean sand in which few other animals are present. It is abundant in certain parts of the Exe estuary, notably on the Bullhill Bank and the Polesands, where it has flourished since at least the beginning of the century, Allen & Todd (1902) having found it in large numbers in the same locality nearly fifty years ago. For a chart of the locality reference should be made to their paper. The development of this species is described separately (Wilson, 1948). In this paper are recorded the results

of experiments designed to test the assumption that the larvae would exhibit a marked preference for sand from the adult habitat and would not readily undergo metamorphosis if other sands, or none at all, were supplied. This having proved true, later experiments were devoted to an attempt to discover how the larvae distinguish between various kinds of sand and to show that actual selection can take place, to some extent at least, in the unnatural confines of a glass dish. *Ophelia* larvae proved very suitable on the whole for experiments of this nature. Apart from their strongly marked reaction to various kinds of bottom they live well crowded in small dishes, and it appears unnecessary to supply food, for though some flagellates were added occasionally their presence does not seem to have made any difference. They are ready to metamorphose within the fortnight, a great advantage over larvae requiring a long rearing period before being ready to settle, and they are just large enough for the main features of the metamorphosis to be visible with a high-power dissecting binocular. The photomicrographs by electronic flash reproduced in Plate XV, figs. 1–3, give a fairly good impression of the appearance of the various stages alive among sand grains from the Bullhill Bank. Ideally the larvae should be just a little larger, as they are undoubtedly difficult to find in most sands until they move. When sand is first removed from an experimental dish, and strewn underwater in a glass tray for searching, the metamorphosed young worms curl up and tend to keep still for a time. After some minutes they begin to crawl about again, and it is then that they are most easily found. Moreover, being smaller than many of the sand grains they are often concealed from view unless active. Their chief drawback is their power of adhesion, strongly developed in the later stages, which causes them to stick to the surface film, to glass, to cotton fragments (Plate XV, fig. 4) and other debris, and to one another by the mucus they secrete. At first they pull themselves free, but later on are unable to do so in the quiet water of a dish. The practical difficulty of supplying some substitute for the strong currents of their natural environment was not overcome in these experiments.

Worms were collected and fertilizations made as have already been described in another paper (Wilson, 1948). The methods adopted will be described under each experiment.

The Preliminary Experiments of 1946

Experiment 1

The results of an early experiment to compare the reactions of larvae in the presence of sand to larvae kept in clean dishes are shown in Table I. Two finger bowls, each containing numerous larvae from the same fertilization, were stood side by side so that as far as possible each was under the same conditions of lighting and temperature. To one bowl sand from the Polesands was added. The water in the bowls was unfiltered outside sea water, and

it contained numbers of small diatoms, flagellates, etc. Little attention was paid to this preliminary experiment, because during the period that it was running the main embryological features of the development were being worked out, but the bowls were examined from time to time. It will be seen that larvae in the bowl with sand soon metamorphosed, whilst the great majority in the clean bowl did not do so. On 6 May the newly metamorphosed worms were crawling actively among the sand grains and seemed particularly healthy in comparison with the unmetamorphosed larvae and the few partially metamorphosed ones sticking to the bottom of the clean bowl. Conditions were similar on 13 May. Owing to pressure of other work these bowls were not disturbed again until 6 June, when it was found, with some astonishment, that the clean bowl still contained many unmetamorphosed larvae which, although stuck to the bottom with the anal papillae, swam when released.

TABLE I. EXPERIMENT 1

(Begun 27. iv. 46 with larvae from a fertilization of 18. iv. 46.)

	Clean bowl	Dish containing Polesand sand	Polesand sand
29. iv. 46	Unmet.	—	? Meting
6. v. 46	Majority unmet.; a few have lost their prototrochal cilia	—	Majority metd
13. v. 46	Majority unmet.	—	All metd
6. vi. 46	Some dead, but many unmet. with strong prototrochs and often telotrochs. Some larvae removed to small dish containing sand	Unmet. larvae introduced from clean bowl	All metd
12. vi. 46	Many dead but living larvae still with prototrochs, telotrochs and sometimes apical tufts	Sand searched; found 21 metd or meting, 2 unmet. and 2 dead larvae	Not examined
5. vii. 46	All dead	All dead	All dead

The following contractions are used in tables: metd, metamorphosed; meting, metamorphosing; unmet. unmetamorphosed; *c.* approximately; *d*, dead.

There was considerable algal growth on the sides and bottom of the bowl testifying to its age, but the bowl was unusually healthy and there were no ciliates visible in spite of the remains of several dead larvae. The sand bowl, on the other hand, was much infected with ciliates, but in the sand there were numerous young worms with long bristles, although still only at the three-setiger stage beyond which none has so far been reared. On this date an uncounted number of unmetamorphosed larvae were removed from the clean bowl and placed in a smaller dish containing Polesand sand. Six days later a search of this sand revealed that the majority had metamorphosed or were metamorphosing, whilst in the clean bowl, in spite of many further deaths, there were still larvae with prototrochs, telotrochs and sometimes apical tufts. Thus, 7 weeks after fertilization, larvae were still able to swim and to

metamorphose, given suitable sand conditions; this, although other larvae from the same fertilization had completely metamorphosed some 5 weeks previously.

There is no doubt that the larvae fertilized on 18 April 1946 were one of the healthiest cultures I have had. They were much used in working out the details of the development and in making the drawings published in the previous paper (Wilson, 1948). I have not since been able to keep larvae unmetamorphosed and healthy over such a long period of time, but quite early in the work it was noted that the healthier the culture the more definite are the reactions of the larvae to the presence or absence of suitable sand. Unhealthy larvae are much more liable to start metamorphosing without sand; particularly do they lose cilia and become unable to swim. This fertilization of 18 April was, on 13 May, the subject of a special note contrasting its health most favourably with other cultures in being at that time. This fertilization was made from worms collected at Exmouth on 13 April and sent to Plymouth by rail.

Experiment 2

Sixty swimming larvae 9 days old were placed in each of three dishes, respectively the clean control, a dish with sand from the Bullhill Bank, and a dish with flocculent mud from Salcombe (Table II). On examination 5 days later only fifty-two larvae were found in the clean control, but fifty of them were unmetamorphosed. In the Bullhill sand twenty-four metamorphosed young worms were found together with seven unmetamorphosed and two dead, one of the latter possibly metamorphosed. In the mud, in spite of a careful search, protracted over 3 hr., only five larvae were accounted for and only one of them was metamorphosed. Three days later the remaining larvae in the clean control were still unmetamorphosed.

TABLE II. EXPERIMENT 2

(Begun 29. v. 46 with larvae from a fertilization of 20. v. 46.)

	Clean dish	Bullhill sand	Salcombe mud
29. v. 46	Unmet. 60	Unmet. 60	Unmet. 60
3. vi. 46	Metd 1 Unmet. 50, *d* 1	Metd 24 Unmet. 7, *d* 2	Metd 1 Meting 2 Unmet. 1, *d* 1
6. vi. 46	All unmet.	Not examined	Not examined

The discrepancy between the numbers of larvae put into each dish and the number found is easily explained. Nine-days-old larvae stick readily to any solid object, and very likely some of them were lost in the pipette and never got into the dishes at all. Too much sand and mud were used in this experiment, making it extremely difficult to carry out a complete search. Larvae are especially easily concealed in the mud, but, nevertheless, it seems highly probable that in the mud the majority were smothered and died.

The difficulty experienced in transferring known numbers of larvae from one dish to another, and more especially in finding them all again in even very small quantities of sand or mud, made it necessary to adopt a somewhat easier technique. It was thought that if a comparatively large, though unknown, number of larvae were put into each experimental dish, it would be sufficient for the purpose of the experiment to recover only a fraction of them. Any marked difference in reaction to various types of bottom deposits would be shown by the proportions of metamorphosed to metamorphosing and unmetamorphosed larvae among those recovered by random sampling. It would not be necessary to search the whole of the sands or mud; this would result in a great saving of time and labour. As it turned out even this method demanded a great expenditure of time and effort, and it was physically impossible for one person to do more than was done by working long hours whilst the experiments were in progress. The results, however, were on the whole satisfactory for the purpose in hand, and marked differences in settlement reactions to the various soils were clearly shown.

Experiment 3

This was the first of the experiments in which tests were made of a number of different types of bottom deposits. Small glass dishes approximately 3 cm. in diameter were thinly strewn with the deposits to be tested. The deposits were sterilized by boiling and well washed in filtered sea water before being used. The dishes were put all together on black paper on a large enamel tray, covered with glass covers and placed in a comparatively cool place. A considerable but unknown number of larvae were put into each. The larvae were 8 days old and were showing the first signs of settling. The experiment is summarized in Table III.

On 21 June, 8 days after the start of the experiment, none of the larvae in the clean dish had metamorphosed. They were attached by their anal papillae to the bottom of the dish, to the surface film, or to cotton fragments or other debris, sometimes in clusters. Almost all had prototrochs and telotrochs, but one or two were seen which had lost the cilia. When water was squirted at them with a pipette the larvae came off the bottom and swam about for a time. In contrast with this was the condition in the dish containing Bullhill sand (Pl. XVI, fig. 1); here, except for a few unmetamorphosed larvae on the surface film, the sand was alive with metamorphosed young worms with long bristles. In a few minutes thirty were counted, but there were many more. One unmetamorphosed and two metamorphosing larvae were also found. It was quite evident that the great majority of the larvae in this dish had metamorphosed, almost the only unmetamorphosed ones being stuck to the surface film. On the other hand, the dish with a few grains of Bullhill sand sprinkled over the bottom contained no metamorphosed larvae, though about 10% had lost or were losing the prototrochal cilia, generally the first stage in meta-

morphosis. The fine 'Gritty' sand (Pl. XVII, fig. 3) consisting of particles of an angular nature with sharp edges and corners had many larvae in or on it, but not one had metamorphosed, although sixteen had lost their prototrochal cilia and may have been beginning to metamorphose. A hundred unmetamorphosed larvae were actually counted and there were still more left in the sand. In the shell gravel a small proportion had metamorphosed and rather more were metamorphosing though a large majority were unmetamorphosed. The mud, as usual, was difficult to search, but in 2 hr. forty-seven unmetamorphosed larvae were seen. Four of these had lost the cilia of the prototroch, but it is doubtful whether they were actually metamorphosing. Not a single metamorphosed worm was found in this dish.

TABLE III. EXPERIMENT 3

(Begun 13. vi. 46 with larvae from a fertilization of 5. vi. 46.)

	21. vi. 46		2. vii. 46
Clean dish	Unmet. *c.* 150	—	Many dead. A few living unmet.
Bullhill sand	(a) Unmet. 10	(c) Metd 30 Meting 2 Unmet. 1	Good number metd, healthy. 1 or 2 unmet.
Bullhill sand (a few grains only)	(a) Unmet. 25	(c) Metd 0 Possibly meting 10 Unmet. 80–90	Mainly dead or dying, unmet. A few may be partially metd
Fine 'Gritty' sand	(a) Unmet. 12	(c) Metd 0 Meting 16 Unmet. 100	None properly metd, but a fair number possibly meting
Shell gravel	(a) Unmet. 6	(c) Metd 4 Meting 29 Unmet. 60	Several metd, a few meting and a few unmet. Some dead.
Salcombe mud	(a) Unmet. 4	(c) Metd 0 Meting 0 Unmet. 47	None seen

(a) on surface film; (c) in gravel, sand or mud.

After the examination on 21 June all the counted larvae and deposits were returned to their respective dishes. On 2 July a further, but briefer, examination was made. The results are summarized in Table III and do not need a detailed explanation.

This experiment shows clearly that larvae will settle readily in Bullhill Bank sand and there metamorphose at an age when they will scarcely do so at all in other deposits. The fact that larvae on the surface film only a little distance above the sand do not metamorphose at the same time as those in it seems to indicate that physical contact with the sand is the main stimulus to metamorphosis. A few thinly scattered and isolated grains of this sand are less effective in bringing about metamorphosis than a deposit of the coarser particles of shell gravel.

Experiment 4

In order to investigate more fully the relation between the physical character of the bottom deposit and metamorphosis a bigger experiment along similar lines to that of Exp. 3 was undertaken. Except for the omission of mud the same types of bottom were repeated with, in addition, several new natural and artificial deposits. Before the actual results set out in Table IV are considered these need some explanation.

Penrhyn Bay sand (Pl. XVII, fig. 1) came from a shore in north Wales where, to the best of my belief, *Ophelia* is absent. It is similar in many respects to Bullhill Bank sand (Pl. XVI, fig. 1), the grains generally being well rounded, though on the whole smaller (see analysis, p. 736), and it contains a considerably higher portion of shell fragments. Eddystone shell gravel consists mainly of relatively large and worn shell fragments; they were well washed so as to be much cleaner than they are in nature. The fine 'Gritty' sand has already been described. The other bottoms were more artificial in nature: Bullhill sand mixed with a roughly equal proportion by volume of well-washed Carborundum grit No. 120 (Pl. XVII, fig. 4); the Carborundum grit alone; Bullhill sand cemented in a single close layer to the bottom of a dish with Murrayite cement, so that each grain was immovably fastened by its base though in contact with neighbouring grains; fragments of broken No. 1 cover-glass; glass wool in a fairly thick layer on the bottom of the dish; fine capillary tubing broken up and in a heap; similarly with coarser tubing; finally, lattices made of criss-crossed strips of No. 1 cover-glass and rather thicker glass. The strips were crossed in layers at right angles and cemented together with Murrayite cement at the points of contact. The larvae could thus get in between the horizontal layers of glass separated by a distance equal to the thickness of the glass used. These thicknesses were: for No. 1 cover-glass about 180 μ; for the thin glass about 330 μ. The larvae used in this experiment came from a very successful fertilization made on 1 July. Almost 100% of the eggs developed and the larvae were very healthy. The experiment was started on 6 July at a time when all the larvae were swimming freely in their finger bowls. They were at a stage when the first two setigers have bristles, but those of the third setiger have not appeared. A large but unknown number of larvae were put into each of the small experimental dishes of approximately 3 cm. internal diameter. As before, these were all covered and stood together on black paper in a cool place not too strongly illuminated.

Two days later the dishes were examined as closely as possible without removing the deposits from the bottom. In almost every dish the great majority of the larvae were swimming actively, but in the dish with Bullhill sand few were swimming, and it was seen that the majority were in the sand metamorphosing or metamorphosed, the latter crawling actively among the sand grains. They already had the characteristic long bristles which none of

TABLE IV. EXPERIMENT 4

(Begun 6. vii. 46 with larvae from a fertilization of 1. vii. 46.)

	8. vii. 46	11. vii. 46			
Clean dish	Almost all swimming. A few stuck to bottom	Some swimming, majority sticking on surface film and bottom, all unmet.			Very healthy
Bullhill sand	A few swimming, but majority in sand meting and metd	(a) Metd 1 Meting 1 Unmet. 15	(b) None	(c) Metd 50+ Meting 0 Unmet. 4	Mainly very healthy
Penrhyn Bay sand	Majority swimming. A few in sand unmet.	(a) Unmet. 35	(b) 15 at least	(c) Metd 20, *d* 2 Meting 11, *d* 3 Unmet. 43, *d* 4	All living fairly healthy
Eddystone shell gravel	All swimming	(a) Unmet. 50	(b) A good number	(c) Metd 1 Unmet. many	Very healthy
Fine 'Gritty' sand	All swimming	(a) Unmet. 6	(b) 97 at least	(c) Metd 5 Meting 7 Unmet. 32	Healthy
Bullhill sand and Carborundum	Majority swimming. A few in mixture, one metd	(a) Unmet. 28	(b) 16	(c) Metd 3 Meting 6 Unmet. 67+	Very healthy
Carborundum	Majority swimming. None metd	(a) Unmet. *c.* 60	(b) 50+	(c) Many unmet.	Very healthy
Bullhill sand cemented in a single layer	1 or 2 swimming, others on surface film or in sand	(a) Unmet. 12	(b) 12	(c) Metd 1 Meting 0 Unmet. 56	Healthy
Broken cover-glass	Majority swimming. Some among fragments. A few metd	(a) Unmet. 7	(b) 4	(c) Metd 8 Meting 2 Unmet. 116	Healthy
Glass wool	1 or 2 swimming. Majority in wool unmet.	(a) Unmet. 10	(b) None	(c) Metd 4 Meting 1 Unmet. 68, *d* 2	Living larvae healthy
Broken fine capillary glass tubing	Majority swimming. Some amid tubing unmet.	(a) Unmet. 32	(b) 2 or 3	(c) Unmet. *c.* 100	Healthy
Broken coarse capillary glass tubing	Almost all swimming	(a) Unmet. 7	(b) None	(c) Unmet. *c.* 100	Healthy
Lattice of No. 1 cover-glass	Majority swimming. Some in lattice unmet.	(a) Unmet. *c.* 60	(b) 2 or 3	(c) All unmet. on bottom of dish or in and about lattice	Healthy
Lattice of thin micro-slide	Majority swimming, some in lattice unmet.	(a) Unmet. 60	(b) 2 or 3	(c) All unmet. on bottom of dish or in and about lattice	Healthy

(a) on surface film; (b) swimming freely; (c) in bottom deposit.

the swimming larvae possessed. Even in the cemented Bullhill sand the larvae were down amid the grains, though here only one larva was seen to be probably metamorphosing, all the others were unmetamorphosed. The glass-wool had attracted, or trapped, many but none was metamorphosed. Amid the broken cover-glass, however, there were a few metamorphosed larvae with long bristles crawling about, though the majority still swam. The difference between the Bullhill sand and the Penrhyn Bay sand was striking.

On the fifth day of the experiment each dish was carefully searched, the various deposits being removed for this purpose. The results are summarized in Table IV, but it should be noted that except for the clean dish, and the various deposits of glass where it was relatively easy to find all the larvae present, a complete count or examination of every larva in the dish could not for certain be made. However, in the half-hour and more devoted to each dish few larvae can have escaped observation. In the Table a + after a figure means that more larvae were seen than were actually counted.

In every dish larvae were trapped on the surface film, sometimes in quite large numbers. These must be ignored when comparing the effect of the different types of bottom, though a word must be said concerning the single metamorphosed and the metamorphosing larva on the film above the Bullhill sand. It is quite probable that these had been carried from the sand below by air bubbles such as are formed when gases come out of solution during a rise in temperature, or in photosynthesis. Indeed, on 11 July there were also grains of sand on the film; these had not been there previously and must have been raised in some such way. There were similar sand grains in the Penrhyn Bay dish and Carborundum grains on the surface film in the two dishes containing that substance. Indeed, the appearance of sand grains on the surface film is a not unusual feature during the course of an experiment, and the presence, therefore, of metamorphosed larvae on the film does not necessarily imply that they metamorphosed in that position. In this experiment there were large numbers of metamorphosed larvae in the Bullhill sand on 6 July, and as since that date sand grains had appeared on the film it is not surprising to find that one or two of these larvae had been carried up with them.

The results as set out in Table IV largely speak for themselves. Once again in the Bullhill sand dish the larvae are far ahead of all others in metamorphosis and in the development of long bristles. In the unmetamorphosed larvae the bristles were much shorter and those on the third setiger were on this same day only just protruding from the seta sacs—the young metamorphosed worms had third setiger bristles many times this length, and those of the first and second setiger were likewise elongated over those of their unmetamorphosed relatives. Penrhyn Bay sand had by this fifth day induced a fair proportion to metamorphose, but was definitely well behind Bullhill sand. A few metamorphosed worms with their long bristles were found in some of the other dishes, but the proportions are much smaller still. It is

striking how the addition of Carborundum grit and the cementing of the grains in an immovable single layer each upsets the metamorphosis-inducing properties of the Bullhill sand.

Experiment 5

The results of the preceding experiments having indicated that the stimulus to metamorphose is probably given by the purely physical nature of the bottom deposit, a further experiment was devised to rule out, as far as possible, the chance that the most effective bottom deposits (Bullhill sand and Penrhyn Bay sand) contained some substance that by slowly dissolving out was perceived by the larvae in a chemical manner. These two sands were therefore treated in various ways. In the acid treatment strong hydrochloric acid was followed by sulphuric bichromate solution such as is used in cleaning glassware, and finally well washed. Sand was also twice boiled, treated with absolute alcohol, and heated to redness for over 10 min. Sands thus treated were compared with the natural sands which were merely washed in fresh and sea water, without sterilization by boiling as is usual in most experiments. In these latter sands a few living nematodes were seen. Unsterilized Penrhyn Bay sand in which some adult *Ophelia* had been kept was also used to see if the adults could impart something to the sand which would make it more attractive to the larvae. A living adult *Ophelia* was also put into an otherwise clean dish. The larvae used were from the same fertilization as those of Exp. 4, but it was 3 days later that this experiment was set up and by that time many of the larvae in the culture bowls were already attached by their anal papillae to the bottom. However, some were still swimming and it was these swimming larvae which were used.

The results of this experiment are shown in Table V. It was not possible to search all the sands exhaustively though the major portion of that in each dish was examined for 20 min. or so. No significant differences are to be noted between any of the results, and it seems evident that previous treatment of the sands in the manner described had no observable effect on the reactions of the larvae towards them. At the end of the experiment the larvae and young worms were several days older than at the conclusion of Exp. 4; this and the fact that their metamorphosis had already been delayed several days before the experiment was set up probably accounts for their often poorer condition. Also in setting up this experiment larvae were removed from two separate culture bowls (both, of course, of the same age), and it may be that those in one bowl were by that time not as healthy as those in the other, with corresponding results in the dishes they were put into. At any rate, there is no obvious correlation of the state of health with the kind of sand used or with its previous treatment. To the extent that the larvae were relatively old when the experiment started and that two separate culture bowls instead of one were used the experiment is unsatisfactory, but the main purpose for which it was devised seems to have been attained. It again shows that the physical size

TABLE V. EXPERIMENT 5

(Begun 9. vii. 46 with larvae from a fertilization of 1. vii. 46.)

15. vii. 46 and 16. vii. 46

Clean dish	(**a**) Unmet. 11	(**b**) *c.* 12	(**c**) Metd 7 Meting 5 Unmet. 61, *d* 7	Fairly healthy. Metd worms lethargic
Bullhill sand washed in fresh water and sea water	(**a**) None	(**b**) None	(**c**) Metd 31 Meting 0 Unmet. 0, *d* 1	Healthy
Penrhyn Bay sand washed in fresh water and sea water	(**a**) Unmet. 3	(**b**) None	(**c**) Metd 31 Meting 1 Unmet. 0, *d* 2	Fairly healthy
Bullhill sand acid treated	(**a**) None	(**b**) None	(**c**) Metd 33 Meting 5 Unmet. 6, *d* 3	Healthy
Bullhill sand twice boiled	(**a**) None	(**b**) None	(**c**) Metd 23 Meting 6 Unmet. 2, *d* 6	Unhealthy
Bullhill sand heated to redness	(**a**) None	(**b**) None	(**c**) Metd 36 Meting 3 Unmet. 9, *d* 12	Majority of metd healthy, all the unmet. unhealthy
Bullhill sand washed in absolute alcohol	(**a**) None	(**b**) None	(**c**) Metd 24, *d* 1 Meting 3 Unmet. 2, *d* 4	Health poor
Penrhyn Bay sand acid treated	(**a**) ? Meting 2	(**b**) None	(**c**) Metd 25 Meting 5 Unmet. 1, *d* 6	Moderately healthy
Penrhyn Bay sand after contact with *Ophelia*	(**a**) None	(**b**) None	(**c**) Metd 21, *d* 1 Meting 1, *d* 1 Unmet. 0, *d* 3	Fairly healthy
Clean dish with adult *Ophelia*	—	—	All unmet.; mainly dead	—

(**a**) on surface film; (**b**) swimming freely; (**c**) in sand or on the bottom.

and shape of the deposit particles rather than the presence of any dissolving chemical substance is most probably the factor inducing metamorphosis, although chemical stimulus is not entirely ruled out by it.

Descriptions of the Sands used

By the conclusion of Exp. 5 the breeding season for 1946 was virtually over and no more really healthy fertilizations were obtained that year. In the following year good fertilizations were not obtained until early in June, the breeding season having been delayed perhaps by the unusually severe weather of the previous winter; it was very cold from about the middle of January to the end of February 1947. The new series of experiments was planned to obtain more precise information about the physical characters of sand in which larvae would readily metamorphose and to determine, if possible, whether anything in the nature of a soluble substance played any part. With this end in view various sands were chosen and graded well in advance of the breeding season. The grading was done by drying the sands and passing them through simple sieves made from selected grades of new bolting silk tightly held between close-fitting metal sleeves. The silks selected were those in stock in the laboratory and had 26, 40, 60, 86, 100 and 200 meshes to the inch. Each sample of sand was washed in fresh water and thoroughly dried; it was then passed in succession through the various silks from the coarsest to the finest, so that eventually its component particles were separated out into a series of grades of nearly uniform particle size. The separated grades were kept in clean screw-stoppered jars ready for use. Each grade is designated according to the silks used to separate it. Thus grade 40–60 mesh means sand which has passed forty meshes to the inch but has been retained by sixty.

The sands treated in this way were as follows. In order to have an independent opinion as to their composition I asked Dr A. G. Lowndes to examine and describe a specimen of each, which he very kindly consented to do.

(1) *Bullhill Bank sand* from an area where adult *Ophelia* were collected in quantity. It is a very clean sand (Pl. XVI, fig. 1), 'homogeneous in size; large grains rounded; mineral chiefly quartz, tourmaline in small quantities; small amount of shell; ferruginous material. The 40–60-mesh grains are distinctly rounded, few fragmented, but in the 86–100-mesh sizes (Pl. XVI, fig. 2) more angular fragments are present, although the majority of the grains are still rounded (A.G.L.).'

The proportions by weight (per 100 g.) of the various grades were:

Mesh	g.
Larger than 26	0·25
26– 40	4·17
40– 60	59·37
60– 86	32·81
86–100	3·12
100–200	0·27
Total	99·99

(2) *Exmouth high-water sand.* This was collected from just below the promenade at Exmouth. It was well above ordinary high-water mark and certainly contained no living *Ophelia.* It was very clean and of the same or very similar mineral content, but contained a higher proportion of small pebbles: 'quite large rounded pebbles, some of which contain crystals of tourmaline; quartzite pebbles and rounded crystals of quartz; many small angular quartz fragments; fragments of shell; calcite; many pebbles of local rock (shale) up to 5 mm. The 40–60-mesh grains are distinctly rounded but in the 86–100-mesh sizes the majority are angular, though a fair proportion are rounded (A.G.L.).'

The proportions by weight were:

Mesh	g.
Larger than 26	46·00
26– 40	9·00
40– 60	22·80
60– 86	13·00
86–100	8·00
100–200	0·64
Total	99·44

(3) *Salthouse Lake sand.* This sand was collected during a brief excursion across the channel separating the Salthouse Lake area from the Bullhill Bank. It was about a quarter of a mile from the main collecting ground for *Ophelia,* but at a slightly lower tidal level. In character the shore where it was taken was quite different from the Bullhill Bank, the sand being firmer and finer with a little admixture of mud. *Arenicola marina* was abundant, with *Tellina tenuis* and a general and quite rich sand fauna. Casual digging did not turn up any *Ophelia,* though in a nearby region this species was present, in much smaller numbers than on the Bullhill Bank (personal communication from Mr N. A. Holme).

An analysis of this small sample (about 25 g.) gave the following composition:

Mesh	g.
Larger than 26	Nothing
26– 40	0·12
40– 60	1·40
60– 86	21·60
86–100	53·40
100–200	22·08
Total	98·60

It will be seen from the figures that this sand was much finer than that of the Bullhill Bank. When thrown into water a slight cloudiness was left behind after the sand had settled, showing the presence of very fine particles. A few grains passed the 200 mesh, but the amount was very small indeed. This sand (Pl. XVI, fig. 3) was 'homogeneous, medium grained, consisting of grains of quartz chiefly, angular not rounded; grains of tourmaline fairly abundant; small fragments of shell (A.G.L.)'. The mineral composition appeared to be very similar to the Bullhill Bank and Exmouth high-water sands.

(4) *Kames Bay sand.* This was sand from Millport, Isle of Cumbrae. It is finer (Pl. XVI, fig. 4) than that of the Bullhill Bank and not quite so clean. 'A clear homogeneous sand impregnated with iron; grains angular with very little rounding; small amount of shell fragments and echinoid spines; no tourmaline; a little zircon (A.G.L.).' The mineral content was not quite the same. The noteworthy feature of this sand is that it was inhabited by an allied species of *Ophelia*, the much smaller *O. cluthensis* McGuire, and the sand used came from a place where these worms were very numerous. The proportions of the various grades by weight were:

Mesh	g.
Larger than 26	0·32
26– 40	1·93
40– 60	24·51
60– 86	52·90
86–100	19·35
100–200	0·96
Total	99·97

(5) *Penrhyn Bay sand.* As already mentioned, this came from a shore in north Wales where *Ophelia*, although not extensively looked for, is almost certainly absent. It is a sand (Pl. XVII, fig. 1), 'homogeneous in size, fairly coarse; quartz and shell fragments; grains angular and rounded in about equal proportion. No tourmaline (A.G.L.)'. There are more shell fragments in this sand than in that from the Bullhill Bank. The proportions by weight of its various grades showed that it was a finer sand than that of the Bullhill Bank. These proportions were:

Mesh	g.
Larger than 26	0·23
26– 40	2·12
40– 60	36·32
60– 86	48·58
86–100	10·37
100–200	2·35
Total	99·97

(6) *Polzeath sand.* A sand (Pl. XVII, fig. 2) consisting of a very high proportion of broken shell fragments. 'At least 50% shell fragments, all polished with rounded corners; angular quartz fragments; grains of local shale and grits; very few small grains (A.G.L.).' The finer mesh sizes contained a higher proportion of angular fragments than the natural sand or the coarser mesh sizes. The proportions of the various grades by weight were:

Mesh	g.
Larger than 26	0·27
26– 40	5·43
40– 60	37·22
60– 86	43·47
86–100	12·77
100–200	0·54
Total	99·70

From this it will be seen that it was rather similar in grade to sand from the Bullhill Bank. In all other features it was a sand of quite a different character.

(7) '*Gritty*' *sand*. This was a sand of uncertain origin; it probably came from a dredging in deep water. It was found in an unlabelled bottle in the laboratory and seemed very suitable for use as a contrast to the other sands. It consisted of sharply angular mineral particles mixed with broken and rather sharp fragments of mollusc shells, *Echinus* spines and plates, etc. 'Rather coarse but homogeneous with a large number of shell fragments, many quartz grains and mica shale; very angular (A.G.L.).' This sand is referred to as 'Gritty' sand, and has already been mentioned by that name when describing the 1946 experiments. In that year, however, the sand was sifted under water to remove the larger fragments, sufficient of the smaller particles being removed with a pipette to form the 'fine gritty sand' (Pl. XVII, fig. 3) of those experiments. The quantity so used was less than half a gram, and hence was not very suitable for grading by the rather rough method used. However, a careful estimation gave the following result, worked out to 100 g. for comparison with other sands:

Mesh	g.
Larger than 26	Nothing
26– 40	Nothing
40– 60	1·6
60– 86	5·4
86–100	27·3
100–200	65·5
Total	99·8

Nothing passed the 200-mesh silk. It will be seen that this artificially selected sand consisted mainly of very small particles.

For the 1947 experiments the 'Gritty' sand in its original state as found in the bottle was graded and several of the grades were used as such, as will be noted under the various experiments. The ungraded sand was not so used, so that an analysis of it is unnecessary.

(8) *B.D.H. sand*, purified by acid. This is a laboratory reagent. Two grades supplied by the British Drug Houses Ltd. were used, 30–40 mesh and 60–80 mesh. By mixing these and regrading through the silks, sands of coarser, finer and intermediate grades were obtained. In composition it consisted of 'large rounded grains of quartz and small angular grains; very little ferruginous material; grains containing sillimanite and natiolite (A.G.L.)'. The sand was pale cream in colour.

The Experiments of 1947

Experiment 6

This is the first of the experiments in which graded sands were used. Various grades of Bullhill Bank sand were compared with natural Bullhill Bank, graded B.D.H. acid purified, and a coarse and fine grade of 'Gritty' sand. A clean dish served as a control.

TABLE VI. EXPERIMENT 6

(Begun 13. vi. 47 with larvae from a fertilization of 9. vi. 47.)

	23. vi. 47 and 24. vi. 47				27. vi. 47	
Clean dish	(a) Unmet. 40	(b) A few	(c) Unmet. a large number	Healthy	None metd though some prototrochal cilia lost. One may be meting	Moderately healthy
Bullhill Bank sand	(a) Unmet. 12	(b) One	(c) Metd 5 Meting 4 Unmet. but possibly meting 12	Healthy	(c) Metd 13 Meting 1 Possibly meting 2 Unmet. 3	Metd fairly healthy, others unhealthy
Bullhill Bank, 26–40 mesh	(a) Unmet. *c.* 60	(b) None	(c) Metd 6 Meting 9 Unmet. but possibly meting 8	Healthy	(c) Metd 15 Meting 1 Unmet. 3	Mainly unhealthy
Bullhill Bank, 40–60 mesh	(a) Unmet. *c.* 30	(b) None	(c) Metd 6 Meting 5 Unmet., some possibly meting 7	Healthy	(c) Metd 21 Meting 6 Unmet. 1	Some fairly healthy, others unhealthy
Bullhill Bank, 60–86 mesh	(a) Unmet. *c.* 35	(b) None	(c) Metd 7 Meting 6 Unmet., some possibly meting 9	Healthy	(c) Metd 14 Meting 6 Unmet. 3	Some fairly healthy, others unhealthy
Bullhill Bank, 86–100 mesh	(a) Unmet. 70–80	(b) Two	(c) Metd 6 Meting 10 Unmet. 42	Healthy	(c) Metd 3 Meting 6 Possibly meting 5 Unmet. 14	Mainly unhealthy

B.D.H. sand, acid purified, 26–40 mesh	(a) Unmet. 10	(b) None	(c) Metd 4 Meting 8 Unmet. 8	Unhealthy	Not examined	—
B.D.H. sand, acid purified, 40–60 mesh	(a) Unmet. 15	(b) None	(c) Metd 2 Meting 9 Unmet. 7	Unhealthy	Not examined	—
B.D.H. sand, acid purified, 60–86 mesh	(a) Unmet. 14	(b) None	(c) Metd 0 Meting 4 Unmet. 9	Unhealthy	Not examined	—
B.D.H. sand, acid purified, 86–100 mesh	(a) Unmet. 8 Possibly meting 1	(b) None	(c) Metd 0 Meting 2 Unmet. 16 Abnormal unmet. 2	Unhealthy	Not examined	—
'Gritty' sand, 40–60 mesh	(a) Unmet. 16	(b) None	(c) Metd 0 Meting 2 Possibly meting 10 Unmet. 15	Fairly healthy	(c) Metd 6 Meting 4 Possibly meting 2 Unmet. 3	Unhealthy
'Gritty' sand, 86–100 mesh	(a) Unmet. 16	(b) None	(c) Metd 2 Meting 2 Possibly meting 2 Unmet. 17, *d* 1	Fairly healthy	(c) Metd 1 Meting 1 Possibly meting 4 Unmet. 5	Fairly healthy

(a) on surface film; (b) swimming freely; (c) in portion of sand or on bottom.

The same volume of sand (a level saltspoonful) was used in each instance, and each quantity was separately boiled, well rinsed in tap water and then given several washings in filtered sea water from outside the breakwater ('outside water'). All dishes were acid-cleaned and well washed. Larvae used were from a batch of eggs naturally shed and fertilized on 9 June 1947. These eggs had been transferred from circulation water to outside water and gave rise to a strong healthy culture of larvae. A small quantity of autotrophic flagellates from laboratory cultures was added to supply food if needed.

To make sure of providing the larvae with opportunities to metamorphose as soon as they were ready to do so, the experiment was set up early at a time when they were not showing any tendency to attach themselves by the anal papillae and the third setiger had not developed bristles. This was probably a mistake, for as it turned out many of the larvae got caught on the surface film, or stuck themselves thereto, before they were ready to metamorphose. Moreover, by starting the experiment early the dishes had to stand without change of water for a longer period than would otherwise have been necessary, and this may have been partly responsible for the poor health of the larvae at the end of the experiment.

In Table VI the results are set out. The larvae on the surface films were removed from the influence of the sands and must therefore be ignored in considering the results. Metamorphosis was seen to have begun in some of the sand pots on 21 June, that is, 8 days after the larvae had first been put in the dishes. A careful examination of each pot was started on 23 June and finished the next day. In every instance all larvae on the surface film were carefully removed with a pipette before a little of the sand was taken out and searched. Searching took about 15 min. or longer; in the 'Gritty' sands the larvae were particularly hard to see, and with each of these the time of searching was extended to about an hour. The 86–100 grade of Bullhill Bank sand was searched for half an hour. In the semi-transparent colourless grains of the B.D.H. sand the larvae were clearly visible, and easily found. The sands which had been removed and searched and the larvae found in them were not returned to the dishes but were discarded, as were all the larvae on the surface films.

It is obvious that only the numerical proportions between unmetamorphosed, metamorphosing and metamorphosed larvae are significant, and this must be borne in mind when comparing dish with dish. In numerous instances it was very difficult to distinguish between larvae which were unmetamorphosed and those which had perhaps begun to metamorphose. Where necessary this is indicated in the table. It will be seen that all the Bullhill Bank sands except the 86–100 grade show very similar results, but the latter seems quite definitely to have a small proportion of its larvae metamorphosed or metamorphosing. Some of the larvae were stuck together in clusters of several individuals, but all were healthy, as, indeed, were all those

in Bullhill sand. On the other hand, all the larvae in the B.D.H. pots were markedly unhealthy, though here again the finest grade used had a higher proportion of unmetamorphosed larvae than did the others. In both coarse and fine 'Gritty' sands only a small proportion had metamorphosed or were metamorphosing; the health of these dishes was fairly good.

On 27 June a final examination was made. In the clean dish the larvae were still unmetamorphosed with some not very active cilia on their prototrochs, and they were moderately healthy. In all the Bullhill sands except the finest grade metamorphosed larvae greatly preponderated over unmetamorphosed, while the reverse was true for the 86–100 grade. The results for the 'Gritty' sands were not good, but they do show something similar when coarse and fine grades are compared, though here the coarser grade does not appear to be as effective in producing metamorphosis as the corresponding grade of Bullhill sand. The B.D.H. sands were unhealthy on the first examination on 24 June and therefore were not re-examined on 27 June.

Experiment 7

This experiment was similar in conception to the last, only here various mesh sizes of Exmouth high-water sand were tested. This sand was the nearest sort to the Bullhill sand in which it was certain that adult *Ophelia* had not been living. In addition, other sands of quite different types were also tested. The same preliminary sterilizations and washings of the sand were carried out as for Exp. 6 and larvae from the same fertilization were used. The experiment was set up 2 days later than Exp. 6, but even so an unduly large proportion of the larvae attached themselves to, and thereby became trapped on, the surface film. The dishes were first looked at 10 days after the experiment began, and the examination of the various dishes took 2 days to complete. The results are shown in Table VII. All the larvae and sands removed from the dishes on 25 and 26 June for counting were discarded and not returned to the experiment. Great care was taken to remove all larvae on the surface film before disturbing the sand. A little filtered sea water was added to several of the dishes to make up for that lost by removal of these larvae. Some of the dishes were examined again on 4 July.

Once again the larvae metamorphosed more readily in the Bullhill sand than in any of the other sorts and, moreover, were, on the whole, considerably healthier than in the other dishes. The various grades of the Exmouth high-water sand gave unexpectedly poor results; it was thought that the 40–60- and 60–86-mesh sizes would have induced a high proportion of larvae to metamorphose. Grains of these sizes form the bulk of the Bullhill sand, and there is little difference in geological character between the latter and the sand from high-water mark a mile or so away. The high-water grains tend to be a little more angular, but except for the smallest sizes this is not very noticeable. The larvae in the dish containing 40–60-mesh size high-water sand were not really

TABLE VII. EXPERIMENT 7

(Begun 15. vi. 47 with larvae from a fertilization of 9. vi. 47.)

	25. vi. 47			26. vi. 47			4. vii. 47	
Clean dish I	(a) Unmet. 33	(c) Unmet. *c.* 70	Healthy	—	—	—	(c) Majority umet, but 3 or 4 metd and a few possibly meting	Health poor
Clean dish II	—	—	—	(a) Possibly meting 1 Unmet. *c.* 35	(c) Possibly meting 1 or 2 Unmet. 70–80	Very healthy	All unmet.	Moderately healthy
Bullhill Bank sand	(a) Unmet. *c.* 70	(c) Metd 14 Meting 5 Unmet. 2	Very healthy	—	—	—	(c) Metd 15 Meting 2 Unmet. 0	Fairly healthy
Exmouth high water retained by 26 mesh	(a) Unmet. *c.* 60	(c) Metd 3 Meting 10 Unmet. 41	Healthy	—	—	—	—	—
Exmouth high water, 26–40 mesh	(a) Unmet. *c.* 100	(c) Metd 1 Meting 0 Unmet. 15	Healthy	—	(c) Metd 0 Meting 1 Unmet. 17	Moderately healthy	—	—
Exmouth high water, 40–60 mesh	(a) Unmet. 70	(c) 1st count 2nd count Metd 5 6 Meting 12 10 Unmet. 5 1	Moderately healthy	—	(c) Metd 5 Meting 4 Probably meting 2 Early meting 9	Unhealthy	—	—
Exmouth high water, 60–86 mesh	(a) Unmet. *c.* 60	(c) Metd 1 Meting 3 Unmet. 16	Healthy	—	(c) Metd 0 Meting 1 Unmet. 5	Moderately healthy	—	—
Exmouth high water, 86–100 mesh	(a) Unmet. *c.* 50	(c) Metd 2 Meting 7 Unmet. 22	Quite healthy	—	—	—	—	—
Exmouth high water, 100–200 mesh	(a) Unmet. *c.* 70 Meting 1	(c) Metd 0 Meting 6 Unmet. 40	Fairly healthy	—	—	—	—	—
Salthouse Lake sand	—	—	—	(a) Unmet. *c.* 30	(c) Metd 0 Meting 2 Possibly meting 4 Unmet. 18, *d* 1	Health poor	(c) Metd 5 Meting 2 Unmet. 0	Health poor
Kames Bay sand	—	—	—	(a) Unmet. *c.* 30	(c) Metd 3 Meting 6 Possibly meting 7 Unmet. 20	Moderately healthy	(c) Metd 17 Meting 1 Unmet. 0	Fairly healthy
Kames Bay recombined in proportions of Bullhill sand	(a) Unmet. *c.* 80	(c) Metd 0 Meting 2 Possibly meting 4 Unmet. 11	Moderately healthy	—	—	—	—	—
Polzeath, 40–60 mesh	—	—	—	(a) Unmet. *c.* 25	(c) Metd 0 Meting 0 Possibly meting 1 Unmet. 20	Very healthy	(c) Metd 5 Meting 1 Unmet. 0	Fairly healthy
Polzeath, 60–86 mesh	—	—	—	(a) Unmet. 50–60	(c) Metd 0 Meting 1 Possibly meting 2 Unmet. 23	Moderately healthy	(c) Metd 10 Meting 10 Unmet. 0	Moderately healthy
Polzeath recombined in proportions of Bullhill sand	—	—	—	(a) Unmet. *c.* 80 1 or 2 may be meting	(c) Metd 0 Meting 1 Possibly meting 3 Unmet. 24	Healthy	—	—
'Gritty' sand recombined in proportions of Bullhill sand	—	—	—	(a) Unmet. *c.* 15	(c) Metd 2 Meting 4 Possibly meting 5 Unmet. 15	Moderately healthy	—	—

(a) on surface film; (c) on bottom or in portion of sand.

healthy, and it may be that some infection in this dish affected the result. The larvae in the 60–86-mesh dish were fairly healthy, however, and yet showed an even more marked reluctance to metamorphose. In the other sands metamorphosis was delayed compared with the Bullhill sand, although in most of them larvae did eventually succeed in metamorphosing. The vast majority of the larvae in the two clean dishes were still unmetamorphosed at the end of the experiment.

A few words should be inserted here on the condition of the unmetamorphosed larvae. On 25 and 26 June those on the surface film of all dishes had strong prototrochal cilia and almost certainly apical tufts and telotrochs as well. With the dissecting binocular used in this work it was not very easy to see cilia other than those forming the prototroch which when present was always clearly visible. On the same dates the unmetamorphosed larvae in the various sands also nearly always had good prototrochs and could generally swim well when disturbed, but in a number the ciliation was rather irregular and a few had lost most of the cilia, though otherwise retaining the prototrochal tissue. By 4 July few of the unmetamorphosed larvae, even those on the surface film, retained any of their cilia, although the other tissues of the prototroch were clearly visible. The general health conditions were, however, poor, and this may have been partly responsible for this loss of tissue. On this date it was, indeed, difficult to classify the larvae properly at all, and some of those put down as metamorphosing may possibly have been fully metamorphosed but imperfectly formed.

Some of the unmetamorphosed larvae on the surface films were stuck together by their anal papillae in little clusters and some surrounded cotton fragments, though a great many were attached to the film singly. In the sands, particularly the two finest grades from Exmouth high water, there were also little clusters of larvae; these were sometimes visible on the surface of the sand before the latter was disturbed.

Experiment 8

The tests of the Exmouth high-water sand made in the last experiment not having proved very satisfactory on account of the unhealthy state of several of the dishes, it was decided to try the various grades again and at the same time to include a graded series of Bullhill sand. In addition to these, the four grades 26–40, 40–60, 60–86 and 86–100 mesh of both Bullhill and Exmouth high-water sands were recombined in the correct proportions by weight to resemble Bullhill Bank sand. These recombined sands lacked only particles larger than 26 mesh and smaller than 100 mesh, both of which, as shown on p. 734, are present in the natural Bullhill sand in very small proportion only. To one of the recombined Exmouth high-water sands a little Bullhill Bank natural sand was added. Some further tests with Carborundum grit No. 120 (Pl. XVII, fig. 4) were also included, but in the mixture with Bullhill natural sand only about a third part was Carborundum—a smaller proportion than in

Exp. 4. The grit did not mix uniformly with the sand, and there were patches of the latter almost free from it.

On the whole this experiment was much healthier than the preceding two and there was never any difficulty in deciding to which category a larva belonged, as was rather often so in Exps. 6 and 7. The unmetamorphosed were strongly ciliated, short in body and without long bristles, the metamorphosing were distinctly elongating with narrow and interrupted prototrochs which still retained some cilia, and the bristles were elongating. The metamorphosed had no less distinctly lost all cilia, were elongated and had long bristles, especially on the third setiger. Individuals rarely departed from these standards[1] which were not always so closely followed in other experiments. This variation in health of different experiments was probably to a large extent due to variation in the state of maturity of the eggs and sperms at fertilization.

The main results of Exp. 8 are set out in Table VIII. The experiment was started on 9 July with 6-days-old larvae which were swimming strongly, though occasionally using the anal papillae to attach themselves to the sides of the glass bowl in which they were kept. Attachment was always only temporary; attached larvae easily released themselves and swam away again. They were strongly negatively phototropic; there were no bristles on the third setiger. The sands and dishes were cleaned and sterilized as described for Exp. 6; a new feature was a black paper collar around each dish so that light came only from above, and the dishes were stood on black paper. It was hoped by this means to drive the negatively phototropic larvae away from the surface film. Unfortunately, many larvae were again trapped, perhaps at night but also certainly by day as well. On 11 July larvae on the surface film were released by dropping freshly filtered outside sea water on to them from a pipette, but they were soon back again. On that day several fully metamorphosed larvae were observed in the sands of some of the dishes. It was intended to make a count on 13 and 14 July, but this could not be done until 15 and 16 July.

All larvae on the surface films were carefully removed before the sands were disturbed. There were always large numbers of these except in one or two instances where the dish was so full of water that the watch-glass dust-cover dipped below the surface and so reduced the area of water-air interface. In future experiments it may be possible to devise some such means of avoiding this particular trouble with the larvae. Before the dishes were disturbed care was always taken to note whether any larvae were swimming freely and whether any could be seen on the surface of the sand. It was impossible within the time available to search all the sands; a portion only was removed from each dish for this purpose.

It had been noted in the previous experiment that larvae often tended to stick together in clusters, especially unmetamorphosed larvae on unsuitable

[1] The general appearance of these stages is shown in Plate XV, figs. 1–3, which are of larvae from an experiment in 1948.

sands. In this experiment therefore clusters are recorded as such, the number of larvae forming each cluster being noted. Such clusters could often be observed lying on the surface of the sand before any of the latter was removed for examination.

Some of the results of this experiment are clear and definite. Larvae in the clean dish and those on the surface films of all the other dishes were still unmetamorphosed some time after many in contact with sand had undergone the critical change. The ungraded, or natural sand from the Bullhill Bank was rarely equalled by any of the graded sands in its property of stimulating larvae to metamorphose. Of the graded sands the 40–60 mesh from Exmouth high water gave a result comparable with that of the Bullhill Bank natural, and there was a marked reduction in efficiency of coarser and finer grades. In the graded Bullhill Bank sand of the 40–60-mesh size the larvae did not seem to be quite as healthy as was usual in this experiment, and this probably affected the result. None the less this grade did on the whole yield a higher proportion of metamorphosed worms than the others, though less than could reasonably be expected. In the two finest grades of both sorts of sand only a very few larvae metamorphosed; in these dishes the great majority of the larvae were unchanged and were often stuck together in clusters of several individuals. The sands recombined from four sifted grades were variable in their effect, though some of the Exmouth recombined sands were almost as efficient as the Bullhill Bank natural. Carborundum grit again had a marked effect, changing the properties of the Bullhill Bank natural sand to which it was added, and in itself proved an unsuitable medium for larval settlement.

It will be noted that there is a difference in result between the two dishes of Bullhill Bank natural sand. In the first dish twenty healthy metamorphosed worms were counted in 5 min. and many more seen, whereas in the second dish 10 min. searching yielded only nineteen metamorphosed and about half as many unmetamorphosed larvae. It is possible that fewer larvae had originally been put into this dish than into the first one. It was noticed that the larvae and worms in the second dish were not as healthy as in the first dish, and this may have been a prime cause in influencing the result. These differences in health between dish and dish may be due to chance bacterial infection; it is impracticable to conduct experiments of this nature under bacteriologically sterile conditions. The small number of larvae on the surface film of the second dish was due to the bottom of the watch-glass cover dipping into the water so as almost to obliterate the air-water interface normally present.

The experiment was completed on 16 July, but the clean dish was kept and examined again on 23 July, the larvae by then being 20 days old. Some of the larvae had metamorphosed, both on the surface film and on the bottom, but were imperfectly formed, and some were metamorphosing. Other larvae were still unmetamorphosed, but had lost most or all of the prototrochal cilia.

TABLE VIII. EXPERIMENT 8

(Begun 9. vii. 47 with larvae from a fertilization of 3. vii. 47.)

	15. vii. 47			
Clean dish	(a) All unmet.	—	(c) All unmet.	Very healthy
Bullhill Bank sand, dish No. 1	(a) Unmet. *c.* 150	(b) None	(c) Single: Metd 20+ Meting 0 Unmet. 0 Clusters: *None*	Very healthy
Bullhill Bank sand, dish No. 2	(a) Unmet., a few	(b) None	(c) Single: Metd 19 Meting 4 Unmet. 9, *d* 2 Clusters: Unmet. *2*	Fairly healthy
Bullhill Bank, 26–40 mesh	(a) Unmet., large number	(b) None	(c) Single: Metd 10 Meting 8 Unmet. 9 Clusters: Unmet. *4, 5, 6*	Healthy
Bullhill Bank, 40–60 mesh	(a) Unmet., many	(b) None	(c) Single: Metd 12 Meting 4 Unmet. 6 Clusters: Unmet. *4, 5, 5*	Some unhealthy, others moderately healthy
Bullhill Bank, 60–86 mesh	(a) Unmet., large number	(b) Several	(c) Single: Metd 11 Meting 7 Unmet. 9 Clusters: Meting *2* Unmet. *4, 8, 3, 4, 7*	Moderately healthy
Bullhill Bank, 86–100 mesh	(a) Unmet., large number	(b) A few	(c) Single: Metd 5 Meting 4 Unmet. 7 Clusters: Meting *2* Unmet. *4, 5, 6, 4, 8, 7*	Very healthy
Bullhill Bank, 100–200 mesh	(a) Unmet. 150–200	(b) None	(c) Single: Metd 0 Meting 0 Unmet. 8 Clusters: Unmet. *4*	Healthy
Bullhill Bank, four grades recombined, dish No. 1	(a) Unmet., large number	(b) Several	(c) Single: Metd 12 Meting 6 Unmet. 10 Clusters: Meting *3* Unmet. *2*	Healthy
Bullhill Bank, four grades recombined, dish No. 2	(a) Unmet., large number	(b) Several	(c) Single: Metd 7 Meting 3 Unmet. 5 Clusters: Unmet. *3, 2, 2*	Moderately healthy
Bullhill Bank and Carborundum	—	—	—	—
Carborundum grit No. 120	—	—	—	—
Exmouth high water, 26–40 mesh	(a) Unmet., large number	(b) Several	(c) Single: Metd 14 Meting 2 Unmet. 8 Clusters: Unmet. *5, 2, 3, 2*	Healthy
Exmouth high water, 40–60 mesh	(a) Unmet., many	(b) None	(c) Single: Metd 28 Meting 2 Unmet. 2 Clusters: None	Healthy
Exmouth high water, 60–86 mesh	(a) Unmet., large number	(b) 1 or 2	(c) Single: Metd 12 Meting 7 Unmet. 11 Clusters: Meting *3* Unmet. *8, 3, 2*	Healthy
Exmouth high water, 86–100 mesh	(a) Unmet., large number	(b) None	(c) Single: Metd 7 Meting 1 Unmet. 7 Clusters: Unmet. *4, 4, 3, 14, 6, 6, 6, 4, 4, 6, 7*	Healthy
Exmouth high water, 100–200 mesh	(a) Unmet., large number	(b) None	(c) Single: Metd 2 Meting 1 Unmet. 9 Clusters: Unmet. *9, 2, 5, 10, 6, 5, 6, 7, 2, 12, 3, 10, 8, 5, 3, 7, 5*	Healthy
Exmouth high water, recombined as Bullhill Bank, dish No. 1	(a) Unmet. 175–200	(b) None	(c) Single: Metd 16 Meting 4 Unmet. 7 Clusters: Unmet. *5, 5, 7, 5*	Very healthy
Exmouth high water, recombined as Bullhill Bank, dish No. 2	(a) Unmet. *c.* 150	(b) None	(c) Single: Metd 30 Meting 5 Unmet. 1, *d* 2 Clusters: Meting *5* Unmet. *6*	Very healthy
Exmouth high water, recombined as Bullhill Bank, dish No. 3	(a) Unmet., large number	(b) None	(c) Single: Metd 22 Meting 1 Unmet. 0 Clusters: Metd 2 Unmet. *5, 6*	Healthy
Exmouth high water, recombined + a little Bullhill sand	—	—	—	—

TABLE VIII. EXPERIMENT 8 (*cont.*)

16. vii. 47

One on bottom meting. Bristles of third setiger very short	Others all unmet. with strong prototrochs and apical tufts.		Healthy
—	—	—	—
(a) Unmet. 70–80	(b) None	(c) Single: Metd 39 Meting 2 Unmet. 5, *d* 11 Clusters: Meting *4* Unmet. *9, 5, 2, 2, 4*	Metd moderately healthy; unmet. unhealthy
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
(a) Unmet., large number	(b) A few	(c) Single: Metd 29 Meting 14 Unmet. 10 Clusters: Unmet. *4, 3*	Fairly healthy
(a) Unmet., fairly large number	(b) A few	(c) Single: Metd 15 Meting 5 Unmet. 15 Clusters: Unmet. *6, 3, 2*	Fairly healthy
(a) Unmet., many	(b) None	(c) Single: Metd 6 Meting 4 Unmet. 23 Clusters: Unmet. *6, 4*	Poor health
(a) Unmet., a few	(b) None	(c) Single: Metd 0 Meting 0 Unmet. 23, *d* 22 Clusters: Unmet. *2, 2, 2, 3, 5, 10, 2, 4, 4* Unmet. *d 3, 2, 2, 2, 2, 2*	Some healthy, but others unhealthy
—	—	—	—
—	—	—	—
—	—	—	—
—	—	—	—
(a) Unmet., a few	(b) None	(c) Single: Metd 0 Meting 0 Unmet. 1 Clusters: Unmet. *3, 5, 7, 10, 6*	Healthy
—	—	—	—
—	—	—	—
(a) Unmet. *c.* 50	(b) 1 or 2	(c) Single: Metd 34 Meting 3 Unmet. 1 Clusters: Meting *5*	Healthy
(a) Unmet., many	(b) None	(c) Single: Metd 38 Meting 4 Unmet. 1 Clusters: Unmet. *2*	Healthy

(a) on surface film; (b) swimming; (c) on bottom or in portion of sand. The italicized figures under 'clusters' give the number of larvae per cluster, each figure representing a single cluster.

Experiment 9

This was a small experiment to test whether freshly collected and unboiled Bullhill sand was more active than sand which had been left a long time and had been boiled. The fresh sand had living *Ophelia* worms in it until used; it was washed only in warm and cold fresh water and filtered sea water. The result (Table IX) reveals no significant difference. In the same experiment two grades of 'Gritty' sand were also tested, and it is to be noted that both had almost no effect in promoting metamorphosis, although one of the grades had a grain size equivalent to that most commonly found in the Bullhill Bank. In all these dishes, and in the clean dish in which no metamorphosis took place, the larvae were strong and healthy, but in a dish containing B.D.H. acid-purified sand recombined in the proportions by weight of the Bullhill Bank sand almost all the larvae were dead or dying and none was in good condition. In all previous experiments with this sand the larvae had been adversely affected in spite of the sand being well boiled and well washed before use. The reason for this apparently lethal action (it seems too improbable to assume chance bacterial infection is the cause here) is unknown.

Experiments on Choice of Bottom

In none of the experiments so far described were the larvae given a choice of sands in which to settle. Each dish contained only one kind of soil, or none at all. In order, therefore, to test the selective powers of the larvae another type of experiment was needed, one in which the larvae were afforded the opportunity to settle in one or more different kinds of sand in the same dish.

Experiment 10

This was designed to test the ability of larvae to find a small area of suitable sand placed in the centre of a large dish. A Petri dish of 9 cm. internal diameter had a small patch of Bullhill sand less than 2 cm. in diameter in the middle of the dish. A large number of actively swimming larvae were put into the dish, which was covered and left undisturbed in a cool place. This experiment began on 12 June 1946 with larvae from a fertilization of 5 June. The larvae were beginning to use their anal papillae for attachment. On 19 June the dish was carefully examined and the result is shown in Table X. There were twenty unmetamorphosed larvae stuck to the surface film, while on the bottom, away from the sand, 226 larvae were counted. Of these four were metamorphosed, but were near the sand and had probably crawled out of it. One other was metamorphosing. All the remainder were unmetamorphosed, some attached singly to the glass, but over half of them stuck to bits of cotton and other debris. One long cotton fragment had about seventy larvae attached. In the sand were seventy-nine metamorphosed healthy-looking worms with others metamorphosing and unmetamorphosed, making in all a total of 140.

TABLE IX. EXPERIMENT 9

(Begun 17. vii. 47 with larvae from a fertilization of 7. vii. 47.)

	21. vii. 47			
Clean dish	(a) Unmet. many	(b) A few	(c) Unmet. many	Healthy
12 months old Bullhill Bank natural	(a) Unmet. *c.* 100	(b) None	(c) Single: Metd 11 Meting 6 Unmet. 14 Clusters: *None*	Healthy
Freshly collected Bullhill Bank natural	(a) Unmet. *c.* 100	(b) None	(c) Single: Metd 11 Meting 7 Unmet. 8 Clusters: *None*	Healthy
'Gritty' sand, 40–60 mesh	(a) Unmet. *c.* 8	(b) Small number	(c) Single: Metd 0 Meting 3 Unmet. 13 Clusters: *None*	Healthy
'Gritty' sand, 100–200 mesh	(a) Unmet. *c.* 60	(b) A few	(c) Single: Metd 0 Meting 2 Unmet. 15 Clusters: Unmet. *2, 6, 3, 10, 12*	Healthy
B.D.H. sand, acid-purified, recombined as Bullhill Bank	(a) Unmet. *c.* 20, several dead or dying	(b) None	(c) Single: Metd 0 Meting 1 Unmet. but dead 5 Clusters: *None*	Nearly all dead or dying

(a) on surface film; (b) swimming freely; (c) in portion of sand. The italicized figures under 'clusters' give the number of larvae per cluster, each figure representing a single cluster.

To these should probably be added the four metamorphosed worms found on the glass close by. A simple calculation shows that in the sand larvae had congregated to the extent of about forty-eight to the sq.cm., whereas on the glass bottom the density was only about 2·4 to the sq.cm. This latter figure, of course, assumes even distribution and ignores the actual great local concentration on cotton fragments, which is probably something that would not occur in the sea.

TABLE X. EXPERIMENT 10

(Result on 19. vi. 46.)

	On surface film	On glass	In sand
Metd	0	4	79
Meting	0	1	25
Unmet.	20	83; *70, 4, 9, 6, 8, 8, 5, 8, 7, 8, 5*	36
Total	20	226	140

When clusters were present, the figures are given separately in italic, each figure representing a single cluster.

From the result it appears that larvae, once they have come into contact with the sand, tend to stay there and metamorphose. As all the larvae in the dish were not in the sand, most of them, indeed, being away from it, it seems unlikely that the sand exerts any sort of chemical attraction for them over a distance. They probably find it by chance contact while swimming about. It is probable, too, that more larvae would have reached the sand had they not first become stuck to the glass or surface film, or trapped by cotton fragments in such a manner that they were unable to detach themselves. In moving water, such as would occur in nature, it is probable that detachment from the bottom would have been facilitated. In nature, too, cotton and other dust particles can hardly be such a menace as they are in laboratory dishes.

Experiment 11

This was similar to Exp. 10, but two patches of sand were used, one of Bullhill Bank sand and the other sand from Penrhyn Bay. Each little heap of sand was about 1·5 cm. in diameter, and their centres were 4·5 cm. apart in a Petri dish of 9·0 cm. internal diameter. The dish was kept in a cupboard in the dark for the first 36 hr. and then on a cool shelf near the sea-water circulation. The experiment began on 11 July 1946 with swimming larvae from a fertilization made on 1 July 1946. The dish was examined and the larvae counted on 16 July 1946. It was found that *Skeletonema* chains and a small naviculoid diatom covered the bottom in large numbers and the larvae both on the glass and in the sands were badly fouled with them, the diatoms sticking to their bristles. A number of larvae were dead, while the living ones were in poor condition. In setting up these early experiments the water was not filtered as it was in later experiments after the necessity for so doing had become apparent.

TABLE XI. EXPERIMENT 11

(Result on 16. vii. 46.)

	On glass	In Bullhill sand	In Penrhyn Bay sand
Metd	4	34 *d* 1	8
Meting	9	2 *d* 2	1 *d* 1
Unmet.	86 *d* 24	2 *d* 5	0 *d* 3
Total	123	46	13

In spite of the poor condition of the larvae, doubtless to a large extent brought about by this excessive concentration of diatoms, the result of the experiment (see Table XI) is interesting. There was a greater concentration of larvae in the Bullhill sand than in the Penrhyn Bay sand and a greater concentration in both sands than on the glass. The figures per sq.cm. give for the Bullhill sand 20 larvae, Penrhyn Bay sand about 5·6 and for the glass 1·3 larvae. On the glass there were a few small clusters of larvae, but most of them were scattered singly about the dish.

The original notes on this experiment make no mention of larvae caught on the surface film. It can be assumed that either none was present or the numbers were small, and not being specially noteworthy were accidentally omitted when recording the result.

Experiment 12

This was similar to the last, but was made the following summer. Some slight changes were introduced in the arrangement. Smaller Petri dishes, only 7 cm. internal diameter, were used, and the sands were confined within shallow glass rings of the kind used in making microscopic mounts of large objects. These rings were of 1 cm. internal diameter; they were placed loosely on the bottoms of the Petri dishes and were not cemented into place. As usual all glassware was acid cleaned and well washed before use.

Three dishes were used; in each one or more sands were tested against Bullhill Bank sand. The experiment began on 14 June 1947 with larvae from a fertilization of 9 June. It was a healthy culture with the larvae still mainly swimming and with few attaching. The larvae actively moved away from a source of light. The dishes were kept on black paper and were covered with glass sheets and tissue paper in a cool place.

The experiment was ended on 30 June and 1 July when the dishes were examined and the larvae in the sands counted. In counting the larvae in the sands great care was taken to ensure that every one was found and it is thought improbable that any escaped observation. The results are shown in Table XII. Larvae on the surface film and bottom were noted, but not counted. In all dishes there was a large number of larvae on the surface film as well as on the bottom; clusters of larvae were often attached to cotton fragments.

Table XII. Experiment 12

(Result on 30. vi. 47 and 1. vii. 47.)

	Dish A		Dish B		Dish C		
	Bullhill Bank sand	Salthouse Lake sand	Bullhill Bank sand	Polzeath sand	Bullhill Bank sand	Kames Bay sand	'Gritty' sand
Metd	23	8	43	21	80	30	30
Meting	3	6	11	11	22	13	12
Possibly meting	1	9	1	9	6	8	10
Unmet.	5; *6*	13	2	15; *3, 7*	14	3; *2*	22; *6, 3*
Dead unmet.	1	1	1	2	1	1	—
Total	39	37	58	68	123	57	83

When clusters were present, the figures are given separately in italic, each figure representing a single cluster.

From Table XII it will be seen at once that as in so many other experiments the Bullhill Bank sand yielded more fully metamorphosed young worms than did sand of other kinds. Moreover, the young worms in the Bullhill Bank sand were always the healthiest of the lot, those in the Salthouse Lake sand and the Polzeath sand in particular being in rather poor condition. The total number of worms and larvae in the Bullhill Bank sand was generally larger than in the others, though unmetamorphosed larvae in some abundance raised the total figure for the Salthouse Lake, Polzeath and 'Gritty' sands. In removing the sands for examination care had been taken to avoid falsification of the result by accidental mixing with unmetamorphosed larvae from the surface film, but this may not have been avoided altogether. Clusters are to be specially suspect as having fallen into the sands from the surface film when the dishes were disturbed.

It was often difficult in this experiment to be sure of the correct classification of unmetamorphosed and metamorphosing larvae. Some of the former had lost their cilia, but no other changes were noticeable. The health of these stages in the sands was not as good as that of most of the fully metamorphosed young worms, or as good as that of the larvae on the surface film or on the glass bottom of each dish.

Although no actual calculation was made, it was obvious to the eye that the concentration of the larvae per unit area of clear glass bottom was much less than in any of the sands.

The larvae on the surface film or on the bottom were almost all unmetamorphosed, though a very few on the bottom were metamorphosed or metamorphosing, and it is just possible they may have crawled out of the sand. It was noted in all three dishes that the larvae on the surface film nearly all had strong prototrochs and apical tufts, whereas those on the glass bottom were not quite so healthy and there was some tendency to loss of cilia, some from

the prototroch but especially the apical tufts, as though contact with the hard surface of the bottom served as a slight stimulus towards metamorphosis. This has also been noticed in other experiments.

While not satisfactory in every respect, this experiment does show once again the relatively greater readiness of the larvae to enter Bullhill Bank sand than any other kind, and that once there they are likely to metamorphose without delay.

Experiment 13

Three small dishes of 3 cm. internal diameter were each divided into two sections by placing across the bottom a narrow strip of glass cut from a microscope slide. On one side of the strip the bottom was covered with Bullhill Bank sand, on the other with a natural sand of another sort. Larvae could readily pass from one sand to the other by swimming over the strip. Sands were sterilized by boiling and then were well washed in fresh and filtered sea water in the usual way; the dishes were filled with filtered sea water. Larvae 5 days old were put into the dishes on 8 July 1947. Each dish was surrounded by a collar of black paper and covered by a glass plate, but as in Exp. 8, which ran concurrently, this method failed to prevent large numbers of larvae attaching themselves to the surface film.

The dishes were not examined until 18 July when it was seen that in each instance 100–200 larvae were on the surface film, almost all of them unmetamorphosed, though a few had rather long bristles on the third setiger whilst still retaining a well-ciliated prototroch. This was unusual. These surface-film larvae were carefully removed and the surfaces of the sands then searched with a low-power binocular. Several clusters of larvae stuck together were seen, as well as single unmetamorphosed larvae sitting upright on their anal papillae attached to sand grains, their prototrochs beating actively, causing heads and bodies to wave about as though endeavouring to get free. Sometimes metamorphosed worms could also be seen. The clusters were removed, as it was considered that they were to a large extent an unnatural formation due to the great concentration of larvae in a relatively small volume of water. The larvae could hardly avoid contact with particles of debris and with one another, and they readily adhered by the mucus they secreted. Thus all clusters seen on the surface were removed, but the subsequent search of the sands showed that many had become buried and the larvae forming them often metamorphosed, though it is possible that some of the clusters were formed after metamorphosis owing to the great concentration in what was relatively a very small amount of sand. Against this is the significant fact that, whereas in dish C the majority of the larvae in the clusters found in the sand were unmetamorphosed (see Table XIII), those in dishes D and E, examined 4 and 5 days later respectively, were mainly all metamorphosed, suggesting that metamorphosis of larvae clustered together does take place when the clusters are buried in sand.

TABLE XIII. EXPERIMENT 13

Dish C (examined 18. vii. 47)

	Bullhill Bank sand		Salthouse Lake sand	
	Singles	Clusters	Singles	Clusters
Metd	37	*2*	12	*None*
Meting	20	*2, 3, 3, 2*	17	*2, 2*
Possibly meting	15	*None*	11	*2*
Unmet.	23	*2, 5, 12, 6, 8, 5, 8, 3, 7, 7, 8, 6, 4, 3, 3*	31	*3, 7, 2, 6, 2, 6, 4, 5, 4, 6, 3, 6, 4, 6, 6, 3, 4*
Dead	2	—	1	*None*
Totals	97	*99*	72	*83*
		196		155

Dish D (examined 22. vii. 47)

	Bullhill Bank sand		Polzeath sand	
	Singles	Clusters	Singles	Clusters
Metd	78	*2, 3, 4, 5, 6, 6, 5, 4, 2, 5, 4, 4, 5, 2*	36	*3, 3, 4, 3, 4*
Meting	3	*2*	3	*3, 4, 2, 2, 8*
Possibly meting	None	*None*	None	*None*
Unmet.	None	*None*	3	*12, 8,* 4
Dead	None	*None*	None	*None*
Totals	81	*59*	42	*60*
		140		102

Dish E (examined 23. vii. 47)

	Bullhill Bank sand		Kames Bay sand	
	Singles	Clusters	Singles	Clusters
Metd	130	*5, 3, 5, 2, 4, 2, 4, 3, 2*	114	*3, 9, 3, 7, 5, 6, 4, 5, 9, 3, 3, 5, 6, 5, 4, 4, 5, 3, 5, 3, 2*
Meting	3	*3*	10	*6, 4*
Possibly meting	None	*None*	None	*None*
Unmet.	None	*None*	3	*4*
Dead	None	*None*	None	*None*
Totals	133	*33*	127	*112*
		166		239

The italicized figures under 'clusters' give the number of larvae per cluster, each figure representing a single cluster.

If in interpreting the results (Table XIII) only single larvae are considered, the usual relative distribution of the larvae among the sands is seen. The Bullhill Bank sand always collects most and induces earlier metamorphosis in the majority of those collected. This is also true in dishes C and D of the clusters as well, but in dish E the usual conditions as regards numbers are reversed. There is no doubt that the formation of clusters in a high concentration of larvae is an unfortunate complication in experiments of this kind, and so is the absence of natural currents to assist the detachment of larvae

endeavouring to pull themselves free from surface sand grains to which they have become too strongly fastened by their anal papillae.

The health of the larvae in dish C was not very good; there were some small ciliates in this dish and some of the larvae were being attacked. In dish D the metamorphosed worms in the Polzeath sand were definitely unhealthy, stumpy and not well formed. Those in the Bullhill sand of the same dish were on the whole healthier and livelier and better formed. The health of dish E was good and the metamorphosed worms in both kinds of sand were in good condition, but again those in the Bullhill sand seemed superior in this respect. They had on the whole larger bodies, longer bristles and a generally better appearance of well-being.

General Conclusions

Additional experiments are planned for the future, and therefore it is not thought fitting at this stage to enter into a complete discussion of the results so far obtained, nor to consider exhaustively the literature bearing on the subject. Some major points have, however, emerged, and it is right that these should be summarized. Some comparison with Jägersten's remarkable results must also be made.

Jägersten (1940) worked with larvae of *Protodrilus rubropharyngeus* Jägersten which he obtained by tow-netting. In a series of extremely interesting experiments he found that in the shell gravel in which this particular species of *Protodrilus* lives, and apparently also in other gravel of similar character, there is a metamorphosis-producing substance, inorganic in nature and extremely resistant to boiling in water, incineration, treatment with alcohol, formalin, acids, etc. It can be destroyed by prolonged soaking in fresh water and by boiling for 2 hr. in nitric acid, but not by several hours' boiling in sulphuric and hydrochloric acids or sodium hydroxide. Jägersten states that quite a small fragment from shell gravel containing the substance will cause *Protodrilus* larvae to metamorphose when it is placed with them in an otherwise clean dish of sea water. Moreover, small stones of granite, etc., can be activated by contact, for one or two days, with active gravel particles, and these small stones will bring about metamorphosis if dropped into a dish containing swimming larvae. Even sea water which has been standing for some weeks over active shell gravel will by itself induce metamorphosis reactions. The metamorphosis-producing substance can be filtered off from such water, the filter paper used becoming active, the filtered water inactive. Thus *Protodrilus* larvae react, not to the physical nature of the bottom soil, but to some obscure chemical substance which dissolves only slowly in water and is remarkably stable when treated with a great variety of reagents.

In a previous paper (Wilson, 1937) I suggested that larvae such as those of *Scolecolepis*, in which the adult occupies a fairly well-defined zone on the shore, select not merely mud as such but that they are perhaps most

strongly attracted to mud inhabited by the adults. I had in mind some sort of chemotaxis to the ancestral home. It has always seemed possible that the larvae of a gregarious species such as *Sabellaria alveolata* (in which, so far as is known, asexual reproduction does not occur), which forms huge honeycomb masses of sandy tubes on suitable shores, may be strongly attracted by the presence of adults or young worms already settled and be induced to settle alongside them. If this be so, it seems likely that the larvae perceive the presence of the adult worms by some sense other than the tactile one. I was thus fully prepared to find that *Ophelia* larvae would show some chemical perception of the sand in which the adults had been living, and some of the experiments were designed to test for this. So far all the results directed to this end have been negative and all positive results have indicated that actual physical contact with the sand, perceived most probably by the tactile sense, is the stimulus to metamorphosis. This stimulus is strongest when the grade of the sand and the shapes of the particles composing it are identical with that of the sand from the Bullhill Bank in which the adults live. The more the character of a sand departs from that of the Bullhill Bank the less readily will larvae metamorphose in it. Mineral composition is probably not so important a factor as shape and size of the sand grains—well-rounded smooth grains, the majority of which pass 40 meshes to the inch but are retained by 86 meshes to the inch, are the main requirement, and the sand must be loose and clean. It is probably not so much the size and shape of the grains which is the stimulus to metamorphosis as the sizes and shapes of the interstices among the grains. It should be remembered that the larvae at metamorphosis are in length one-third to one-half the diameter of the commonest sizes of sand grains present in the Bullhill Bank sand (see Plate XV, figs. 1–3). It may well be, therefore, that smooth rounded grains, each in diameter two to three times the length of the larvae, have among them interstices of sizes and shapes giving degrees of contact with the body of the larva crawling amongst them that induce it to remain there and metamorphose. In other words, if it *feels* right, it *is* right, and the larva seeks no further.

The experiments described in this paper give no indication at all that Bullhill Bank sand, or any of the other sands such as that from Penrhyn Bay which is a moderately efficient stimulus to metamorphosis, contain any slowly dissolving substance that brings about metamorphosis as in the manner of the shell gravel which is active for Jägersten's *Protodrilus*. The indications are, indeed, all against it. The fact that by mixing Carborundum grit with the Bullhill sand metamorphosis is long delayed or prevented altogether is more easily explained on the physical theory than the chemical. So, too, is the effect of cementing the sand in a single layer on the bottom of the dish so that the grains are immovable, though only bedded in the cement on their undersides, leaving most of their surfaces free to release any soluble substances they might contain. It seems that the grains must be movable as well as of the

right shapes and sizes; a single layer of grains anyhow will hardly produce interstices comparable to those in a pile of sand. Larvae on surface films just above Bullhill sand hardly ever metamorphose, though they may be there for several days, and the same is true of larvae on the glass bottoms of dishes containing restricted piles of the sand. Larvae are not chemically attracted to these piles but seem to find them by chance contact. Moreover, the finest grades of Bullhill sand, though composed of the same minerals and presumably containing the same, if any, soluble matter as the coarser grains are almost as inactive in a metamorphosis producing sense as are Carborundum grit and sands of sharp angular particles. On the other hand, a proportion, though admittedly a very small proportion, of larvae can be induced to metamorphose by supplying fragments of broken cover-glass or glass wool (Exp. 4), substances unlikely to contain a soluble metamorphosis-producing substance but which might now and again produce interstices of appropriate sizes and shapes which, if found by larvae, would be mistaken for the proper environment. The same remark applies, of course, to the Eddystone shell gravel, gritty sands of angular particles and other unsuitable soils where some of the larvae metamorphosed.

This difference between the reactions of *Ophelia* larvae and those of *Protodrilus* as reported by Jägersten is, of course, in no sense a contradiction of Jägersten's work or of the conclusions he has drawn from it. Neither does my work rule out entirely the possibility of some chemical perception of the grains at close range being employed by the larvae, although it makes such a possibility seem improbable.

Ophelia larvae kept indefinitely under clean conditions or with the wrong kind of substratum either die without metamorphosing or eventually make some attempt to metamorphose. This often consists only in the loss of cilia, but sometimes metamorphosis is successful and more or less normal young worms are produced. Much seems to depend on the health of the larvae at the time, and really healthy larvae seem to last longer without showing signs of metamorphosis than do less healthy ones. In clean dishes the larvae on the bottom as a rule show incipient signs of metamorphosis sooner than do those on the surface film; it is as though contact with something solid does in itself constitute some degree of stimulus quite apart from consideration of shape and size.

The possession by pelagic larvae of the ability to choose the right substratum during a period of time that may amount to several weeks in some species, as in *Ophelia*, is undoubtedly of especially great advantage to those species that are confined when adult to a particular kind of bottom soil, or any other form of restricted type of habitat. It is not intended here to enter fully into the implications on ecological distribution and similar fields of inquiry which this discovery opens up. Points concerning it were made in an earlier paper (Wilson, 1937), and Thorson (1946) has recently discussed the subject

at some length and has described some experiments with bottle collectors that 'seem to support the conjecture that marine bottom invertebrates are able to actively choose their substratum' (p. 465).

In the Exe estuary there are a variety of bottoms, some differing widely from the conditions on the top of the Bullhill Bank where *Ophelia* reaches its maximum abundance. The larvae, by their ability to distinguish between the various types and by their selection only of those which are appropriate for adult life, are led to concentrate in the latter and so maintain the normal distribution of the species in the estuary. The pelagic stages will be carried to and fro in and out of the estuary with the tidal currents, and whilst some may be lost out to sea it seems probable that the main swarm does not get dispersed to distant places but remains about the estuary mouth. This must be so, otherwise the species would not be able to maintain itself in that locality, for as far as is known it is not present on outside shores or grounds in the immediate vicinity of the Exe, though full investigation has not yet been made.

Among the grounds over which *Ophelia* larvae will be carried will be the Salthouse Lake area already mentioned. The sand of this area is, as we have seen, generally of a finer grade, more compact and not quite as clean as is the looser sand of the Bullhill Bank. It supports a normal sand fauna with a relatively few *Ophelia* present in some areas. The samples of sand from these areas which have so far been analysed showed a preponderance of grains between the 60- and 100-mesh sizes, but there was a higher proportion of grains between the 40- and 60-mesh sizes than in the Salthouse Lake sample used in the experiments and whose composition is given on p. 735. This latter sand is, as was seen in Exps. 7, 12 and 13, not as effective in bringing about metamorphosis as is the Bullhill Bank sand, and it may be presumed that the rather similar sand from the Salthouse Lake area where a few *Ophelia* may be found (about 12 per m.^{2} as against up to 268 per m.^{2} on the Bullhill Bank, according to Mr N. A. Holme's figures—private communication) would likewise be relatively unattractive to the larvae. If this be so, we have a reasonable explanation of the observed distribution of *Ophelia* in the Exe estuary, a heavy concentration in the metamorphosis-stimulating sand of the Bullhill Bank and the Polesands, with a much lower concentration in the less stimulating Salthouse Lake area. As the larvae in the later pelagic stages drift over the banks the majority of these coming into contact with the Bullhill sand will enter it and stay there, but of those washed over the Salthouse Lake only a small proportion will settle, the majority will leave the sand after testing it and, continuing pelagic life, may later on eventually reach the Bullhill Bank or the almost equally suitable Polesands nearer the open sea. This explanation is at least as reasonable as supposing that there is an even settlement over the whole area followed by greater destruction of the young worms in the unfavourable soils, and the results of these experiments support it.

Summary

Experiments with larvae of *Ophelia bicornis* Savigny have shown that they metamorphose most readily in sand from their natural habitat and with hesitancy or not at all in sands from other sources. Their natural sand consists largely of smooth rounded grains of quartz, very uniform in size; sands of smaller and more angular grains are unfavourable to settlement and metamorphosis. It appears that size and shape of the sand grains, or perhaps, more likely, the sizes and shapes of the interstices among the grains, perceived probably by the tactile sense, is the main stimulus to metamorphosis. Chemical substances dissolving out of the sands do not seem to be responsible for this.

There is a period of time, amounting under favourable conditions to several weeks, during which an *Ophelia* larva is able to settle and metamorphose as soon as it comes into contact with a substratum suitable for adult life.

The ability of the larvae to distinguish bottom deposits suitable for adult life from those which are unsuitable must be of great advantage to the species in maintaining normal distribution and in conserving larvae.

Larvae kept indefinitely in glass dishes without sand, or with a deposit of the wrong kind, eventually either die without metamorphosing or attempt to do so with greater or less success.

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EXPLANATION OF PLATES

PLATE XV

Photomicrographs of living *Ophelia* larvae, × 50.

Fig. 1. Unmetamorphosed larva attached to a sand grain by the anal papillae. The larva is squat in shape and the region of the prototroch is dark and distinct.

Fig. 2. Larva in early metamorphosis crawling on the bottom of a glass dish. The larva is elongating and the dark prototrochal tissues are less distinct.

Fig. 3. Two metamorphosed larvae on a large sand grain; one is attached by the anal papillae, the other is crawling round the grain. The body is longer and the head narrower than before and no dark prototrochal tissue remains. The central portion of the gut is dark and distinct. In the original photograph the long bristles are visible, but are likely to be lost in the reproduction.

Fig. 4. Cluster of about one hundred unmetamorphosed larvae attached to a cotton fragment.

All larvae were from the same experiment and were 13 days old. The cluster was from a clean dish without sand, the others were from a dish containing Bullhill Bank sand. Photographed in July 1948 with electronic flash apparatus using a Mullard LSD3 flashtube. Duration of exposure about $\frac{1}{3000}$ sec.

PLATE XVI

Photomicrographs of sands, × 21.

Fig. 1. Bullhill Bank sand.

Fig. 2. Bullhill Bank sand, 86–100 mesh.

Fig. 3. Salthouse Lake sand.

Fig. 4. Kames Bay sand.

PLATE XVII

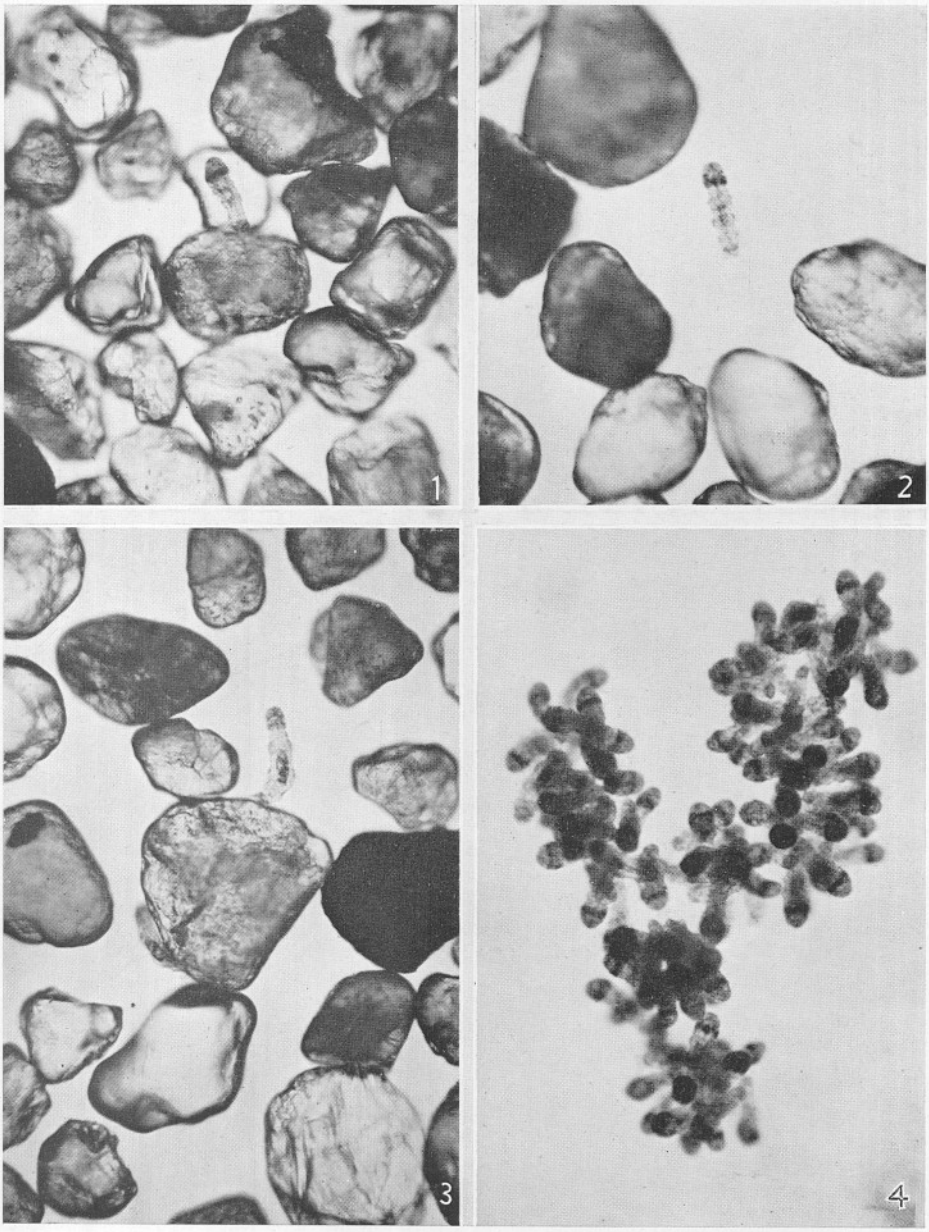
Photomicrographs of sands and 'Grits', × 21.

Fig. 1. Penrhyn Bay sand.

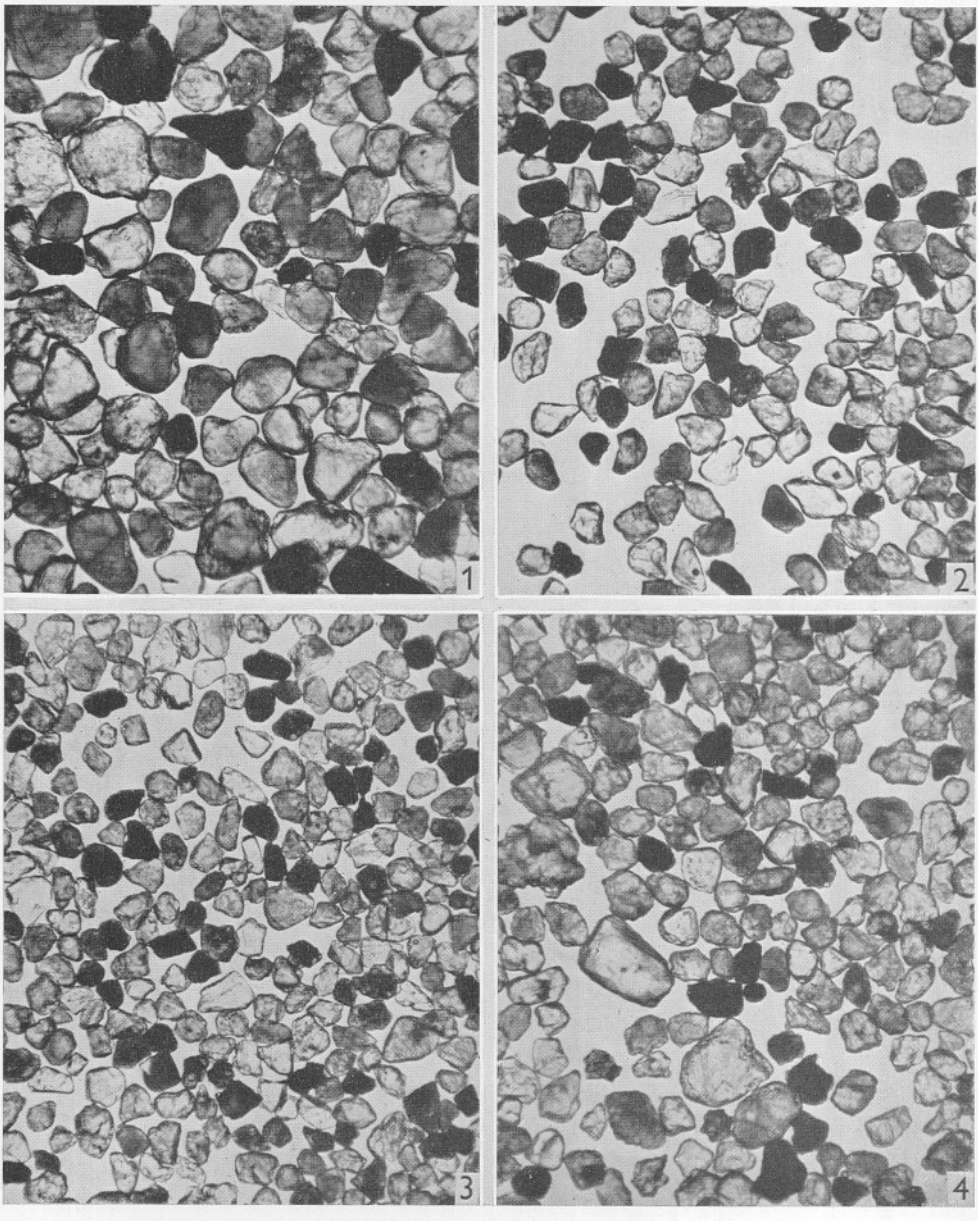
Fig. 2. Polzeath sand.

Fig. 3. Fine 'Gritty' sand.

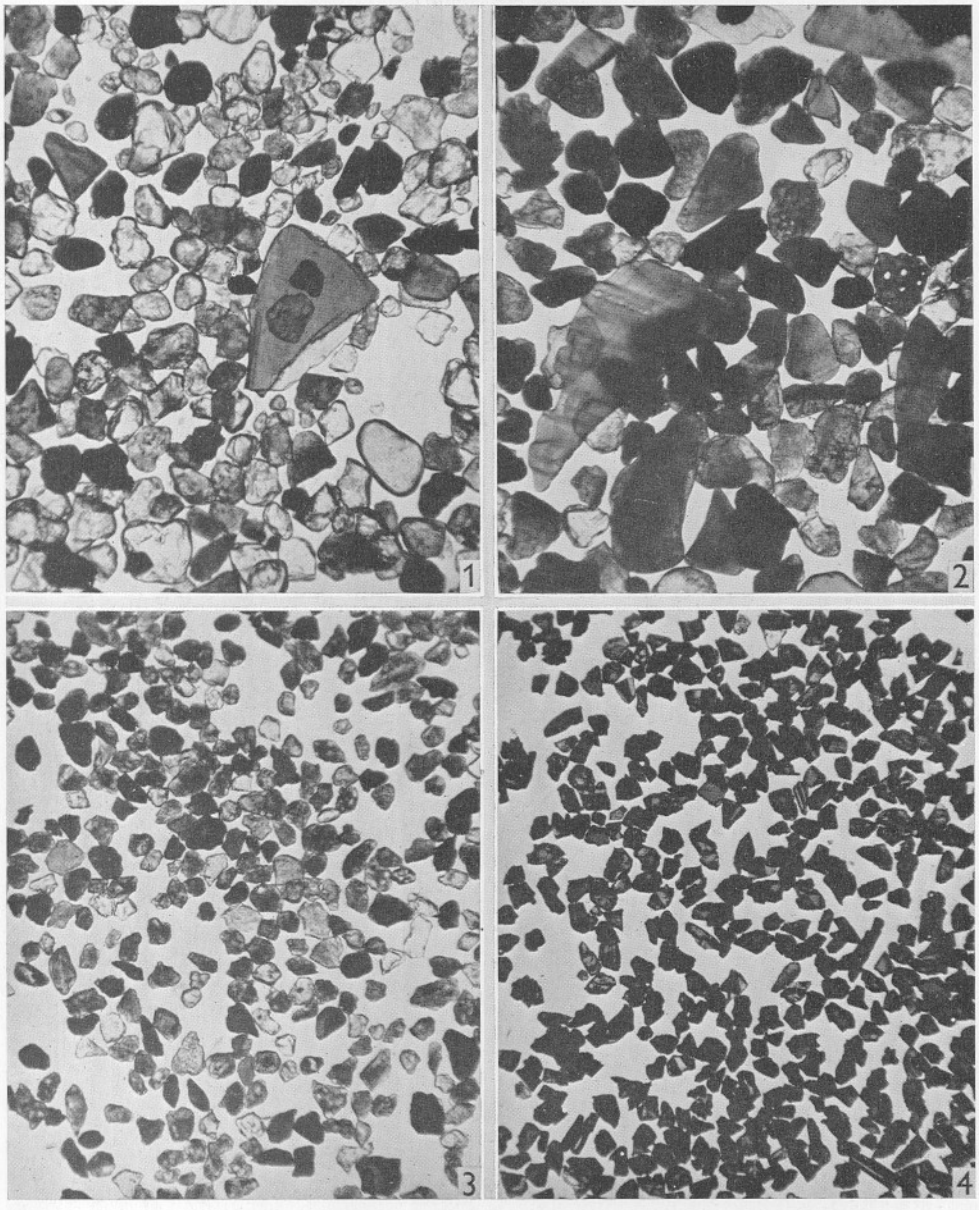
Fig. 4. Carborundum grit No. 120.



Figs. 1–4.



Figs. 1–4.



Figs. 1–4.

THE PLYMOUTH LABORATORY OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM[1]

By F. S. Russell, F.R.S.

Director of the Plymouth Laboratory

(Plates XVIII–XXV and Text-fig. 1)

In *The Times* of 31 March 1884, it was announced that a meeting would be held that day in the rooms of the Royal Society for founding a society having for its purpose 'the establishment and maintenance of a well-equipped laboratory at a suitable point on the English coast, similar to, if not quite so extensive as, Dr Dohrn's Zoological Station at Naples' (M.B.A., 1887*a*). With Prof. T. H. Huxley in the chair a gathering of distinguished gentlemen gave reasons why such a laboratory should be built. All stressed what its value would be from the purely scientific viewpoint, and all were agreed that both by fundamental research and by more direct investigations on our food fishes, knowledge of economic import would be gained. The last speaker, Mr George J. Romanes, said that there was one function of the proposed laboratory which had not received the attention it appeared to deserve; he meant the investigation of invertebrate physiology. 'In the invertebrate forms of life', he said, 'we saw life in its simplest shape, and in the shape which best admitted of observation and experiment, with the view of throwing light upon most of the great questions relating to the processes of life' (M.B.A., 1887*b*).

As a result of this meeting a corporate society, the Marine Biological Association of the United Kingdom, came into being. It was decided that the laboratory should be built at Plymouth where a rich and varied fauna was available. The building, which was opened on 30 June 1888 (M.B.A., 1888), is situated under the walls of Charles II's Citadel in a commanding position overlooking the waters of Plymouth Sound.

The Association, which owed its inception largely to the initiative and energy of Sir E. Ray Lankester, received and still receives financial support from persons interested in the study of biology and the sea, who are the members of the Association. In addition, considerable financial backing was given by a number of Universities and other public bodies, and notably the Fishmongers' Company. From its beginning an annual grant was made by H.M. Treasury,

[1] This lecture was delivered to the Royal Society on 6 March 1947 (*Proc. Roy. Soc., London*, B, Vol. 135, pp. 12–25, 1947), and is reprinted in this Journal by kind permission of the Council of the Royal Society.

and after the 1914–18 war this grant began to assume considerable proportions when it came under the control of the Development Commissioners.[1]

In 1902 the Association was asked by H.M. Treasury to undertake the English share of the scientific investigations which formed part of the programme of the International Council for the Exploration of the Sea (M.B.A., 1903). The English share of these international fisheries investigations was divided under two heads.

I. A survey of the trawling grounds and fisheries in the southern North Sea, together with scientific observations on migrations, feeding and rate of growth of the more important fish. For this purpose the Association also ran a laboratory at Lowestoft.

II. A hydrographic and plankton survey of the western half of the English Channel.

After the 1914–18 war the Lowestoft laboratory 'was re-established under the Ministry of Agriculture and Fisheries for the purpose of studying problems having a direct bearing on the commercial fisheries. At the same time a substantially increased grant was made to the Marine Biological Association for the maintenance of the Plymouth laboratory, so that researches of a more general or fundamental nature concerning life in the sea might be developed on a larger plan' (Allen & Harvey, 1928). The years between the two great wars saw an increased staff at the Plymouth laboratory, and constant additions to the buildings and improvement of facilities for research of all kinds.

Over the period that the Association has been in existence it is possible to trace a sequence in the development of the work from the titles of the many papers in the Association's own *Journal* and its other publications (M.B.A., 1928). It should be remembered that in the earliest days practically nothing was known about the life histories and habits of even our commonest food fishes, and few carefully compiled accounts of the commercial fisheries were in existence. Since the avowed objects of the Association (M.B.A. 1887*b*) were to establish one or more laboratories on the British coasts 'where accurate researches may be carried on leading to the improvement of zoological and botanical science, and to an increase of our knowledge as regards the food, life, conditions and habits of British food fishes, and molluscs in particular, and the animal and vegetable resources of the sea in general', it was only natural that the emphasis in the beginning had to be on fishes. Accordingly, we find that a large number of the earlier papers were devoted to observations on the habits of fishes, shellfish and other products from the sea, and to the collection of information on the methods and results of commercial fishing. This was very necessary, because the few naturalists concerned had to have a general picture of these matters to be able to answer with some feeling of authority the many questions that must have been put to them once the Association was founded.

[1] An interesting account of some of the early history of the Plymouth laboratory is given by G. P. Bidder (1943) in his obituary notice of Dr E. J. Allen.

I have no doubt that quick results were expected in those days as they still are in certain quarters to-day.

But in addition to doing fishery research, the few naturalists of the staff, together with a number of enthusiastic visiting workers, were building up a knowledge of the marine fauna and flora off Plymouth and its neighbouring coasts. This again was a first requirement, because in all branches of science the systematic observations must come first. More direct fishery research also naturally received considerable attention as a result of the assumption of the English share of the investigations under the International Council for the Exploration of the Sea. But some of the programme of these investigations gave opportunities for increasing the pure scientific observations and studying the environmental factors in the sea over a wide area. Thus much of the foundation was laid for our knowledge of the hydrological conditions round the British Isles, of the fauna of the sea floor, and of the microscopic plants and animals which drift with the water and form the plankton.

Looking back over the first twenty years of the Association's life it is remarkable how much ground was covered by the few research workers available and how well balanced on the whole had been the distribution of the investigations. A most valuable fauna list (M.B.A. 1904, 1931) had been produced, a beginning had been made in the study of the distribution of the animals in relation to their environment, and fishery research had been put on a solid basis. Many papers on the morphology and development of marine organisms had been published, and, in addition, here and there appeared a paper somewhat before its time which gave advanced indications of other possible uses to which the Plymouth laboratory might be put.

After the 1914–18 war there was a noticeable change in the subject matter of the contents of the Association's *Journal*. With the taking over of fisheries research by the Ministry of Agriculture and Fisheries the work at Plymouth became for the greater part fundamental in nature. All the emphasis was on the study of the chemical and physical conditions of the environment, the life histories and development of marine invertebrate animals, and the distribution in space and time of the animal populations. But at the same time the economic aims were not entirely lost sight of and a certain amount of research on the biology of fishes was continued. Such a preservation of a link with more direct fishery research is of value if only because it necessitates that contact shall be kept with current work elsewhere. The Association has, for instance, undertaken research on the breeding and habits of the mackerel, the distribution of seals, the effects of T.N.T. on oysters, and other problems, at the request of the Ministry of Agriculture and Fisheries. But such research should not nowadays be needed as a justification for receiving a Government grant. All fundamental researches in the long run justify themselves, and the bulk of the work done at Plymouth is essentially fundamental in nature.

Thanks to the valuable work of the Fisheries Departments our factual know-

ledge of the important food fishes is such that the populations of fish on which our food supply depends can now be watched with a view to the regulation of the catches. The major picture of the distribution, migrations, growth and spawning habits of the common fish is now well known. But what the underlying factors may be, on which the fishes' lives and habits depend, remain to a large degree unsolved, and their solution lies more in the realms of pure science. It seems likely, therefore, that all fisheries research will become more fundamental in nature and aimed at understanding the great natural fluctuations in the fish populations and the causes of the habits of the fish themselves.

It may be noted that most of the researches that have been undertaken in recent years by the staff of the Plymouth laboratory can be built around two main underlying themes. The first is how much living matter can the sea produce, what are the variations and causes of variation in productivity, and how do the organisms obtain the materials necessary for life? The second is how do marine animals in general live, how do they fit their various individual environments, and what alterations in the conditions in their environment can they appreciate? Both require a knowledge of the physical and chemical conditions in the sea. Where the productivity of the sea is concerned the sea water is the medium which contains all the ingredients necessary for the successful growth and development of the living organisms; in so far as the general biology of the animals is being studied it is the conditions in the sea water which determine their distribution, habits and migrations.

The Plymouth laboratory is therefore equipped for studying the physics and chemistry of the sea. Researches of the staff are aimed at the development of methods for estimating the quantities of nutrients in the sea water upon which the unicellular plants depend and following the changes they undergo throughout the year and from place to place in relation to the plant crop. The approximate yearly cycle of the more abundant constituents, phosphorus, nitrogen and silicon is now known. But much remains to be done in studying their rate of turn-over, and long-term investigations have shown periodic fluctuations in the amounts available. This is now being linked with hydrological observations on the movements of water masses and their origins, for much will depend upon whether the water is drawn from the rich deep ocean layers upwelling on the continental shelf or from the more depleted surface waters.

One of the first necessities in this research is a knowledge of the amount of photosynthesis; photoelectric methods have therefore been adapted for the measurement of the penetration of light into the sea, and the extinction by absorption and scattering of its component wave-lengths at varying depths.

In order to solve some of the problems thus posed it is necessary to work with pure cultures of diatoms and flagellates, and for many years attention has been given to this side of the work. Advances have thus been made in our

knowledge of the utilization of combined nitrogen and phosphorus by the plants, these constituents often being present in such exceedingly low concentrations in the sea as to limit plant growth. Research is also being made on other substances, necessary only in minute quantities as trace elements, now known to play a vital part in the growth of land plants. Thus the concentration of both iron and manganese is probably suboptimal in some waters and may indeed limit plant production.

It is on the production of these unicellular plants that all the animal life in the sea depends, and ultimately those fish which form so valuable a part of man's food supply. The first link in the chain from plant to fish is the minute animal life of the plankton. Not only are these eaten directly by such fish as the herring and the mackerel, but they are of direct importance to nearly all species of fish, because when first they hatch the young fish are too small to eat anything larger. Researches on distribution, abundance, growth and habits of the many species of animals in the plankton therefore form a necessary part in the general problem of productivity. The effects of grazing off the plant crops by these animals can be studied at sea by evaluation of their numbers in measured volumes of water, and in the laboratory by experiments on the rate the animals eat the plants when cultured.

Observations on the distribution of the plankton organisms are made also in connexion with the hydrological surveys. It is found that some species are restricted to certain types of water, and they can thus be used as indicators of their respective water masses. Some waters in the Plymouth area, which are thus clearly characterized biologically, are not readily distinguishable by the usual hydrological features such as salinity and temperature. Such biologically distinguishable waters may differ markedly between one another in the amount of life they carry. This must in turn be related to their chemical content.

Other links in the chain are the bottom animals upon which the growing fish feed. It is necessary first to know the distribution of these animals. The bottom deposits of the sea are not uniformly distributed, ranging as they do from the finest mud to the coarsest gravel according to the movements of the overlying water. Each kind of deposit has its characteristic fauna; and recent researches have shown that the microscopic larval stages of some animals will only undergo their normal metamorphosis if they can find the individual grade of soil they live in. The estimation of the food available in different deposits has received attention, and attempts have been made to evaluate the animal contents of standard samples of deposit.

There is another link in this productivity chain whose connexion may not at first appear obvious. Quite early in the history of the Marine Biological Association the opportunity was taken, while studying the distribution of bottom animals, to examine also the stones and rocks dredged up in order to throw light on the geology of the English Channel. A knowledge of the configuration

of the sea floor is of importance for the study of water movements. The shape of the continental edge where it passes over from the shelf to the steeper continental slope may be of critical importance, for it is here that the deeper waters of the ocean, rich in nutrient salts, are brought towards the surface at times by upwelling and reach the photic zone. It may well be that embayments resulting from submerged valleys may cause submarine waves to increase their amplitude and thus reach higher levels.

Let us now consider the second major line of research, the biology of marine animals. Every species of animal in the sea can form a subject for enquiry, and each alone can pose nearly all the problems of biology. The sea provides a greater variety of animals than any other environment. In it are to be found representatives of all the groups of the animal kingdom, the insects alone being scarcely represented. Many groups indeed are found almost exclusively in the sea. The facilities offered by the Plymouth laboratory therefore afford an inexhaustible mine for any biologist, and it becomes difficult to canalize the work into any single objective line. There is scope for systematists, for morphologists and embryologists, for students of life histories and behaviour, for geneticists and so on. In general it may be said that, once the ground has been laid open by the systematists, research has chiefly been directed towards the description of the life histories of animals important in the general economy of the sea, of their food and methods of feeding, of their breeding and rate of growth, their parasites, and of their relationships with their animate and inanimate environment. Many of the results of investigation obviously have also a bearing on the general problem of productivity. In this wide field for research the emphasis tends to vary from one direction to another according to the predilections and aptitudes of the individual workers, but, apart from their value as contributions to general biology, any one of them can be shown directly or indirectly to have its practical bearing. Knowledge of the life histories and habits of fishes in general has obvious value, even where species of no commercial interest are concerned, since they are all competitors for the common food supply. Very useful results have accrued from investigations on the herring, which at one time formed an important winter fishery at Plymouth, attracting a hundred or more steam drifters from the east coast ports. In the early 1930's the herring ceased to come in their usual numbers to the grounds near Plymouth, and it became possible by local observations to warn the industry of the reduced chances of a successful fishery and thus save the considerable expense of sending ships to the area. The causes of the disappearance of the herring are, however, of the greater fundamental interest and the answer may be found when our knowledge of water movements grows.

Apart from the more obvious necessity of research on the biology of crabs, oysters, mussels and other shellfish used for food, knowledge gained about invertebrate animals in general has proved its worth. The annual cost to the nation resulting from damage to underwater structures by boring organisms

and by the fouling growths on ships' bottoms is immense. All attempts to reduce this wastage by improved methods require at the start a knowledge of the natural history of the organisms concerned. Other departments are now taking up antifouling problems, but they begin with a basic knowledge already supplied by fundamental researches.

It is not wise in the long run to restrict observations only to those organisms known to be of economic interest. It has been noteworthy that our common coastal seaweeds attracted little attention in the past. In relation to the general economy of the sea as a whole the narrow fringe of weeds around our coasts is of small importance; probably largely for this reason the seaweeds were neglected. But during the war, when supplies of certain raw materials were cut off, seaweeds were needed as a source of supply of alginic acid, agar and mannitol. It was then realized that we knew practically nothing of the rate of growth and breeding of our commonest weeds, and investigations were immediately begun.

I think this necessity for the accumulation of knowledge without regard for its immediate practical value should be stressed, for it has proved itself abundantly worth while. The Association has often advised Government departments with resulting savings in expense. A knowledge of the effects of temperature on the rate of growth of marine organisms was incidental in the destruction of fouling organisms and their prevention for many succeeding years in a large basin in one of our naval dockyards. And, in passing, it is worthy of mention that research on the preservation of ropes and nets, besides enabling the Plymouth laboratory to make considerable economy in the use of expensive silk plankton nets, resulted in great saving for the Ministry of Home Security when proven methods were adopted for preserving sand bags.

But marine animals live not only in the open sea. They inhabit the intertidal zones of the shore and they invade the estuaries. Work cannot therefore be limited to offshore waters; the shores and estuaries must also receive attention. The examination of the estuarine fauna is of great interest physiologically, and a detailed knowledge of the distribution of the different species in relation to the normal changing conditions is of value in assessing pollution. As a result of a close study of a water shrimp (*Gammarus*), primarily as a subject for genetics, certain species are proving to be valuable estuarine indicators.

From the point of view of life in the sea as a whole it should be realized that work at Plymouth touches only the borders of the great oceans, whose study lies within the province of the highly organized oceanographical expeditions. Nevertheless Plymouth plays its part in the promotion of oceanographical research. This is especially so in the development of methods. Many of the methods used on ocean-going expeditions have been developed at Plymouth. This is an essential part of the laboratory's work. Once an oceanographical expedition is equipped and its programme planned it is necessary that the

majority of the observations should be carried on by routine methods, for results lose comparative value if they are constantly varied en route. At Plymouth, however, there is full opportunity to develop methods in the laboratory and test them out at sea. Each succeeding cruise by the ocean-going research vessels may therefore take advantage, and employ the improved methods and attack new problems for which the necessary technique had been awaiting development at a shore laboratory.

This brief review of the problems open to investigation shows some of the field of research available to the Plymouth staff. The scientific staff is small, only a dozen or so in number. The most that can be done is to distribute this staff in a balanced manner so that there is one engaged in each of the possible major lines of inquiry. Some might argue that it would be better to concentrate all the energy on to one specific problem. This could only be done by the formation of a school and the interests of the leaders of this school might determine a one-tracked course for many years.

This should never be at Plymouth, because there is another most important side of the laboratory's work upon which I have not yet touched. It has been a tradition of the Plymouth laboratory that it shall attract visiting research workers. The constant flow of visitors gives life to the buildings and, with its ever changing interests, affords invaluable points of contact for the staff. It is essential, therefore, that the interests and experience of the staff should cover as wide a field as possible so that visitors may receive assistance and mutual benefit be derived.

The additions to scientific knowledge produced by the many visitors must exceed those of the staff itself and they are for the most part published in journals other than that of the Association. Much of this work has been on traditional biological lines, but it may be noted that, even on the day of the Association's foundation, the words of Romanes pointed to other fields. When the time was ripe the scope was broadened to include the comparative physiology of marine animals. In this direction Plymouth has always been understaffed, but it has for long been the aim as far as space will allow to equip the building with the necessary facilities and apparatus so that visiting workers may fill this gap.

The physiological researches made at Plymouth have been very varied, and mention only can be made here of some of the subjects which have received attention. The common spider crab (*Maia*) has been much used for studying the heat formation in nerves and other problems of the physiology of nerves; the same animal also supplies material for the study of the respiratory blood pigment, haemocyanin. The sea urchin (*Echinus*) has been a fruitful animal for experiments on fertilization and development since its eggs are most suitable in nature. Advances have been made in our knowledge of the nervous coordination of the movements of fishes and on the physiology of the regulation of their colour changes. The functions of the lateral line system in fishes have

been partly elucidated, and our knowledge of the labyrinth has been advanced owing to the unique suitability of the dogfish (*Scyllium*) as a subject for experiments.

Nervous systems in their simplest form have been studied in the sea-anemone, and in recent years the squid (*Loligo*) and cuttlefish (*Sepia*) have received prominent attention because they possess giant nerve fibres on which much can be done which is not possible with other nerve fibres; these giant fibres are also to be found in other marine animals, notably some polychaete worms and Crustacea.

Much remains to be done on the physiology of marine animals, and one direction perhaps in which our knowledge is especially lacking is that of the sensory perceptions and environment of animals in the sea.

From these few examples it can be seen that the practical benefits resulting from the founding of the Marine Biological Association may have a wider application than is expressed in its original aims, for these physiological researches have a very definite connexion with the medical sciences.

In this account I have omitted to mention by name the many distinguished men of science whose researches have resulted in the success of the Plymouth laboratory, and who, together with the Association's many devoted benefactors, have raised the laboratory to its present position of world repute. I cannot, however, let the occasion pass without reference to the late Edgar Johnson Allen who, as Director for 42 years, was the guiding genius to whom the Marine Biological Association owes so much of its success (Bidder, 1943; Kemp & Hill, 1943). It is interesting to recall Dr Allen's published works. These were comparatively few, but it is noteworthy that they touched on nearly all the main fields of research covered by the laboratory. To him was due the pioneer work on the culture of diatoms which made possible the great advances in our knowledge of the productivity of the sea. He produced the first important publication on the bottom fauna with his work on the Eddystone-Start grounds, and he was an acknowledged authority on the systematics of polychaete worms. His writings cover many problems concerning fish and other products of the sea. He co-operated in work on development and heredity, and had a deep interest in evolution; and it is perhaps significant that his first researches were on the nervous system of Crustacea. I think this is sufficient to show why the Plymouth laboratory never developed into a one-sided institution.

It would be unfitting also if I failed to include the name of the late Director, Stanley Kemp, whose death came as so tragic a blow just as the war was ending (Hardy, 1946). Dr Kemp's name will go down in history as that of the leader of one of the greatest oceanographical expeditions of all time. The *Discovery* Expedition has become a living institution, and the loss of Dr Kemp is deeply felt by all biologists and most by the staff of the Plymouth laboratory.

I should like also to record one name out of those of the Association's many

benefactors, that of George Parker Bidder, for whose wisdom, generosity, and unfailing help in times of need we shall always remain in debt.

The laboratory is managed by a Council of elected members and annual Governors appointed by certain governing universities and other bodies, including the Royal Society, which have given sums of £500 or more. A number of Universities also contribute to the Association by renting tables to which they can nominate research workers. All foreign visitors are welcomed as guests free of charge and every year sees an increasing number of foreigners coming to Plymouth to work and discuss common interests with members of the staff.

The private sources of income of the Association are from these grants and donations, from membership subscriptions and the proceeds of the sales of specimens, collecting gear and journals. By far the largest contributor at the present time is the Government which voted an annual maintenance grant last year of over £25,000. The grant is sanctioned by H.M. Treasury as a draft from the Development Fund, and the Association is deeply in debt to the Development Commissioners, their advisers, and their Secretary, E. H. E. Havelock, for the wisdom and foresight they have always shown in their recommendations for the laboratory's support.

The Laboratory is built of Devonian coral limestone of which the Plymouth Hoe is formed, and marine animals of a past age are clearly visible in the weathered stone. It is not very large; accommodation is restricted by the limited area available between the Citadel walls and the road. It consists of a main south building with the two upper floors divided into working rooms in which about twenty-four workers can be accommodated. Connecting with it is a north block containing the chemical and physiological laboratories. Underneath are cellars excavated from the solid rock which, on account of their uniform temperature and freedom from vibration, are most suitable for research requiring very delicately adjusted apparatus. There is a small constant temperature building with two compartments for controlled low temperatures.

The north block can take about sixteen research workers. The whole laboratory can thus accommodate some forty people[1] at one time, although this number can always be increased by a little 'crowding up'. The present permanent scientific staff numbers twelve, and there are also usually half a dozen or so investigators on long-term grants of a year or more duration. Over and above these about twenty visiting research workers can therefore be accommodated at one time, and it is of course normal for the laboratory to be especially crowded during the summer months when University staffs are on long vacation and visitors come to this country from abroad.

[1] The eastern block of the south building, which was the Director's house, was gutted by fire in a bomb attack. It is being rebuilt as a laboratory and should increase the working accommodation by ten rooms.

There is a valuable library, which is probably the most complete in the country in publications concerned especially with marine biology and oceanography. The library also takes a number of other periodicals likely to be needed by visiting research workers. Many visitors remark on the pleasure of using a library of so compact a nature and with such careful selection of publications.

On the ground floor of the main south building there is an aquarium which is open to the public. Apart from its educational value for the many adults and children who visit the aquarium, the tanks with their living exhibits are a never failing source of interest to the research worker on the habits and behaviour of animals. The exhibits are restricted to the local fauna and provide a representative view of the chief fishes and larger invertebrates of the district.

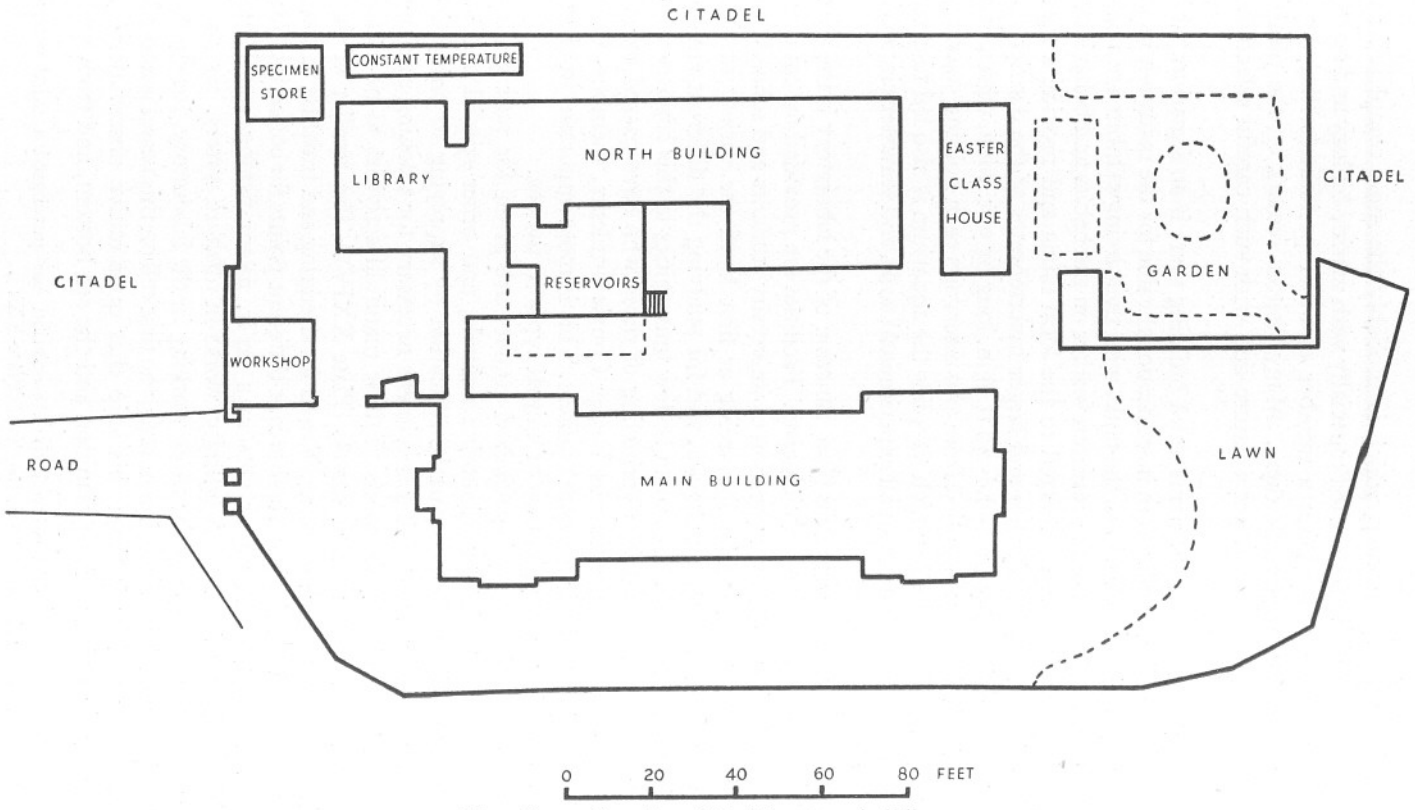
The tanks, the largest of which is 30 ft. 6 in. long by 9 ft. wide, with a depth of water of 4 ft. 6 in., are supplied from two reservoirs each holding 50,000 gal. of sea water. This sea water which supplies the aquarium is also led to certain parts of the laboratory where small experimental tanks and seawater circulation benches are available.

A subsidiary, but nevertheless vital, function of the laboratory is the part it plays in the general training of biologists. Facilities are provided for courses of instruction during the Easter vacation to university students and schools, who have unrivalled opportunities for seeing at first hand the variety of living organisms which abounds in the sea, and for studying the different environments in which they live. There can be few universities in this country whose zoology staffs do not contain a sprinkling of those who have passed some of their time at Plymouth, either as Easter Course students, members of the scientific staff, or visiting research workers. This is most important in view of the overwhelming preponderance of animal types in the sea.

From time to time more specialized courses are given for post graduate students on the physiology of marine animals, and other special subjects. Plymouth also plays another part in education by supplying to universities and schools preserved and living specimens necessary for teaching purposes.

In order to enable the demands of these manifold activities to be met the Association runs two research vessels (Plate XXIV).[1] The smaller of these, a 25 ft. motor boat, the *Gammarus*, is used for dredging and trawling in waters close inshore, and for visiting the shores at different points for collecting intertidal specimens. The larger, at present a 90 ft. motor fishing vessel (R.V. *Sabella*) on charter from the Admiralty, works in offshore waters. As well as making collections generally for those working in the laboratory, for stocking the aquarium, and for the specimen trade, the first call on this vessel is naturally for research at sea. It is from this ship that quantitative observations are made on the organisms of the plankton and the sea bottom, and from which

[1] Since this lecture was first printed the Association has purchased a third research vessel, a 61½ foot motor fishing vessel, the *Sula* (Plate XXV).



Text-fig. 1. Site plan of the laboratory buildings.

physical and chemical investigations are made at sea. The ship also makes periodical cruises farther afield to study the hydrology over a larger area including the western approaches to the English Channel.

I hope I have said enough to give some idea of the general activities of the Plymouth laboratory and the possibilities it affords for work. One might sum it up by saying that it aims to give facilities for any research, not necessarily only biological, on problems for which the sea can provide the materials or the environment required. Its position is unique, lying as it does between the extremes of a fishery research laboratory and of an oceanographical institution, yet serving both, and at the same time offering facilities for visitors like the laboratory at Naples on whose pattern it was first founded. Let us hope it may be allowed to continue to hold this focal position and attract all those interested in the science of the sea and indeed of life itself.

Note. There have been extensive alterations to the Plymouth laboratory since the account written by Allen & Harvey (1928). A new library was built in 1931, and in 1932 the north block was farther extended to the eastward, to give increased accommodation for physiological and chemical laboratories, and improved photographic darkroom facilities. A small constant temperature building was added in 1938. In 1939 the centre of the south building, the original main laboratory, was completely renovated and a new floor added. A site plan as at the present date is shown in Text-fig. 1.

I wish to thank Miss E. J. Batham, Mr D. P. Wilson and Mr G. A. Steven for permission to reproduce the photographs.

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EXPLANATION OF PLATES

PLATE XVIII

View of the Plymouth Marine Biological Laboratory, taken from the Smeaton Tower on the Hoe looking eastwards towards the Cattewater (summer, 1946).

PLATE XIX

Fig. 1. Tank room on the first floor of south building (south side).

Fig. 2. Tank room on first floor of south building (north side).

PLATE XX

Fig. 1. Museum on second floor of south building

Fig. 2. Typical work room in south building.

PLATE XXI

Fig. 1. Reading room on first floor of library.

Fig. 2. Corner of physiological laboratory.

PLATE XXII

Fig. 1. Chemical laboratory.

Fig. 2. Yard between north and south buildings showing reservoirs for sea water on left, outside tanks and circulation bench on right, and end of Easter Course building in distance on left.

PLATE XXIII

Fig. 1. General view of aquarium.

Fig. 2. Anemone tank in aquarium.

PLATE XXIV

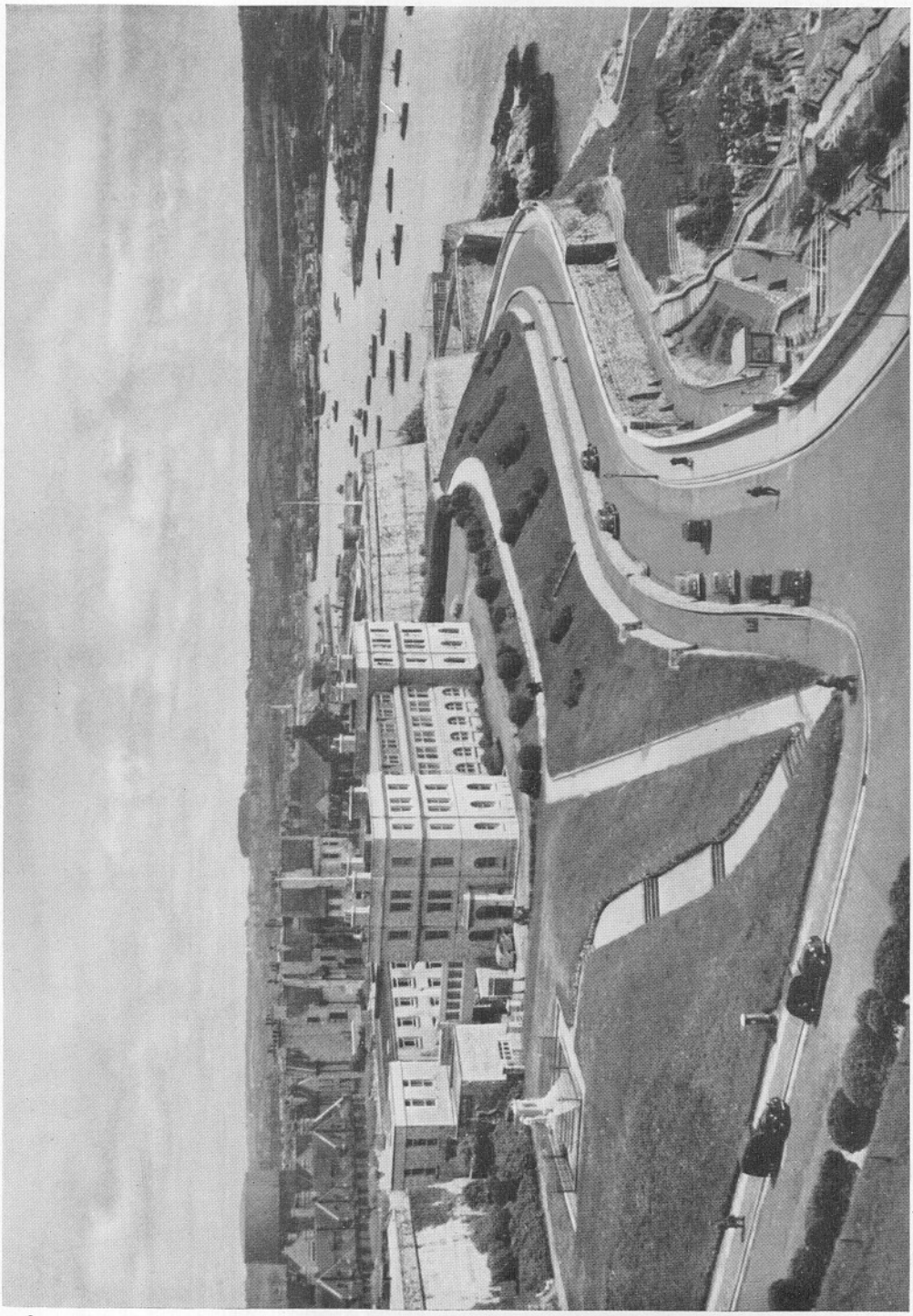
Fig. 1. R.V. *Sabella*.

Fig. 2. Motor Boat *Gammarus*.

PLATE XXV

M.V. *Sula*.

The photographs for Plates XVIII and XXV were taken by Miss E. J. Batham. All the other photographs are the work of D. P. Wilson, except Pl. XXIV, figs. 1 and 2, which were taken by G. A. Steven.



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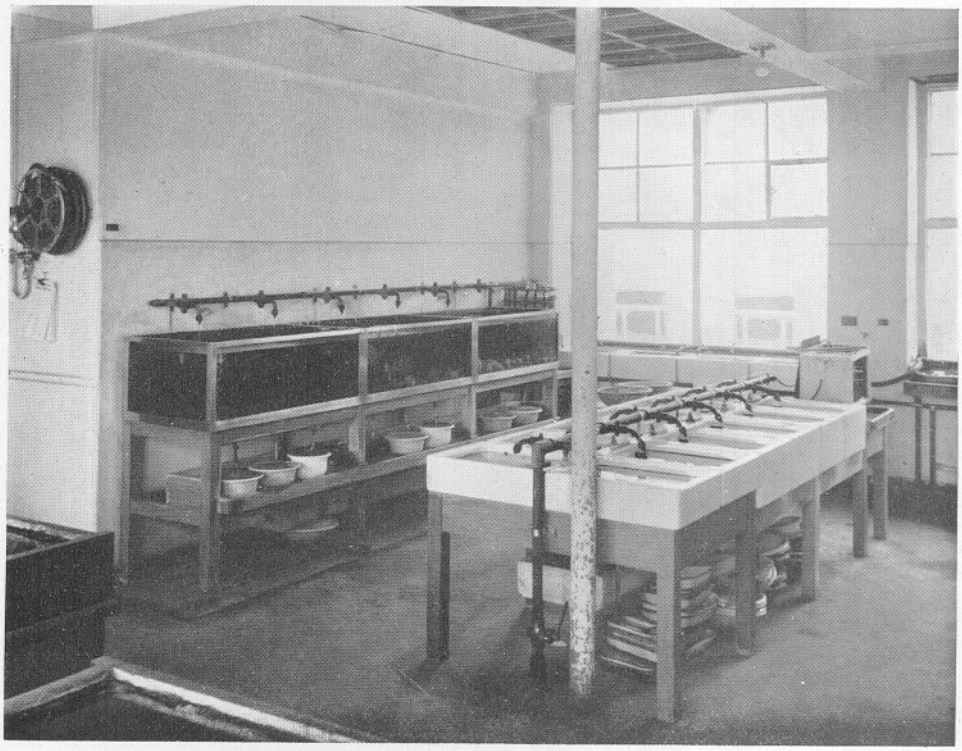

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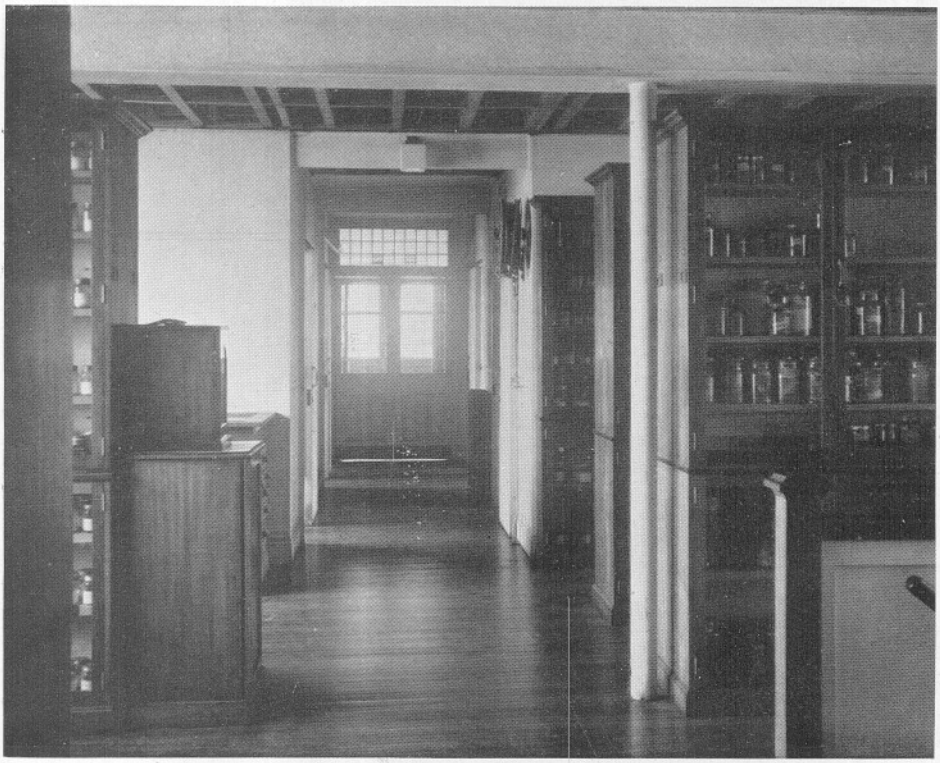

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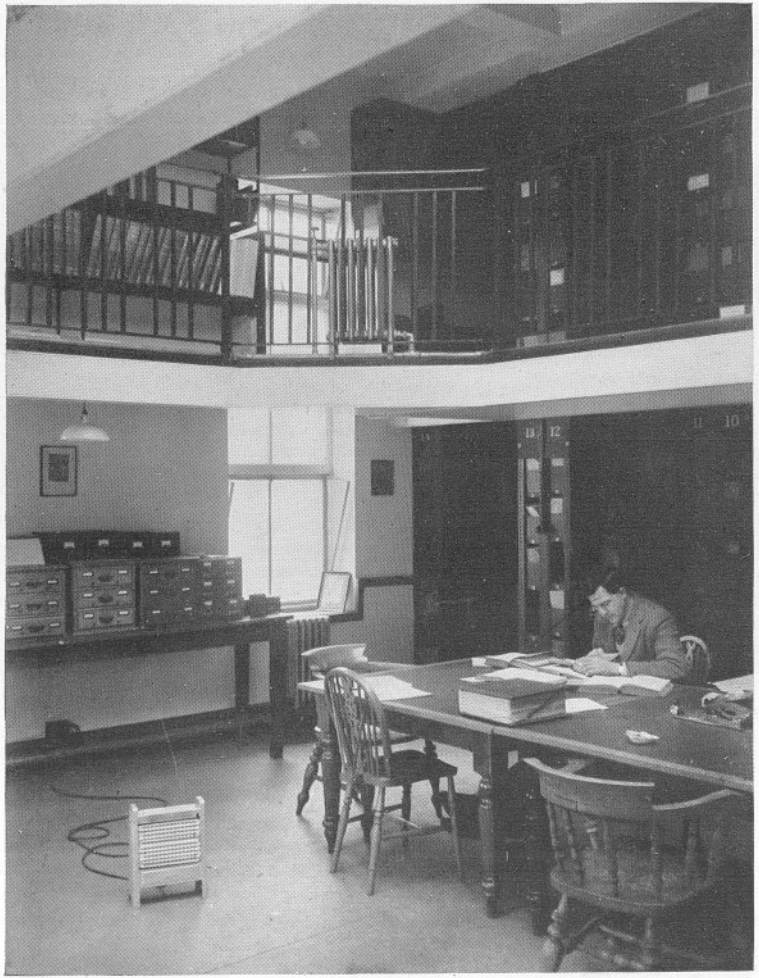

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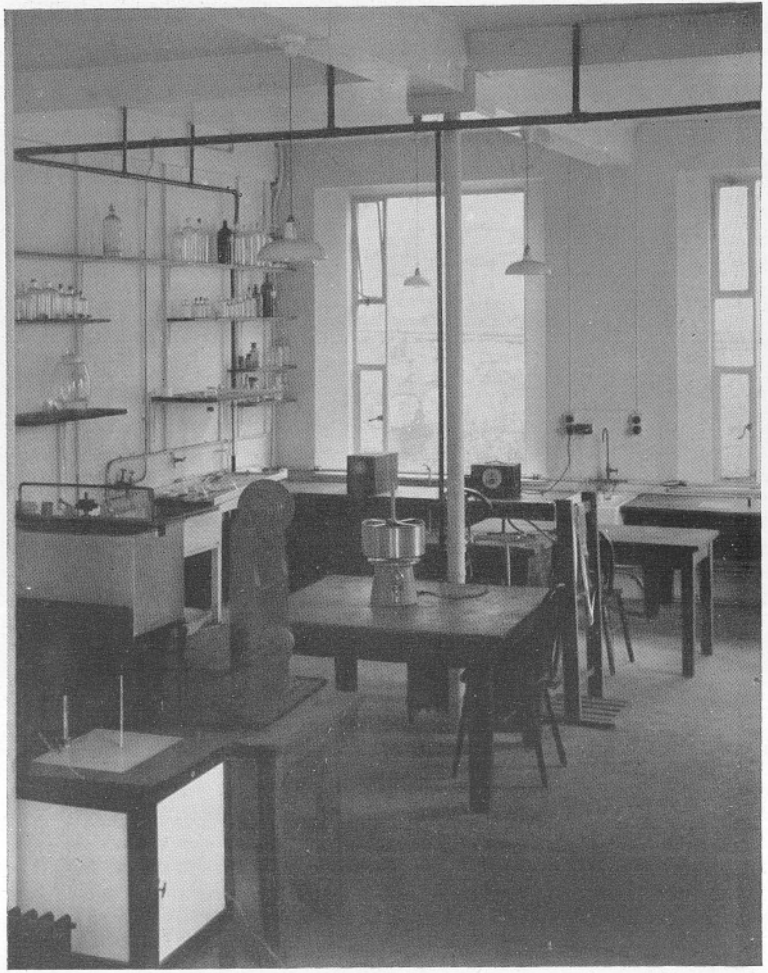

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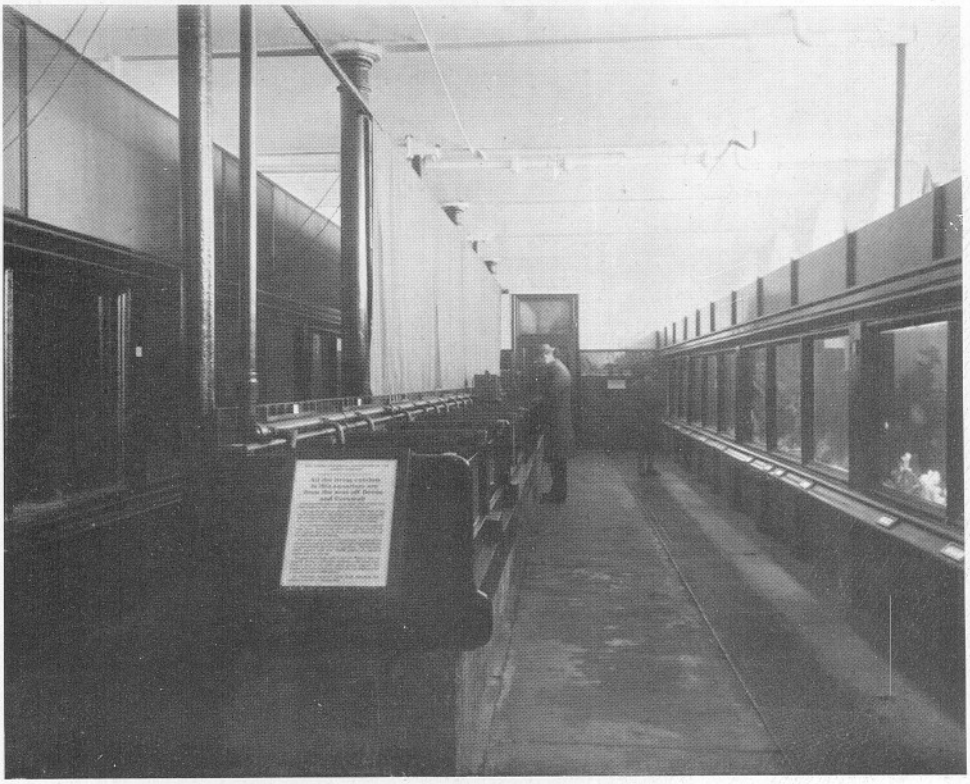

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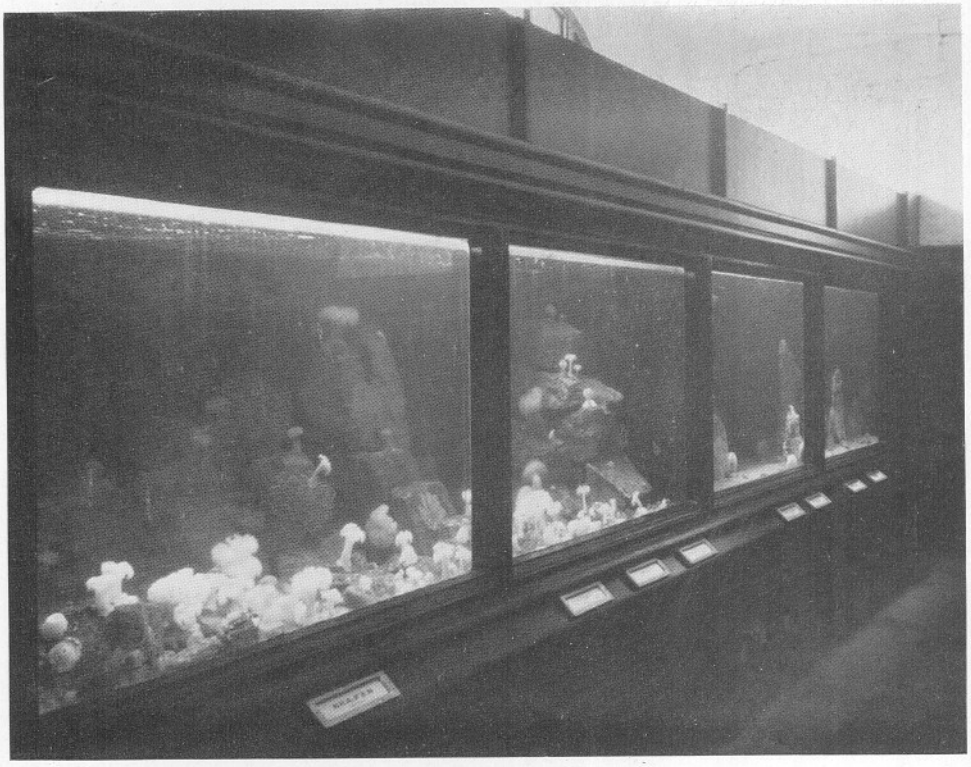

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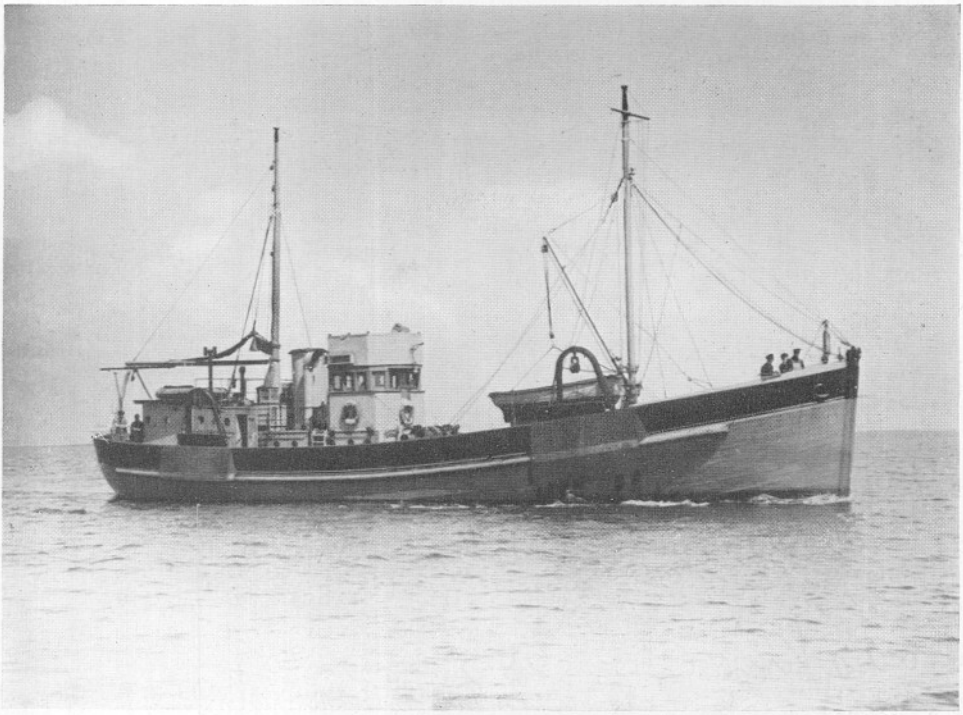

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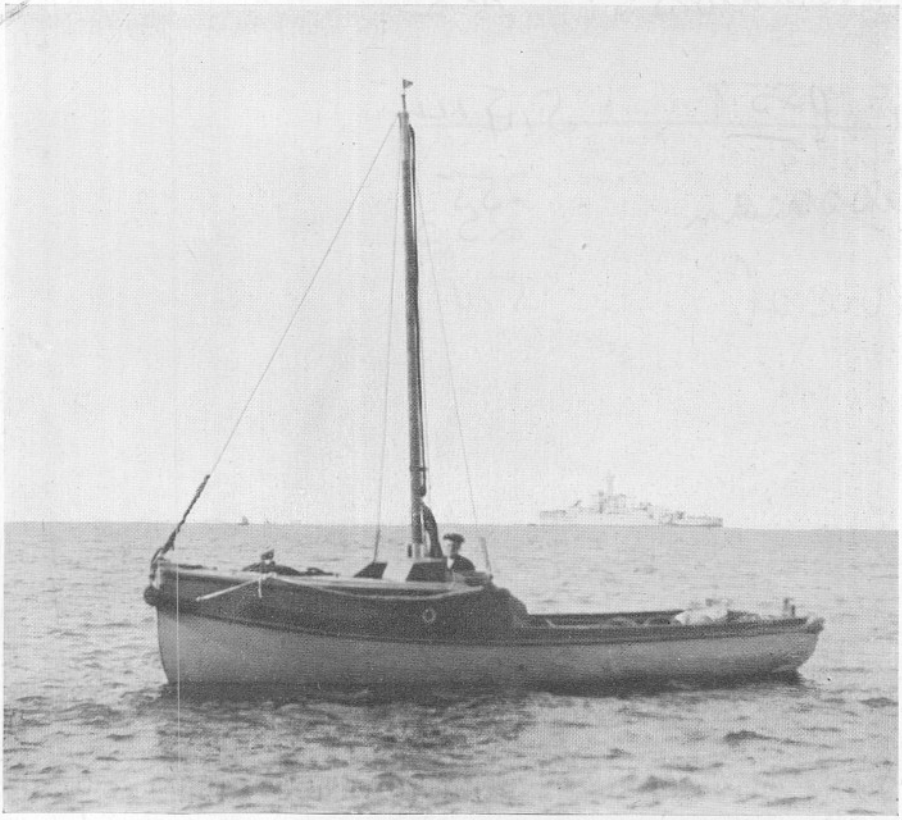

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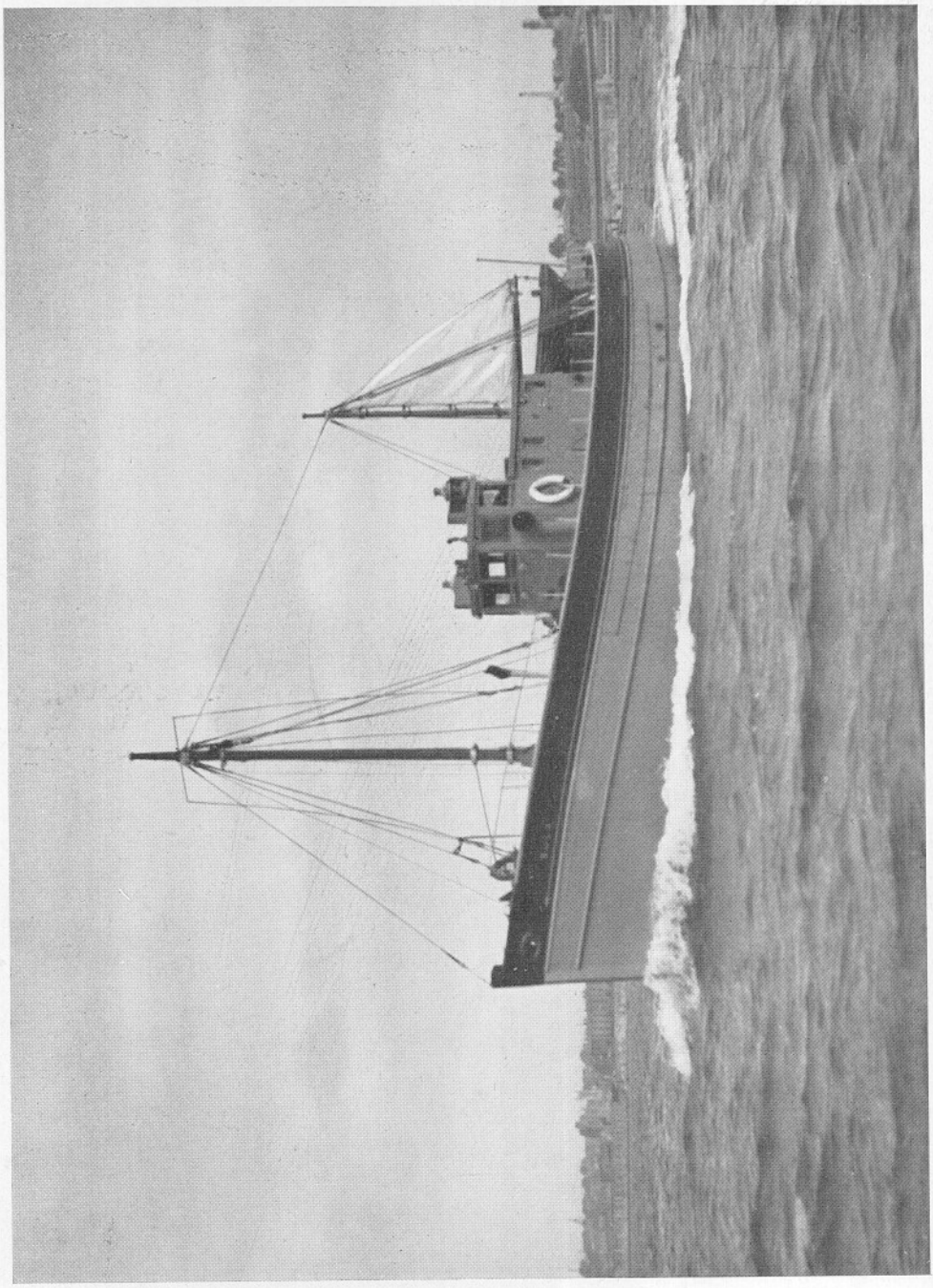

ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

GALATHEA

By Richard B. Pike

L.M.B.C. Mem. XXXIV, *L'pool*, 1947, *pp.* 1–179, 20 *plates*

This work follows the usual form of the *L.M.B.C. Memoirs*, giving a fairly complete description of the external and internal anatomy of *Galathea squamifera* Leach (Decapoda), with some histological detail of most structures described. The larvae have been omitted, as they are dealt with adequately by other authors. Some notes on reproduction and growth rate have been included. Attention has been paid to comparisons of the anatomy of the main organ systems of *Galathea* with that of corresponding systems, both in other members of the Anomura and also in other Decapoda. This has led to a tentative suggestion on the possible origin of the Anomura from a thalassinid ancestor and on their relationship with the rest of the Decapoda. R.B.P.

FACILITATION IN SEA ANEMONES. I. THE ACTION OF DRUGS. II. TESTS ON EXTRACTS

By D. M. Ross

J. Exp. Biol., Vol. 22, 1945, *pp.* 21–36

About twenty-five drugs, mostly those which act on vertebrate neuromuscular systems, were tested on *Calliactis parasitica* in an attempt to throw light on the mechanism of neuromuscular facilitation described by Pantin. No direct contractions of the musculature were elicited, but a few of the drugs which act at adrenergic junctions, tyramine, tryptamine and 933 F, caused responses to single stimuli. This might be described as a sensitizing or 'facilitating' effect, since two stimuli are required to initiate contractions of the sphincter in untreated animals. Adrenaline itself was inactive in this respect, but other drugs belonging to this group, cocaine and ergotoxine, had potentiating and inhibitory effects respectively which closely resembled their action at sympathetic junctions in vertebrates. Acetylcholine and allied drugs had no significant effects on facilitation. Extracts of *Calliactis parasitica* and *Metridium senile* also caused responses to single stimuli, but these differed from the tyramine effect in certain respects and it is unlikely that the two effects occur in exactly the same way. The results are consistent with the view that there are two processes taking part in neuromuscular transmission in these animals and that at least one of these processes involves sensitization of the muscle or the junctions by a chemical substance liberated by each nerve impulse. D.M.R.

The Pallial Organs in the Aspidobranch Gastropoda and their Evolution throughout the Mollusca

By C. M. Yonge

Phil. Trans. Roy. Soc., B, Vol. 232, 1947, *pp.* 443–518

The probable conditions in the mantle cavity of the primitive Mollusca are described in the light of work on all available aspidobranch Gastropoda. Ctenidia, hypobranchial glands and osphradia are shown to constitute a functional unit. The nature of the primitive ctenidium precluded life on soft substrata; this was made possible in the Gastropoda by the evolution of the pectinibranch ctenidium. The effects of (1) torsion and (2) asymmetrical coiling of the shell on the pallial organs in the Gastropoda are discussed. These include important effects on the reproductive as well as on the respiratory system. In the aspidobranchs four conditions are shown to have resulted from the initial asymmetrical coiling of the shell. These include the acquisition of a secondarily symmetrical limpet form which has been independently achieved four times by them as well as several other times by higher Gastropoda. In the Patellacea a functional series, *Patelloida-Lottia-Patina-Patella*, is described. The evolution throughout the molluscan classes of the various types of ctenidia is described. Attachment may be either by the efferent or afferent side of the axis, but the arrangement of the afferent and efferent blood vessels remains constant throughout. It is the further elaboration of frontal and abfrontal cilia, originally concerned with cleansing the ctendia, that is responsible for the evolution of the food-collecting ctenidia of the majority of the Lamellibranchia. Further evidence is provided in support of the view that the osphradia are tactile organs concerned with estimating the amount of sediment carried in with the inhalant current. C.M.Y.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1947–48

The Council and Officers

Four ordinary meetings of the Council were held during the year, three in the rooms of the Royal Society and one at Plymouth. At these the average attendance was sixteen. The Association is indebted to the Council of the Royal Society for the use of its rooms.

The Council has to record with great regret the death of the Earl of Stradbroke, K.C.M.G., C.B., C.V.O., who was a Vice-President of the Association from 1910.

The Plymouth Laboratory

The rebuilding of the east wing of the main building as laboratory accommodation has proceeded slowly but steadily. The major construction is now completed, and the work on the interior is proceeding.

Aquarium

The tanks in the aquarium have been kept well stocked and they have attracted a considerably larger public than in pre-war days. During the year 83,237 tickets of admission have been sold, the receipts from which amount to £1770.

The sea water appears to be in better condition than before the war, large numbers of the tunicates, *Ciona* and *Molgula*, and the sponge *Sycon* growing naturally in the tanks and reservoirs. Objects of special interest displayed during the year have been sea horses from Arcachon and a turtle which came ashore in November 1947 at Newlyn.

A new edition of the abridged *Aquarium Guide* by Mrs E. W. Sexton and Mr D. P. Wilson has been printed, and it includes some of Mr Wilson's own photographs. Over 6800 copies have already been sold.

Research ships

The research vessel *Sabella* has been in commission all the year and is in excellent condition. During a survey in the summer considerable galvanic corrosion was found in the neighbourhood of the rudder caused by the presence of the copper sheathing on the hull. It is hoped that the special treatment given will keep this in check.

The motor boat *Gammarus* has run continuously throughout the year, and the motors and hull are in first-class condition.

Approval has been obtained from the Development Commissioners for the purchase by the Association of an additional research vessel intermediate in size between the *Sabella* and the *Gammarus*. A half-completed Admiralty 61½ ft. motor fishing vessel fitted with a 105 h.p. Lister engine has been purchased. The vessel is being completed by the Sittingbourne Shipbuilding Company in whose yard she was built, and Mr G. A. Steven has given much time to the planning of this vessel and superintending her completion. It is hoped that, with an extra research vessel available, the *Sabella* will be enabled to spend more time on scientific cruises and exploration of grounds farther afield. During the year the off-survey and sale of the *Salpa* have been effected. The Ministry of Transport lump-sum compensation and purchase monies together amount to about £4500.

Government Surplus and other Equipment

The Association has continued to take advantage of the opportunities afforded for obtaining apparatus from surplus Government stores, and use has especially been made of facilities given locally by the Devonport Dockyard. The Association is especially indebted to Mr J. L. Parkinson of the Biophysics Research Unit, University College, London, for assistance and advice regarding surplus apparatus. The thanks of the Association are also due to the Admiralty for the loan of a depth-recording instrument for use with plankton nets, and also of an outboard echo-sounding installation for use on the *Sabella*. The latter loan arose out of a recommendation by Mr M. N. Hill, who has been using it in submarine seismic investigations undertaken from the Plymouth laboratory in collaboration with Mr P. L. Willmore of the Department of Geodesy and Geophysics, Cambridge.

A Geiger-Müller counter has been lent to the Association by the Ministry of Supply for use at the Plymouth laboratory.

The Staff

Dr Mary W. Parke has been appointed to the staff as Botanist; she took up her appointment on 1 April 1947.

The recommendations submitted by the Development Commissioners for the assimilation of the staff to the grades of the Scientific Civil Service have now been approved by H.M. Treasury. The new grading is as follows: Senior Principal Scientific Officers: Mr E. Ford, Dr W. R. G. Atkins, F.R.S., and Dr H. W. Harvey, F.R.S.; Principal Scientific Officers: Mr G. A. Steven, Mr D. P. Wilson and Dr L. H. N. Cooper; Senior Scientific Officers: Mr G. M. Spooner, Dr Mary W. Parke and Mr P. G. Corbin; Scientific Officer: Mr H. G. Vevers; Experimental Officers: Mr S. M. Nunn and Mr F. J. Warren.

Dr W. R. G. Atkins, Mr G. M. Spooner and Mr F. J. Warren spent a few days in December 1947 at the Atomic Energy Research Establishment at Harwell, gaining experience in the use of the Geiger-Müller counter.

Mr G. A. Steven attended the thirty-fifth meeting of the International Council for the Exploration of the Sea held at Copenhagen in October 1947.

Mr D. P. Wilson has been awarded the Rodman Medal of the Royal Photographic Society for photomicrographs of the development of *Ophiothrix*.

Occupation of Tables

The following seventy-three workers have occupied tables at the Plymouth laboratory during the year:

Dr N. AMBACHE, London (Nerve net of Scyphomedusae).
Miss E. J. BATHAM, Cambridge (Nerve net of *Metridium*).
Dr ANNA M. BIDDER, Cambridge (Digestive system of *Loligo*).
Dr C. FRANCIS-BOEUF, Paris (Chemistry of iron and chemical hydrography).
L. R. BRIGHTWELL (Aquarium).
Miss E. M. BROWN, London (Parasitic and saprozoic Protozoa).
Dr M. BURTON, British Museum (Nat. Hist.) (Sponges).
K. H. CHAPMAN, Manchester (Morphology and bionomics of *Machilis*).
K. CHIDAMBARAM, Cullercoats (Fisheries).
J. S. COLMAN, Sheffield (Shore ecology).
Dr S. M. DAS, Cullercoats (Excretion in Tunicates; *Folliculina*).
P. R. DAY, London (Marine Algae).
Dr G. E. R. DEACON, Teddington (Library).
P. S. B. DIGBY (Planktonic Copepods).
E. B. EDNEY, Birmingham (General zoology).
Dr M. A. ELLISON, Sherborne (Photo-electric cells).
D. ETHERINGTON, London (Sporozoan parasite in *Phascolosoma*).
Miss G. C. EVANS, Leicester (Behaviour of *Lepidochiton*).
J. E. FORREST, London (Digestion in Dorids).
Dr V. FRETTER, London (Molluscs).
D. J. FRYER, London (Elasmobranch and teleost nerve fibres).
K. D. GIBSON, Cambridge (Plankton).
Dr ISABELLA GORDON, British Museum (Decapod Crustacea).
Miss U. M. GRIGG, Cambridge (Biology of Trochids).
N. GUPPY, Cambridge (Library).
Dr T. J. HART, Discovery Investigations (Ice diatoms; hake).
P. H. T. HARTLEY, Oxford (Blennies).
M. R. HAYWOOD, Leicester (Mechanism of the heart-beat of Tunicates).
H. F. P. HERDMAN, Discovery Investigations (Oceanographical Apparatus).
M. N. HILL, Cambridge (Seismic prospecting of sea-bed).
A. L. HODGKIN, Cambridge (Nerve fibre of *Loligo*).
F. S. J. HOLLICK, Cambridge (General zoology).
N. A. HOLME, Cambridge (Bottom fauna).
Dr G. F. HUMPHREY, Cambridge (Inhibition of respiration of flagellates).
A. H. AL-HUSSAINI, Alexandria (Alimentary canal of fish).
J. D. JONES, Colonial Office (Physics and chemistry of sea water).
Dr C. B. JÖRGENSEN, Copenhagen (Water transport through animals).
Dr B. KATZ, London (Nerve fibre of *Loligo*).
K. L. KERMACK, London (Spatangoids).
F. G. W. KNOWLES, Marlborough (Pigment movement in Crustaceans).

Dr T. LEVRING, Göteborg (Plymouth marine flora).
Dr O. C. J. LIPPOLD, London (Nerve net of Scyphomedusae).
Dr O. LOWENSTEIN, Glasgow (Electro-physiology of the elasmobranch labyrinth).
Dr A. G. LOWNDES (Density of aquatic organisms).
Dr A. MARCOTTE, Quebec (General Marine Biology).
M. D. MENON, Madras (Fisheries).
H. P. MOON, Leicester (Mechanism of the heart-beat of Tunicates).
Miss V. MOYLE, Cambridge (Excretion in Amphipods).
A. R. NATESA IYER, Manchester (Library).
Prof. J. H. ORTON, Liverpool (*Patella*).
Dr C. F. A. PANTIN, Cambridge (Nerve net of *Metridium*).
P. E. PURVES, British Museum (Methods of Echinoderm preservation).
Q. H. QURESHI, London (Fish embryology).
Dr J. READ, London (Action of radon on *Echinus* eggs).
Dr W. J. REES, British Museum (Mollusca).
J. D. M. ROBERTS, Edinburgh (Electro-physiology of the elasmobranch labyrinth).
Miss H. G. Q. ROWETT, Plymouth (Library).
Miss M. SHARMAN, London (Biology of Veneridae).
Prof. C. J. SHEN, Peiping (Colour changes in *Crangon* larvae).
Miss J. SINGER, Cambridge (Regeneration in Hydroids).
Dr R. STAEMPFLI, Berne (Nerve fibre of *Loligo*).
Miss F. A. STANBURY, Plymouth (Library).
R. SUBRAHMANYAN, Liverpool (Library).
Miss M. TAYLOR, London (Schizogregarine parasite in *Phascolosoma*).
P. K. THOMAS, London (Elasmobranch and teleost nerve fibres).
Y. R. TRIPATHI, Allahabad University (Parasites of fishes).
D. W. TUCKER, Liverpool (*Patella*).
Miss VIDYA VATI, Lucknow University (Fish embryology).
R. VENKATARAMAN, Madras (General).
Dr E. J. WILKIE, Portsmouth (Antifouling compositions).
P. L. WILLMORE, Cambridge (Seismic prospecting of sea-bed).
Dr and Mrs CLAUDE E. ZOBELL, Scripps Institution, La Jolla (General).

Again this year a very large number of visitors have taken the opportunity of spending a day or two in Plymouth to see the work of the laboratory. Among these, the following have come from overseas: Prof. A. B. L. Beznak, Tihany; Dr A. F. Bliss, Boston; Prof. Maurice Fontaine, Paris; D. T. C. Gillespie, Australia; Dr Sven Hörstadius, Uppsala; Dr and Mrs I. Bohus Jensen, Copenhagen; Prof. C. C. John, Travancore; K. F. King, Fisheries Officer, Palestine; Dr A. Lindenberg, Paris; Dr R. Overman, Tennessee; Prof. Carlos Peaz Perez, Colombia; Dr A. Punt, Utrecht; Prof. P. Sawaya, San Paulo; R. J. Swaby, New South Wales; Dr K. F. Vaas, Buitenzorg, Java; Prof. F. R. Zuniga, Chile.

The usual Easter Vacation Courses were conducted by Mr D. P. Wilson and Mr G. A. Steven, and were attended by forty students from the following Universities and University Colleges: Oxford, Cambridge, London, Edinburgh, Glasgow, Liverpool, Birmingham, Bristol, Leicester, Cardiff, Sheffield, Exeter and Newcastle.

Also during the Easter Vacation Mr R. Bassindale brought nineteen students from Bristol University. This was followed by a class of twenty-six boys brought by six masters from the following schools: Bradfield College, Christ's Hospital, Clayesmore School, Harrow and Wellington College.

During August a Refresher Course for biology teachers was conducted by Dr J. E. Smith and Dr G. E. Newell, at which the attendance, which included some students, was twenty-three.

A joint meeting of the Challenger Society and representatives from Marine Laboratories, under the Development Commissioners' Scheme, was held at the Plymouth laboratory on 10 and 11 July 1947. Members of the staff provided the papers and demonstrations for the meeting which was attended by some 90 persons.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea Water

Dr W. R. G. Atkins has been occupied in preparing for publication work done before or during the war, and in overhauling of general apparatus and electrical equipment. The entire assembly for photoelectric measurements has required careful examination; in particular he and Dr H. H. Poole are following up the ageing of rectifier cells and the suitability of newer types for use at sea. Some submarine measurements have also been made, partly in connexion with preliminary work on under-water visibility, partly for a comparison of two quite distinct physical measurements, the vertical extinction coefficient and the extinction coefficient as determined in a narrow tube. The latter is being measured by Dr Cooper with the Pulfrich photometer. Work on the preservation of nets has been held up pending the restoration of access to the Pier Cellars basin, but nets in use here and those sold to other institutions are treated with a copper soap mixture.

Observations now extending over a period of seventeen years have continued to show a well-marked relation between the quantity of plankton and young fish in the water off Plymouth and the quantity of phosphate in the water when at a maximum at the beginning of each year. Consequent upon this Dr H. W. Harvey has been engaged upon an investigation of the cycle of phosphorus in the sea, with the aim of finding whether the total phosphate and organic phosphorus compounds in the water at other times of the year than winter is related to the potential fertility of the water mass. Data are being obtained in collaboration with Mr P. G. Corbin's survey of plankton in the English Channel and in collaboration with Mr R. S. Wimpenny, of the Ministry of Agriculture and Fisheries' Laboratory at Lowestoft, in the North Sea. These data do not yet extend over a sufficient period of time. Some experiments have also been made on the rate of phosphate excretion by two species of animals filter-feeding on varied concentrations of phytoplankton.

The initial step in the investigation was to find fairly rapid methods of estimating the dissolved organic phosphorus in sea water and of estimating phosphate in solution with maximum accuracy. A suitable photoelectric instrument has been developed, a critical examination of the molybdenum-blue reaction in sea water has been made, and particulars of methods of estimation are being published in Vol. XXVII, No. 2 of the *Journal*. Means of storing water samples while in transit to the laboratory have also received attention in order to preclude adsorption of organic phosphorus compounds on the glass and to stop change in the phosphate content of the water.

During the course of this examination of methods of analysis it was found that the sea off Plymouth contained an unexpectedly low concentration of arsenic. This may prove of interest in view of recent work by Swedish botanists who find that this element is necessary for, or greatly stimulates, algal growth.

A method of estimating manganese in sea water is also under investigation. It has been found that several species of flagellates would not make continued growth in water from this area without the addition of 1 mg. or less manganese per cubic metre. Crude preliminary estimations are indicating that the water contains only a fraction of 1 mg. of manganese per cubic metre in this area.

The survey of quantitative physical, chemical and biological data from the English Channel started by Dr L. H. N. Cooper last year has been continued. In the earlier years of the nutrient salt investigations at Plymouth the whole of the western English Channel was usually occupied by a uniform body of water of which the station E1, 10 miles south-west of the Eddystone, was typical. In 1930, in the neighbourhood of Plymouth, phosphate-rich 'elegans' or 'western' water was replaced by 'setosa' or 'Channel' water. It had become doubtful whether station E1 was any longer so widely representative. In January 1947 R.V. *Sabella* was based on the port of Newlyn where a temporary chemical laboratory was set up. In spite of bad weather Mr Corbin worked twenty-three stations. In three areas the water was markedly different from that at E1. Two were phosphate-richer, one phosphate-poorer. High salinity and temperature, combined with the biological indicators, showed this latter to be 'south-western' water which had recently entered the Channel. These results provide the first indication of the phosphate content of 'south-western' water.

As a secondary theme, Dr Cooper studied the distribution of iron. These results are being published in Vol. XXVII, No. 2 of the *Journal*, and they indicate that iron is present in the sea as particles distributed at random.

In another paper landings of spurdog and of rays and skates have been compared with the yearly fluctuations of stocks of phosphate. Close parallels have been found.

The study of tidal kinetic energy has been continued. Many planktonic species able to live in the western English Channel cannot penetrate into the eastern half. The barrier seems to be—or to be associated with—the

notable increase in kinetic energy of the tides in about 2° W. Publication has been delayed since the Admiralty have placed additional very useful tidal measurements at his disposal. These have still to be worked up.

Understanding of the present-day hydrology of the Channel and adjacent waters requires an intimate knowledge of the bottom topography. When studying banks and currents, it would be of much value to know which is caused by which. Sea-levels, temperatures and possibly salinities have changed much during the Pleistocene period, providing a series of differing environments for plants and animals. These changes ought to be considered in any study of the relationship of living organisms and their chemical and physical environment. The chaetognath *Sagitta setosa* provides an example. To-day this has its centre of distribution in the waters around the British Isles and North Sea, and it does not occur on the western side of the Atlantic. During the maximum withdrawal of the sea the area of its present habitat was mostly dry land, much of it heavily glaciated. To explain its present distribution, a knowledge of its evolution and whereabouts during the Ice Ages would seem essential.

Plankton

Mr F. S. Russell has resumed his work on the monograph of British medusae which was nearly completed before the war. He has brought it up to date as regards results published during the war by other authors on species which occur in the British fauna.

The observations which have been made for many years on the abundance of young fish and other plankton animals caught in weekly half-hour hauls with the 2 m. stramin ring are now being carried on by Mr P. G. Corbin. The results of this year's collections have been similar to those of last year, with *Sagitta setosa* dominant, but at no time numerous. *Muggiaea atlantica* appeared in considerable numbers in the late summer, but no *M. kochi* were present. The scarcity of young fish has continued.

Plankton collections taken with the 2 m. ring-trawl on a cruise in December 1946, and on three cruises in January 1947, all in the western Channel mouth area, are also being examined by Mr Corbin. Four cruises were originally planned for January, but the full programme was not carried out owing to bad weather. Conditions in January were severe, and the fact that it was possible to complete three cruises is in large measure due to the special weather forecasts which were provided twice daily for a particular sea area by the R.A.F. Meteorological Station, Mount Batten.

Mr Corbin is continuing work on the young fish of the 1937–9 mackerel investigation cruises. Some seventy-five species have been recorded, including a number of interesting oceanic species taken at stations near the edge of the Continental Shelf. The young stages of *Ammodytes* from these cruises are separable into four types, each of which can be distinguished by marked pigmentation differences. Types I and IV are respectively *A. lanceolatus* and

A. tobianus, type II appears to be *A. marinus*, while type III, although not yet identified, is not attributable to *A. cicerellus*, the young stages of which were described by Louis Fage from the Mediterranean. Adult *A. cicerellus* are, however, now known to occur in the Plymouth area, on three separate occasions this year single specimens being caught by R.V. *Sabella*. In the above researches Mr Corbin has been assisted by an Indian State Scholar, Miss Vidya Vati.

During the year Mr P. S. B. Digby has been working on a Development Commission Grant studying life histories of the smaller planktonic copepods. The work is based on weekly collections made at the International station L4, 5 miles from Plymouth breakwater, with the Harvey measuring net, the Clarke and Bumpus plankton sampler, and townets. Cruises have been made in January, June and July to other parts of the Channel to give information on whether the breeding periods are advanced or retarded elsewhere.

The species investigated have been *Paracalanus parvus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia clausi and Oithona similis*. Less complete data have been obtained for *O. nana* and *Centropages typicus*, and for the cyclopoids *Corycaeus* and *Oncaea*. The collections from August until October and most of the cruise samples are still to be worked up.

The winter plankton of early 1947 consisted of *Paracalanus*, *Pseudocalanus* and *Oithona* in roughly equal numbers, the only nauplii present in quantity being those of *Pseudocalanus*. Similar conditions prevailed on the south side of the Channel and in the area to the west of the Scillies, apart from the addition of late stages of *Metridia* and *Calanus* in the latter. By the end of February small numbers of *Acartia* and *Temora* had appeared and a brood of nauplii of the five main species occurred (with the possible exception of *Acartia*, found in very small numbers at this time of the year). A great increase in the number of nauplii of all species appeared in May and June, *Pseudocalanus* being first in May, *Paracalanus*, *Acartia* and *Temora* in May and June, and *Oithona* in June and July. The nauplii of all species were present continuously from February, and it is not yet clear whether in general there is a single long development period of $2\frac{1}{2}$–$3\frac{1}{2}$ months from February to May or June, or whether there are two shorter periods, from February to May and from May to June or July, of about $2\frac{1}{2}$ months and 1 month or 6 weeks respectively. If this latter is the case, the development times are closely comparable to those found by Fish in the Gulf of Maine, and the usual large spring increase of smaller copepods is due to the combined second and third generations of the year. This is expected to be clarified by further work on the samples.

Mr D. P. Wilson's investigations into the occurrence of the Portuguese Man-of-War (*Physalia physalis*), in the south-western area of England and Wales during the summer and autumn of 1945, have been completed and published in Vol. XXVII, No. 1 of the *Journal*. He shows, from a consideration of meteorological data for the period involved, that winds more than water

currents move the swarms towards the British Isles and are mainly responsible for determining on what parts of the coastline they shall be stranded. It has not been possible to determine precisely the place of origin of the swarms, but the available evidence suggests that they are more likely to come to us from a region in mid-Atlantic west of the Azores than from the area between the Canaries and Gibraltar. The literature of the past hundred years has been searched for records of previous visitations to the Atlantic coasts of Europe, and these reveal that strandings in abundance may be expected to occur three or four times a century, with visitations in small numbers every several years. Some previously unpublished records for 1912, 1913, 1934 and 1935 were discovered in the laboratory, and these are listed and discussed in the paper.

Cultures of marine planktonic diatoms and flagellates have been maintained in the Plymouth laboratory by Dr Mary Parke. Much culture material has been used by research workers in the laboratory and subcultures have been sent to Norway, Holland, France and many institutions in Britain for research purposes.

Fauna and Flora of the Sea Floor

During the breeding season of the polychaete worm *Ophelia bicornis*, many more experiments were made by Mr D. P. Wilson in an endeavour to determine the nature of the stimulus initiating metamorphosis of the larva. The data so accumulated have still to be examined critically, but it would appear that the main factor responsible is the physical size and shape of the sand particles, or, put another way, the sizes and shapes of the interstices between the grains. Sands much finer or coarser than that of the natural adult habitat or sands of angular instead of rounded grains, are definitely less attractive to the larvae than is sand from the natural habitat. Unsuitable sands delay metamorphosis and the larvae may die without metamorphosing at all. So far no indication has been obtained that sand from the adult habitat contains any slightly soluble substance able to initiate metamorphosis in the absence of suitable sand particles, but it is intended to make further experiments on this and other aspects next breeding season. Some experiments were made to test the ability of the larvae to distinguish between sands of various sorts contained in separate compartments of the same dish. While the results were not entirely satisfactory they did yield some positive evidence of ability to choose aright, but the absence in the experimental dishes of strongly flowing water, such as would be present in nature, seems to have affected adversely these particular tests.

The paper by Mr G. M. Spooner dealing with the taxonomic side of estuarine *Gammarus* species was published in Vol. XXVII, No. 1 of the *Journal*, and an interesting development immediately arising out of it has been followed up. The necessity for splitting *G. zaddachi* (as described in last year's Report) had been independently recognized by Dr Segerstråle of Helsingfors, with whom there have been some useful exchanges of material and opinions. Agreement

has been reached on the status of the northern marine populations hitherto assigned to *G. locusta*. These have clearly to be transferred from that species, from which they differ in many important respects, to be included under *G. zaddachi*. A third subspecies, *G. z. oceanicus*, is erected by Segerstråle to include them.

G. z. oceanicus is told mainly by the form and setation of the first antenna which is intermediate between typical *zaddachi* and *locusta* and, apparently, by the lack of pigment bands on the hinder part of the body, a feature which disappears in preserved material. The northern cold-water populations are distinguished readily enough by their larger size, but at the southern limit of their range they are much closer in appearance to *G. z. salinus*. It occurs abundantly along the coast of Norway, and in the Baltic Sea in much lower salinities.

G. zaddachi is thus a widely spread arctic-boreal species which ranges into temperate waters where it becomes an exclusively brackish water, or even fresh-water, animal.

In Britain *G. z. oceanicus* has been recognized in material from the northern half of Scotland. It occurs in the Tay estuary at the level normally inhabited by *G. z. salinus*. In some parts of Scotland there is presumably an overlapping of its range with that of *salinus* (as occurs widely in the Baltic), but this matter requires investigation. It has also yet to be shown that *oceanicus* and *salinus* are intersterile, as *salinus* and typical *zaddachi* have been shown to be.

Over most of the British Isles, however, only *G. z. zaddachi* and *G. z. salinus* appear to be present. Their occurrence in population samples from estuaries and other brackish waters is the main subject of Part II of the material which is in preparation for publication.

With *G. locusta* (*sens. strict.*) these two provide useful 'indicators' for zoning habitats of estuaries. Passing from the sea to the upper limit of tidal influence there are six zones. In (1) at the seaward end the population consists entirely of *G. locusta*; in (2) of a mixture of *G. locusta* and *zaddachi salinus*; in (3) in the middle reaches (where the fluctuation of salinity is greatest and where the fauna and flora is least varied) of *G. z. salinus* only; in (4) of a mixture of *G. z. salinus* and *G. z. zaddachi*; in (5) of *G. z. zaddachi* only, living normally; and in (6) *G. z. zaddachi* present but not breeding and *G. pulex* often present. Changes in the population follow the major seasonal fluctations, such as occur between summer and winter. The distribution of other members of the fauna, such as the crustaceans *Marinogammarus marinus* and *Cyathura carinata*, and the molluscs *Cardium edule*, *Scrobicularia plana*, *Hydrobia ulvae* and *H. jenkinsi*, and *Littorina* spp., etc., can be related to these zones.

Mrs E. W. Sexton, with the kind collaboration of Mr D. M. Reid, has been preparing the results of the investigation of the diversity of form in the amphipod species *Jassa falcata* (Montagu). It is hoped the work will soon be ready for publication.

Mr H. G. Vevers has continued his studies on the breeding biology of the common starfish *Asterias rubens*, in the waters off Plymouth. The main work has been carried out on population samples of this species taken throughout the year from two different areas to the south of Plymouth. The populations in these areas were very distinct in size composition, those from the inshore area being medium-sized (as defined by size ranges and means), while those on the offshore grounds (to the south and south-west of Eddystone) were more numerous and consisted of essentially large starfishes, reaching in some cases over 30 cm. in radius. Examination of the gonads showed a further marked difference between the two populations. In the inshore area less than 30% of the females reached full maturity between the beginning of April and the middle of June, whereas in the offshore population over 60% of the females reached this stage and showed ripe eggs between mid-March and mid-May with a peak in the middle of April. Townet catches taken throughout the season contained bipinnaria larvae between the middle of April and the end of May.

The bottom temperatures in the two areas do not differ greatly and there does not appear to be any direct correlation between temperature and the differences in ovarian maturity observed in the two areas. The high value for ripe ovaries in the offshore population is tentatively regarded as a direct reflexion of the richer food resources (especially the shoals of *Chlamys* (*Pecten*) *opercularis*) available in this area as compared with those available farther inshore. The successful maturing of the offshore population is not dependent upon the large size of the individuals, but both these attributes are considered to be the direct result of the rich food supply. In further support of this view it was found that in a third area (closer inshore) where there was a rich stock of food lamellibranchs, the starfishes were smaller (half the size) than those of the 'inshore' population, and yet they were in full breeding condition at the end of May. From laboratory observations on rate of growth it appears that these small but breeding starfishes could easily have reached this size in one year from metamorphosis.

The parasitic ciliate, *Orchitophrya stellarum* Cépède, was found in the gonads of up to 20% of the 'offshore' males during the breeding season. This parasite was first recorded as very rare on the north coast of France and has since been recorded in two related species of *Asterias* in North America; it has not previously been recorded at Plymouth. It causes parasitic castration in the testes where it is present, and its distribution throughout the population has been studied in some detail.

Further research on bottom animals has been started by two students at the laboratory on D.S.I.R. Maintenance Grants, Miss U. M. Grigg and Mr N. A. Holme, who began their work on 1 October. Miss Grigg is studying the ecology of the four species of Trochid molluscs occurring on our shores, and Mr Holme is devoting his attention to problems connected with the bottom fauna.

Dr Mary Parke has continued working up the results of the investigations on seaweeds, and the first paper dealing with *Laminaria saccharina* (L.) Lamour. is nearly completed.

Further points of interest have emerged from the detailed study of the data relating to *L. saccharina* which were amassed during the practical side of the work. It has been shown that the variation that can be found in this species on the British coast can be related to the variation in the rate of growth of the plants with changes in age, season, habitat and geographical position. Not only can growth forms be classed as varieties of the species, some of the forms obtained during the work agree even with descriptions of distinct species.

The differential growth rate in length at successive levels up the frond of plants of *L. saccharina* has been worked out. The results show that the primary or basal growth never drops below 70% of the total frond growth in length. On the Argyll coast primary growth shows the highest percentage of the total increase from October to April with the peak from December to February. In the frond tissue above the base the highest percentage increase (secondary growth) is from August to October, when the lowest percentage of primary growth is recorded. It has been found that in plants growing on the Devon coast the peaks of primary and secondary growth occur one month earlier than on the Argyll coast.

The figures for the width of the frond of plants at different ages, in different habitats and geographical positions, show that the width of the frond tissue produced is in direct relation to the rate of growth in length of the frond. It has been shown that with the variation in the rate of growth in frond length and width throughout a yearly cycle a change takes place in the shape of the base of the frond, so that the rapidity or the slowness of the frond growth at any time can be assessed roughly from the shape of the frond base.

The regenerative powers of different-aged plants of this species have been investigated. It has been found that when the whole frond is removed from a plant no regeneration occurs, and that when a frond is cut or torn off near the base complete regeneration of the frond occurs only in plants up to the age of one year.

Dr Parke is building up a collection of preserved specimens of marine algae at the Plymouth laboratory, and she has made a number of additions to the recorded species. She has also been engaged in compiling a summary and bibliography of all work done on marine algae in Great Britain and Ireland during the war for publication in the *Revue Algologique*.

Fishes and Fisheries

In last year's report Mr E. Ford briefly described a method of defining the spatial form of the neurocranium in species of gadoid fishes by means of a geometric network passing through the natural centres of the individual skull bones. During the present year, the work has been extended to cover some

twenty different species, in order to determine the nature and extent of variation between them. Comparisons have also been made between skulls of cod caught in widely separated localities, to test the possibility that skull-form in the one species is subject to geographical variation. A necessary development of the technique was to study the form and disposition of the individual skull-bones. For although the geometric network depicts the orientation of the bones by means of their centres, it does not take into account their varying size and shape, and the degree of overlap between them, which is often quite considerable. To obtain information of this kind it is necessary to examine the interior of the skull as well as the exterior, and to disarticulate the skull, bone by bone.

Mr Ford has collaborated with Miss Vidya Vati in a study of the keeled scales in young herring, sprat and pilchard. The keeled scales lie in a median row along the ventral edge of the body from the throat backwards to the anus, and normally they are in meristic register with the myocommata, ribs and vertebrae. In the region of the pelvic fins, however, this agreement is liable to break down. Until further information is available concerning the extent to which this breakdown occurs, statistical counts of keeled scales in population studies will be subject to error of unknown magnitude. Comparison between the keeled scales of young herrings from Plymouth and those from the Clyde revealed distinctive differences in form—so much so that a mixed sample of the two could be resorted by mere inspection of the keeled scales in each individual.

Mr G. A. Steven has continued to work up the results of his mackerel investigations in the south-western area. A paper has been completed and will shortly be published on 'Mackerel Migrations in the English Channel and Celtic Sea'. In the light of this work it is believed that the hitherto imperfectly understood migratory habits of the *Scomber scombrus* on both sides of the North Atlantic will be found to fit into one coherent and relatively simple picture. There is each year a demersal period, a pelagic migratory period during which spawning takes place, and a brief transition period in which the fish return from the surface waters to winter quarters on the sea floor.

There is a very long spawning season extending from March till July with maximum intensity in April. This is due to the fact that the mackerel of the area do not all spawn at the same time. Another contributory factor is that in these fish the eggs mature in batches that are spawned in succession over an extended spawning period. Ripe, translucent eggs appear in the ovary distributed widely and irregularly amongst the still unripe, yellowish ova, giving rise to a peculiar speckled appearance that, for lack of a better term, has been called the 'plum pudding' stage. These ripe ova are dehisced into the lumen of the ovary which then, on superficial examination, shows no trace of ripe eggs. Unless opened up, such an ovary may well be, and often has been, described as 'unripe'. In the mackerel, in fact, a fully 'ripe' ovary is never

present; the most that is ever found is an ovary containing small numbers of ripe eggs.

These observations are being worked up, but additional information is needed on some difficult points. Unfortunately, as there has been no spring mackerel fishery since the war, no samples of spawning fish have been obtainable. It is hoped that fishing will be renewed next spring so that further investigations can then be made.

The Library

The thanks of the Association are again due to numerous foreign Government Departments, and to Universities and other Institutions at home and abroad, for copies of books and current numbers of periodicals presented to the Library, or received in exchange for the *Journal*. Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

During the year the periodicals in the Library have been checked and listed for inclusion in the next edition of *The World List of Scientific Periodicals*.

Published Memoirs

Vol. XXVI, No. 4 of the *Journal* was published in June 1947, Vol. XXVII, No. 1 in November 1947, and Vol. XXVII, No. 2 is nearing completion.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ATKINS, W. R. G., 1947. Disappearance of *Zostera marina*. *Nature*, Vol. 159, p. 477.

ATKINS, W. R. G., 1947. Size versus colour in air-sea rescue. *Nature*, Vol. 159, pp. 612–13.

ATKINS, W. R. G., 1947. Electrical conductivity of river, rain and snow water. *Nature*, Vol. 159, p. 674.

ATKINS, W. R. G. & ELLISON, M. A., 1947. Photoelectric measurements of the seasonal variations in daylight at Plymouth, from 1938 to March 1941, compared with the years 1930 to 1937. *Proc. Roy. Soc., London*, A, Vol. 191, pp. 467–84.

COOPER, L. H. N., 1947. Internal waves and upwelling of oceanic water from mid-depths on to a Continental Shelf. *Nature*, Vol. 159, pp. 579–80.

COOPER, L. H. N., 1947. Recent work of the Marine Biological Laboratory, Plymouth. *British Science News*, Vol. 1, pp. 8–10.

HART, T. JOHN, 1948. The distribution and biology of hake. *Biological Reviews*, Vol. 23, pp. 62–80.

HILL, M. N. & WILLMORE, P. L., 1947. Marine seismic prospecting. *Nature*, Vol. 159, pp. 707–8.

JEPPS, MARGARET W., 1947. Contribution to the study of the sponges. *Proc. Roy. Soc., London*, B, Vol. 134, pp. 408–17.

LEBOUR, MARIE V., 1947. The oyster. II. *School Science Review*, Vol. XXVIII, pp. 216–19.

NICOL, J. A. C. & YOUNG, J. Z., 1946. Giant nerve fibre of *Myxicola infundibulum* (Grube). *Nature*, Vol. 158, p. 167.

PIKE, RICHARD B., 1947. *L.M.B.C. Memoir*, XXXIV. *Galathea* (in part). Liverpool University Press. 178 pp.

REES, W. J., 1947. On the systematic position of the Hydroid genera *Hippolytus* Murbach, 1899, and *Dahlgrenella* Miles, 1937. *Ann. Mag. Nat. Hist.* (11), Vol. XIII, pp. 102–6.

RUSSELL, F. S., 1947. The Plymouth Laboratory of the Marine Biological Association of United Kingdom. *Proc. Roy. Soc., London*, B, Vol. 135, pp. 12–25.

SPOONER, G. M., 1947. Further extension of the range of *Crepidula fornicata* (L). *Journ. of Conchology*, Vol. 22, p. 243.

STEVEN, G. A., 1947. The British Raiidae. *Science Progress*, Vol. XXXV, pp. 220–36.

STEVEN, G. A., 1947. *Report on the Sea Fisheries of Sierra Leone.* (Freetown, 1945.) Crown Agents for the Colonies, Millbank, London, 1947. 66 pages.

STEVEN, G. A., 1948. The Plymouth Marine Biological Laboratory. *Discovery*, February 1948, pp. 43–9.

WILSON, D. P., 1947. *They Live in the Sea.* Collins: London. 128 pp.

YONGE, C. M. 1947. The pallial Organs in the Aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. Roy. Soc., London*, B, Vol. 232, pp. 443–518.

Membership of the Association

The total number of members on 31 March 1948 was 458, being 46 more than on 31 March 1947; of these the number of life members was 69 and of annual members 389. The number of Associate members is now three, Dr H. Muir Evans having died during the year.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income. The Council gratefully acknowledges the following generous grants for the year:

From the Fishmongers' Company (£500), the Royal Society (£50), British Association (£50), Physiological Society (£30), the Ray Lankester Fund (£20), the Cornwall Sea Fisheries Committee (£10); the Universities of Cambridge (£125, and £20 balance for 1946-7), London (£210), Oxford (£100, and £52. 10*s.* for 1946–7), Bristol (£50), Birmingham (£31. 10*s.*), Manchester (£10. 10*s.*), Leeds (£20), Nottingham (£10. 10*s.*), Leicester (£10. 10*s.*), Exeter (£10. 10*s.*), Southampton (£10. 10*s.*), Sheffield (£5) and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1948–49:

President

Prof. JAMES GRAY, C.B.E., M.C., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Sir SIDNEY F. HARMER, K.B.E., Sc.D., F.R.S.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
Prof. WALTER GARSTANG, D.Sc.
The Rt. Hon. TOM WILLIAMS, M.P.
G. P. BIDDER, Sc.D.
W. T. CALMAN, C.B., D.Sc., F.R.S.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S.
E. S. RUSSELL, O.B.E., D.Sc.
Sir EDWARD J. SALISBURY, Kt., C.B.E., Sec.R.S.
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.

COUNCIL

To retire in 1949

G. E. R. DEACON, D.Sc., F.R.S.
Prof. J. E. HARRIS, Ph.D.
N. A. MACKINTOSH, D.Sc.
EDWARD HINDLE, Sc.D., F.R.S.
R. S. WIMPENNY

To retire in 1950

H. CARY GILSON
C. F. HICKLING, Sc.D.
MORLEY H. NEALE
Prof. LILY NEWTON, Ph.D.
Prof. J. Z. YOUNG, F.R.S.

To retire in 1951

ANNA M. BIDDER, Ph.D.
Prof. J. ROGERS BRAMBELL, D.Sc.
J. N. CARRUTHERS, D.Sc.
O. D. HUNT
J. E. SMITH, Ph.D.

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

F. S. RUSSELL, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
P. D. H. DUNN, C.M.G., O.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Major E. G. CHRISTIE-MILLER
ALFRED R. WAGG
Prof. A. C. HARDY, D.Sc., F.R.S. (Oxford University)
C. F. A. PANTIN, Sc.D., F.R.S. (Cambridge University)
Prof. H. GORDON JACKSON, D.Sc. (British Association)
H. G. MAURICE, C.B. (Zoological Society)
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

BALANCE SHEET 1947–48

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1948

	£ s. d.	£ s. d.
SUNDRY CREDITORS:		
Accrued Expenses	386 2 11	
Subscriptions received in advance	40 12 4	
Grant received in advance	125 0 0	
Admiralty—Hire of R.V. 'Sabella'	2530 0 0	
Equipment for R.V. 'Sula'	326 14 0	
		3408 9 3
AQUARIUM SINKING FUND:		
As at 31st March 1947	332 3 11	
Add: Donations for rebuilding Aquarium Tanks:		
£ s. d.		
Plymouth Corporation ... 100 0 0		
Aquarium Visitors ... 33 17 1		
	133 17 1	
	466 1 0	
Less: Transfer to Income and Expenditure Account	332 3 11	
		133 17 1
E. T. BROWNE—BEQUEST FUNDS:		
Building Fund, as at 31st March 1947	1265 1 9	
Add: Interest on Investment ...	38 7 3	
Profit on Redemption of Investment	13 14 0	
	1317 3 0	
Library Fund, as at 31st March 1947	1118 2 1	
Add: Interest on Investment ...	34 0 10	
Profit on Redemption of Investment	16 14 5	
	1168 17 4	
Special Apparatus Fund, as at 31st March 1947	2540 17 4	
Add: Interest on Investment ...	76 19 11	
Profit on Redemption of Investment	25 13 3	
	2643 10 6	
Scientific Publications Fund, as at 31st March 1947...	1905 12 8	
Add: Interest on Investment ...	57 15 0	
Profit on Redemption of Investment	19 8 0	
	1982 15 8	
		7112 6 6
'SALPA' DEPRECIATION FUND:		
As at 31st March 1947	6477 3 8	
Add: Amounts received from Ministry of Transport Compensation on De-requisitioning	3927 0 0	
Hire	33 10 0	
	3960 10 0	
Interest on Investments	238 15 6	
	10676 9 2	

	£ s. d.	£ s. d.	£ s. d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director at 31st March 1941 plus Additions at Cost:			
S/S 'Salpa':			
As at 31st March 1947		2000 0 0	
Less: Net proceeds of sale ...	614 5 9		
Loss on sale	1385 14 3		
		2000 0 0	
Motor Boat 'Gammarus':...		200 0 0	
Nets, Gear and General Equipment:			
As at 31st March 1947	50 0 0		
Additions during the year ...	50 0 0		
		100 0 0	
			300 0 0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director at 31st March 1941, plus additions at cost:			
As at 31st March 1947		4800 0 0	
Additions during the year		250 0 0	
			5050 0 0
LIBRARY, at valuation by Mr Ridgill Trout in January 1941, plus additions at cost:			
As at 31st March 1947		16100 0 0	
Additions during the year		250 0 0	
			16350 0 0
STOCKS ON HAND, as valued by the Director:			
Specimens		600 0 0	
Chemicals		250 0 0	
Journals		400 0 0	
			1250 0 0
SUNDRY DEBTORS:			
Sales of Specimens, etc.			673 10 1
PREPAYMENTS			247 3 4
RECOVERABLE EXPENDITURE:			
Research Fund—Miss N. G. Sproston:			
As at 31st March 1947		165 17 10	
Less: Grant received	165 11 8		
Transfer from Income and Expenditure Account ...	6 2		
		165 17 10	
Research Fund—P. S. B. Digby:			
Expenditure		581 6 4	
Less: Balance at 31st March 1947	7 13 10		
Grant received	533 16 8		
		541 10 6	
		39 15 10	
ON BUILDINGS RECONSTRUCTION:			
Expenditure:			
Rebuilding East Wing	5018 0 0		
Reconstruction of Main Building	1830 3 1		
	6848 3 1		

Less: Maintenance to date of Sale	53 0 0			
Loss on Sale	1385 14 3			
Loss on Redemption of Investment	113 6 9			
Transfer to Vessels' Hire and Capital Expenditure Fund	9124 8 2			
		10676 9 2		
VESSELS' HIRE AND CAPITAL EXPENDITURE FUND:				
Transfer from 'Salpa' Depreciation Fund ...		9124 8 2		
Add: Transfer from Income and Expenditure Account		850 0 0		
		9974 8 2		
Less: Hire of R.V. 'Sabella' for year to date	1380 0 0			
Modifications to R.V.'Sabella'	800 0 0			
Equipment for R.V. 'Sula'...	326 14 0			
		2506 14 0		
			7467 14 2	
'GAMMARUS' REPLACEMENT FUND:				
As at 31st March 1947		564 15 4		
Add: Interest on Investment		16 12 0		
		581 7 4		
Less: Loss on Redemption of Investment ...		11 6 10		
			570 0 6	
COMPOSITION FEES FUND:				
As at 31st March 1947		472 10 0		
Add: Fees Received		110 5 0		
		582 15 0		
Less: Loss on Redemption of Investment ...		9 6 10		
			573 8 2	
BIOLOGICAL INVESTIGATIONS ON 'ALGAE' FUND:				
As at 31st March 1947			8 1 3	
MACKEREL RESEARCH FUND:				
As at 31st March 1947		9 15 11		
Add: Transfer from Income and Expenditure Account		1 10 6		
		11 6 5		
Less: Repaid to Ministry of Agriculture and Fisheries ...	9 15 11			
Expenditure	1 10 6			
		11 6 5		
SPECIAL SQUID TANK FUND:				
Grant received from Rockefeller Unit of Neurophysiology, Cambridge			70 0 0	
CAPITAL RESERVE ACCOUNT:				
As at 31st March 1947			21688 8 2	
SURPLUS ACCOUNT:				
As at 31st March 1947		3419 18 11		
Less: Excess of Expenditure over Income for the year...		1537 9 8		
			1882 9 3	
			£42,914 14 4	

Less: Balance on Building Reconstruction Fund at 31st March 1947	1372 3 5			
Grant received	5018 0 0			
		6390 3 5		
			457 19 8	
				497 15 6
GENERAL FUND INVESTMENT at Book Value £352. 2*s.* 3*d.* 2½% Treasury Stock ... ... (Market value at date £269. 7*s.* 0*d.*)				232 7 10
E. T. BROWNE—BEQUEST FUNDS INVESTMENT, at Cost: £7242. 14*s.* 10*d.* 3% British Transport Stock (Market value at date £7025. 0*s.* 0*d.*)				7112 6 6
VESSELS' HIRE AND CAPITAL EXPENDITURE FUND INVESTMENT, at cost: £4846. 11*s.* 9*d.* 2½% Treasury Stock ... ... (Market value at date £3717. 17*s.* 0*d.*)				4433 10 9
'GAMMARUS' REPLACEMENT FUND INVESTMENT, at cost: £580. 9*s.* 6*d.* 3% British Transport Stock ... (Market value at date £563. 1*s.* 0*d.*)				570 0 6
COMPOSITION FEES FUND INVESTMENTS, at cost:				
£18. 18*s.* 6*d.* 2½% Treasury Stock			15 15 0	
£567. 17*s.* 8*d.* 3% British Transport Stock ... (Market value at date £564. 19*s.* 0*d.*)			557 13 2	
				573 8 2
CASH AT BANK AND IN HAND:				
Coutts and Company			4919 0 10	
Lloyds Bank Limited			632 16 5	
Cash in Hand			72 14 5	
				5624 11 8

TO THE MEMBERS THE OF MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

We report that we have examined the above Balance Sheet with the Books of the Association and have obtained all the information and explanations we have required. Capital Expenditure on erection of Buildings on Land held on Lease from the War Department is excluded. Subject to this remark we are of opinion that the Balance Sheet is properly drawn up so as to exhibit a true and correct view of the state of the Association's affairs as at 31st March 1948 according to the best of our information and the explanations given to us and as shown by the books of the Association.

PRICE, WATERHOUSE & Co

Prudential Buildings, George Street, Plymouth.
19th May, 1948.

G. E. R. DEACON }
JOHN E. HARRIS } *Members of the Council.*

£42,914 14 4

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1948

	£ s. d.	£ s. d.
To SALARIES, including Association's Contributions to Superannuation and War Bonuses ...		14357 1 0
,, LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, Contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance		8941 17 4
,, UPKEEP OF LIBRARY		238 6 7
,, SCIENTIFIC PUBLICATIONS, LESS SALES ...		994 15 2
,, UPKEEP OF LABORATORIES AND AQUARIUM:		
Buildings and Machinery	411 12 1	
Electricity, Oil, Gas, Coal and Water ...	501 5 5	
Chemicals and Apparatus	837 5 9	
Fire Insurance, Tithe, Ground Rent and Rent of Store	114 6 5	
Travelling Expenses	344 2 7	
Stationery, Postages, Telephone, Carriage and Sundries...	725 17 10	
Specimens	292 7 1	
		3226 17 2
,, EXPENDITURE IN CONNECTION WITH R.V. 'SABELLA'		— — —
,, MAINTENANCE AND HIRE OF BOATS:		
Petrol, Oil, Paraffin, etc.	232 1 1	
Maintenance and Repairs to Nets, Gear and Apparatus	1183 10 8	
Purchase of Materials for Nets, etc. for Resale	321 14 5	
Boat Hire, Collecting Expenses and Upkeep of Truck...	106 12 1	
Insurances	395 10 0	
Hire of R.V. 'Sabella'...	— — —	
		2239 8 3
,, ENTERTAINMENT EXPENSES		24 6 6
,, BANK CHARGES		9 4 0
,, TRANSFER TO VESSELS' HIRE AND CAPITAL EXPENDITURE FUND		850 0 0
,, TRANSFER TO MISS N. G. SPROSTON RESEARCH FUND, Irrecoverable balance		6 2
,, TRANSFER TO MACKEREL RESEARCH FUND, Irrecoverable balance		1 10 6
,, TRANSFER TO REPAIRS AND RENOVATIONS FUND		— — —
,, TRANSFER TO AQUARIUM SINKING FUND ...		— — —
		£30,883 12 8

	£ s. d.	£ s. d.	£ s. d.
By GRANTS:			
Ministry of Agriculture and Fisheries Grant from Development Fund	22600 0 0		
Fishmongers' Company	500 0 0		
British Association	50 0 0		
Royal Society	50 0 0		
Physiological Society	30 0 0		
Cornwall Sea Fisheries Committee	10 0 0		
		23240 0 0	
,, SUBSCRIPTIONS (excluding Subscriptions received in advance)		404 6 7	
,, DONATIONS			
,, FEES FOR TESTS OF MATERIALS		86 8 6	
,, SALES:			
Specimens	2221 14 7		
Photographs (*less* purchases)	27 6 2		
Fish	105 18 10		
Nets, Gear and Hydrographical Apparatus ...	399 17 9		
		2754 17 4	
,, TABLE RENTS (including Universities of Cambridge £145 (including £20 for 1946/47); London £210; Oxford £152. 10*s.* 0*d.* (including £52. 10*s.* 0*d.* for 1946/47); Bristol £50; Birmingham £31. 10*s.* 0*d.*; Leeds £20; Manchester £10. 10*s.* 0*d.*; Leicester £10. 10*s.* 0*d.*; Exeter £10. 10*s.* 0*d.*; Nottingham £10. 10*s.* 0*d.*; Southampton £10. 10*s.* 0*d.*; Imperial College £10; Sheffield £5; Trustees of Ray Lankester Fund £20 and Ministry of Works £104)		1029 18 8	
,, INTEREST ON INVESTMENTS		20 4 8	
,, SALE OF DR M. V. LEBOUR'S BOOK		5 7 6	
,, SALE OF 'PLYMOUTH MARINE FAUNA'		12 4 6	
,, AQUARIUM:			
Admission Fees...	1770 7 3		
Sale of Guides	193 0 2		
Sale of Postcards	19 12 8		
Transfer from Sinking Fund	332 3 11		
	2315 4 0		
Less: Expenditure:			
Maintenance of Buildings	160 13 1		
Printing	214 8 2		
Food	75 8 0		
Wages	71 19 6		
	522 8 9		
		1792 15 3	
,, BALANCE BEING EXCESS OF EXPENDITURE OVER INCOME FOR THE YEAR		1537 9 8	
		£30,883 12 8	

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1948

GOVERNORS

The British Association for the Advancement of Science, *Burlington House, W.* 1
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 48 *Fenchurch Street, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
The Prime Warden. (**Council**, 1886→)
Wagg, Alfred R., *The Hermitage, East Grinstead.* (**Council**, 1948→)
Christie-Miller, Major E. G., 38 *Hyde Park Street, W.* 2. (**Hon. Treasurer**, 1941→)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, *St Stephen's House, Victoria Embankment, S.W.* 1
Bayly, Robert (the late). (**Council**, 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council**, 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council**, 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner, Hills Road, Cambridge.* (**Council**, 1899→; **President**, 1939–45; **Vice-President**, 1948→)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President**, 1929; 1939–45; **President**, 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary.) (**Council**, 1895–1942; **Secretary**, 1895–1936; **Hon. Governor**, 1937–42)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall*, 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.* 2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council**, 1884–92; **Hon. Treasurer**, 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary**, 1884–90; **President**, 1891–1929)
1884 Lord Masham (the late)

1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road, Bournemouth West*
1888 The Worshipful Company of Drapers, *Drapers' Hall, E.C.* 2
1889 The Worshipful Company of Grocers, *Grocers' Hall, Princes Street, E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., M.Inst.C.E., 32 *Thornhill Road, Plymouth, Devon*
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square, S.W.* 1. (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc., *Bayworth Corner, Boars Hill, Oxford.* (**Council**, 1932–5)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens, W.* 8
1920 Lord Buckland of Bwlch (the late),
1920 Llewellyn, Sir D. R. (the late),
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., *Ocean House, Pudding Lane, E.C.* 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1
1925 Discovery Committee, *Colonial Office, Downing Street, S.W.* 1
1927 Bidder, Miss Anna M., Ph.D., *Cavendish Corner, Hills Road, Cambridge.* (**Council**, 1948→)
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co., Ltd., P.O. Box* 331, *Alexandria, Egypt.* (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W., *Sharvells, Milford-on-Sea, Hants*

MEMBERS

* Life Members

1939 Abercrombie, M., *Department of Anatomy, University College, Gower Street, London, W.C.* 1
1945 Aberdeen University Library, *The University, Aberdeen*

1941 Aberystwyth (*see* Wales)
1947 Achimota College, *Department of Zoology, Achimota, Gold Coast Colony*
1934 Adam, Mrs K. M. G., 21 *Belgrave Crescent, Edinburgh* 4
1940 Adrian, Prof. E. D., O.M., M.D., D.Sc., LL.D., F.R.S., *St Chad's, Grange Road, Cambridge*
1947 Affleck, R. J., 847 *Brighton Road, Purley, Surrey*
*1927 Amirthalingam, C., Ph.D., *Director of Fisheries, Colombo, Ceylon*
1932 Aquario Vasco da Gama, *Estação de Biologia Maritima, Cais do Sodré, Lisbon, Portugal*
1944 Ashby, D. G., *P.O. Avondale, Salisbury, S. Rhodesia*
1947 Astill, D. R. D., *Newball and Mason, Ltd., Beech Avenue, Nottingham*
*1911 Viscount Astor, 3 *Elliot Terrace, Plymouth, Devon* (**Vice-President**, 1911→)
1929 Atkins, Miss D., D.Sc., *Oak Cottage, Chichele Road, Oxted, Surrey*
*1939 Atkins, W. R. G., O.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S., *The Old Vicarage, Antony, Torpoint, Cornwall*
*1910 Atkinson, G. T., *Apsley House, Esplanade, Lowestoft, Suffolk*

1948 Baal, H. J., 3 *Bel Royal Villas, Jersey, C.I.*
1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow, India*
*1920 Baker, J. R., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1936 Baldwin, E., Ph.D., *School of Biochemistry, Sir William Dunn Institute, Tennis Court Road, Cambridge.* (**Council**, 1946–48)
1939 Barnes, H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1930 Barrett, W. H., *Roxeth Farm, Bessborough Road, Harrow, Middlesex*
1939 Barrington, E. J. W., *Department of Zoology, The University, Nottingham*
1946 Barter, W. Y., 29 *Sea View Avenue, Plymouth, Devon*
1939 Bassindale, R., *Department of Zoology, The University, Bristol*
1932 Bateman, J. B., Ph.D., *Physical and Chemical Division, Camp Detrick, Frederick, Ind., U.S.A.*
1946 Batham, Miss E. J., *c/o Department of Zoology, Downing Street, Cambridge*
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
*1929 Bayliss, L. E., Ph.D., *Department of Physiology, University College, Gower Street, London, W.C.* 1
1934 Beadle, L. C., *Department of Biology, College of Medicine, University of Durham, Newcastle-upon-Tyne* 1, *Northumberland*
1928 Beer, Prof. G. R. de, D.Sc., F.R.S., *University College, Gower Street, London, W.C.* 1
1947 Berrill, Prof. N. J., *Department of Zoology, McGill University, Montreal, Canada*
1947 Best, A. C. G., 6 *Station Road, Loudwater, High Wycombe, Bucks*
1948 Betts, Slade, 100 *Avondale Road, Bromley, Kent*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames, Oxon*
1947 Bilton, Leslie, *c/o* 158 *Howard Road, Clarendon Park, Leicester*
*1945 Bingley, F. J., *Broomhill, Herringswell, near Bury St Edmunds, Suffolk*
1925 Birkbeck College, *Fetter Lane, London, E.C.* 4
1931 Birtwistle, W., 73 *North Street, Skibbereen, Co. Cork, Eire*
1947 Bishop, M. W. H., *Meadow Farm, Waterbeach, Cambs.*

1945 Black, J. A., *Ash House, Caton, near Lancaster, Lancashire*
1947 Black, Miss M. K., *c/o F. Band, High Street, Benwick, March, Cambs.*
1930 Blaschko, Dr H., *Department of Pharmacology, South Parks Road, Oxford*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1936 Bogue, Prof. J. Yule, D.Sc., *Heyscroft, Hartley Road, Altrincham, Cheshire*
1932 Bolitho, Capt. R. J. B., *Gorey, Jersey, C.I.*
1945 Boney, A. D., *Ivydene, Grosvenor Road, Crownhill, Plymouth, Devon*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1947 Bossanyi, J., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1944 Boyd, Lt. David, R.N.V.R., 261 *Woodstock Road, Oxford*
1940 Brambell, Prof. F. W. Rogers, D.Sc., *Department of Zoology, University College of North Wales, Bangor, Caernarvonshire.* (**Council**, 1944–47, 1948→)
1924 Brightwell, L. R., *White Cottage, Chalk Lane, East Horsley, Surrey*
1933 Bristol University, *Department of Zoology, Bristol*
1948 British Cod Liver Oils (Hull and Grimsby) Ltd., *P.O. Box No.* 18, *Hull*
1941 British Celanese Ltd., *Celanese House, Hanover Square, London, W.* 1
1939 British Ropes Ltd., *Western Avenue, Cardiff*
1946 Brough, Prof. James, D.Sc., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*
*1946 Brown, Miss C. H., *Girton College, Cambridge*
1928 Brown, Miss E. M., 6 *Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey*
1936 Brown, Herbert H., O.B.E., Ph.D., *Manager, Fisheries Division, Colonial Development Corporation,* 33 *Dover Street, London, W.* 1
*1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1920 Burne, R. H., F.R.S., *Monkschester, Blue House Lane, Limpsfield, Surrey*
1948 Burrows, Mrs E. M., *Hartley Botanical Laboratories, The University, Liverpool* 3
1947 Burton, Miss J. M., 55 *Popes Grove, Twickenham, Middlesex*
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1936–39)
1947 Burton, R. F., 55 *Popes Grove, Twickenham, Middlesex*

1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester.* (**Council**, 1927–30, 1932–34, 1937–41, 1942–45)
1927 Carruthers, J. N., D.Sc., *Hydrographic Department, Admiralty, Cricklewood, London, N.W.* 2. (**Council**, 1948→)
1923 Carter, G. S., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1945 Carter, P., *Littlewood, Beadon Road, Salcombe, Devon*
1948 Carthy, J. D., 161B *Hills Road, Cambridge*
*1931 Cattell, Dr McKeen, *Cornell University Medical College,* 477 *First Avenue, New York City, U.S.A.*
*1948 Cattley, J. G., *Fisheries Laboratory, Lowestoft, Suffolk*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1947 Cheng, Prof. Chung, Ph.D., *Department of Oceanography, National Amoy University, Amoy, China*
*1947 Chidambaram, K., *c/o Mr R. Vaidyalingom Pillai, Retd. Dewan Peishkar, Jagathy, Trivandrum, S. India*

1946 Chipperfield, Philip N. J., *Hillside, Manor Road, Brixham, Devon*
1942 Christie-Miller, Major E. G., 38 *Hyde Park Street, London, W.* 2. (**Hon. Treasurer**, 1941–)
1924 Clark, R. S., D.Sc., *The Cottage, Bieldside, Aberdeenshire.* (**Council**, 1938–41)
1947 Clarke, Miss D. H., *Hoe Garden House, Hoegate Street, Plymouth, Devon*
1944 Clarke, Robert H., *'Discovery' Investigations, Queen Anne's Chambers,* 41 *Tothill Street, London, S.W.* 1
1936 Clothier, Peter, *Hill Close, Street, Somerset*
1939 Clowes, A. J., *Division of Fisheries, Beach Road, Sea Point, Cape Town, S. Africa*
*1886 Coates and Co. (Plymouth), Ltd., *Black Friars Distillery, Southside Street, Plymouth, Devon*
*1945 Cobham, Lt.-Cdr. A. J., R.N., 44 *Strand-on-the-Green, London, W.* 4
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *The Royal South Hants and Southampton Hospital, Centenary Appeal Office,* 105 *Graham Road, Southampton*
1933 Cole, H. A., *Fisheries Experimental Station, Castle Bank, Conway, Caernarvonshire*
1948 Collier, Albert, 826 *Maison Blanche Building, New Orleans, La., U.S.A.*
*1885 Collier and Co., 53 *Southside Street, Plymouth, Devon*
1947 Collis, Miss M. M., 27 *Mowbray Road, Cambridge*
1930 Colman, J. S., *Department of Zoology, The University, Sheffield* 10
1947 Cook, Miss P. M., 51 *Runnymede Crescent, Streatham, London, S.W.* 16
1940 Cook, R. H., 24 *Luard Road, Cambridge*
1939 Cooper, Major Brian, *Countess Weir House, Countess Weir, Exeter, Devon*
*1933 Cooper, L. H. N., D.Sc., F.R.I.C., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, P. G., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, Mrs P. G., *Dostabrook, Horrabridge, S. Devon*
1946 Corlett, John, M.Sc., *Fisheries Laboratory, Lowestoft, Suffolk*
1937 Cosway, C. A., 20 *Maurice Road, King's Heath, Birmingham* 14
1941 Cott, H. B., D.Sc., *University Museum of Zoology, Cambridge*
1948 Council for Promotion of Field Studies, *Dale Fort Field Centre, Haverfordwest, Pembs*
1936 Crawford, G. I., 18 *East Drive, Carshalton Beeches, Surrey*
*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Usher Institute, Warrenden Park Road, Edinburgh* 9
1929 Crofts, Miss D. R., D.Sc., *Deerbank, Noisey Wood, Billericay, Essex*
*1930 Cuthbertson, Norman, *King's College School, Windsor, Nova Scotia, Canada*

1922 Dale, Sir Henry H., O.M., G.B.E., M.D., LL.D., F.R.S., *The Royal Institution,* 21 *Albemarle Street, London, W.* 1. (**Council**, 1922–28)
1948 Dales, R. Phillips, 67 *Westmoreland Avenue, Squirrels Heath, Essex*
1947 Dall, William, *Grace Street, Corinda, S.W.* 4, *Brisbane, Queensland, Australia*
*1919 Damant, Capt. G. C. C., C.B.E., R.N., *Thursford, Cambridge Road, East Cowes, I. of W.* (**Council**, 1928–31, 1937–40)
1939 Danielli, J. F., D.Sc., *Chester Beatty Research Institute, Royal Cancer Hospital, London, S.W.* 3. (**Council**, 1944–45)
1947 Danmarks Akvarium, *Charlottenlund, Denmark*
1929 Darby, Dr H. H., *Carnegie Institution of Washington,* 5241 *Broad Branch Road, N.W., Washington* 15, *D.C., U.S.A.*
1948 Dartmouth, The Royal Naval College

1946 Das, S. M., D.Sc., *Department of Zoology, The University, Lucknow, India*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay*
1943 Davies, D. J., 1 *Mayfield Terrace, Cwmburla, Swansea*
1931 Dawes, B., D.Sc., *Department of Zoology, University of London, King's College, Strand, London, W.C.* 2
1944 Day, Prof. J. H., D.F.C., *Department of Zoology, University, Rondebosch, Cape Town, S. Africa*
1948 Day, Lionel E., 24 *Inverness Avenue, Westcliffe-on-Sea, Essex*
1948 Day, Peter R., 36 *Templeton Avenue, Chingford, London, E.* 4
1938 Deacon, G. E. R., D.Sc., F.R.S., 55 *Broadhurst, Ashtead, Surrey*. (**Council**, 1946→)
1939 Dennell, Ralph, *Department of Zoology, The University, Manchester* 13
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, S. Africa*
1944 Digby, P. S. B., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1910 Dobell, C. C., D.Sc., F.R.S., *National Institute for Medical Research, Hampstead, London, N.W.* 3
1939 Dobson, A. T. A., C.B., C.V.O., C.B.E., *The Elms, Walsham-le-Willows, Bury St Edmunds, Suffolk*. (**Council**, representing Ministry of Agriculture and Fisheries, 1938–46)
1948 Dodd, J. M., *Gatty Marine Laboratory, The University, St Andrews, Fife*
1942 Dollner, H., 3516 *Northcliffe, Montreal, N.D.G., Canada*
1946 Douglas, Leslie, 11 *Harbour View, Seahouses, Northumberland*
1940 Dowson, Capt. W. B., *Agricultural Service, Nigeria, c/o Crown Agents for the Colonies*, 4 *Millbank, London, S.W.* 1
1946 Duly, S. J., 68 *Richmond Hill Court, Richmond, Surrey*
1939 Dundee University College Library, *Dundee, Forfar*
1947 Dunne, B., 53 *Headland Park, Plymouth, Devon*
1937 Dyke, Frederick Montague, *Branksome, Boreham Wood, Elstree, Herts*

1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1933 Eastham, Prof. L. E. S., *Department of Zoology, The University, Sheffield* 10
1945 Edgell, Vice-Admiral Sir John A., K.B.E., C.B., F.R.S., 1 *Glenalmond House, Manor Fields, Putney, London, S.W.* 15. (**Council**, 1945–48, **Vice-President**, 1948→)
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
1948 Elgood, J. H., 159 *Purley Oaks Road, Sanderstead, Surrey*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, Devon*
*1944 Elmhirst, Richard, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1931 Enoch, C. E. D., *Rayman Lodge, Sherborne Road, Parktown, Johannesburg, S. Africa*
*1947 Evans, Miss G. C., *Gerrans, Portscatho, near Truro, Cornwall*
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*
1942 Ewer, D. W., *Department of Zoology, Natal University College, P.O. Box* 375, *Pietermaritzburg, Natal, S. Africa*

1929 Faouzi, Dr Hussein, *Faculty of Science* (*Department of Zoology*), *Farouk I University, Moharram Bey, Alexandria, Egypt*
1922 Farran, G. P., *Knocklyon, Templeogue, County Dublin, Eire*. (**Council**, 1922–26)
1948 Faulkner, I. J., Ph.D., *I.C.I. Billingham Division, Billingham, E. Durham*

1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1940 Foote, Miss V. V. J., *Achimota College, Achimota, Gold Coast Colony*
1928 Ford, E., *The Laboratory, Citadel Hill, Plymouth, Devon*
1935 Ford, E. B., F.R.S., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1939 Fowell, R. R., *Municipal Technical College, Mount Pleasant, Swansea, Glam*
1912 Fox, Prof. H. M., F.R.S., *Bedford College for Women, Sussex Lodge, Regent's Park, London, N.W.* 1. (**Council**, 1928–30, 1931–34, 1944–47)
1942 Foxon, G. E. H., *Department of Biology, Guy's Hospital Medical School, London Bridge, London, S.E.* 1
1924 Fraser, Miss E. A., D.Sc., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1935 Fraser, F. C., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
*1935 Fraser, James H., *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1939 Fretter, Miss Vera, Ph.D., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
*1930 Fritsch, Prof. F. E., D.Sc., F.R.S., *Department of Botany, Queen Mary College, Mile End Road, London, E.* 1. (**Council**, 1931–34, 1937–40, 1943–46)
1948 Furness, W. J., *Inglewood, Abbey Park Road, Grimsby, Lincs.*

1941 Gardiner, Mrs A. C., *c/o Mrs Walter Gardiner*, 4 *Grange Road, Cambridge*
*1907 Garstang, Prof. W., D.Sc., *Five Elms, Apsley Road, Oxford.* (**Council**, 1907–10, 1923–28; **Vice-President**, 1940→)
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Biological Laboratories, Harvard University, Cambridge* 38, *Mass., U.S.A.*
1948 Gatty Marine Laboratory, (The Principal), *The University, St Andrews, Fife*
1947 Gay, Miss M. V., *Lowerfield, Lapford, Devon*
1932 Ghardaqa Marine Laboratory of the Egyptian University, *Ghardaqa, Red Sea District, Egypt*
1947 Gibson, R. O., 3 *Gascoyne Place, Plymouth, Devon*
1935 Gilson, H. Cary, *Freshwater Biological Association, Wray Castle, Ambleside, Westmorland.* (**Council**, 1940–43, 1947→)
1945 Glasgow University, Zoology Department, *Glasgow, W.* 2
1946 Glover, R. S., *Department of Oceanography, University College, Hull*
1945 Goodland, W. S. L., 20 *Trinity Terrace, Weymouth, Dorset*
1939 Goodrich, Dr Helen Pixell, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1943 Gourock Ropework Co., Ltd., 92 *Bay Street, Port Glasgow, Renfrew*
1931 Graham, Prof. Alastair, D.Sc., *Department of Zoology, Birkbeck College, Fetter Lane, London, E.C.* 4
1931 Graham, Michael, O.B.E., *Fisheries Laboratory, Lowestoft, Suffolk.* (**Council**, 1931–32, 1933–36, 1943–46)
1930 Gray, Sir Archibald M. H., C.B.E., M.D., F.R.C.P., F.R.C.S., 39 *Devonshire Place, London, W.* 1
1912 Gray, Prof. J., C.B.E., M.C., Sc.D., LL.D., F.R.S., *Department of Zoology, Downing Street, Cambridge.* (**Council**, 1920–24; representing Cambridge University, 1928–45; **President**, 1945→)

1943 Great Grimsby Coal, Salt and Tanning Co., *Fish Dock Road, Grimsby, Lincs*
1948 Grigg, Miss Ursula M., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1946 Gross, Fabius, Ph.D., *Department of Zoology, West Mains Road, Edinburgh*
1948 Grove, A. V., 48 *Carlton Terrace, Swansea, Glam*
1947 Guiler, E. R., *Department of Zoology, University of Tasmania, Hobart, Tasmania*
1947 Gundry, Joseph, and Co., *Bridport, Dorset*

1946 Haifa: *Sea Fisheries Research Station, P.O. Box* 50, *Haifa, Palestine*
*1946 Hamond, Richard, *Morston, Holt, Norfolk*
1947 Harbott, A. J., *Wensleydale*, 7 *Manorcrofts Road, Egham, Surrey*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford.* (**Council**, 1938–41, 1942–45; representing Oxford University, 1946→)
1929 Harington, Sir Charles R., Ph.D., F.R.S., *National Institute of Medical Research, Mount Vernon House, London, N.W.* 3
1946 Harling, Miss K. E., *The Arches, Looe, Cornwall*
*1885 Harmer, Sir Sidney F., K.B.E., Sc.D., F.R.S., 5 *Grange Road, Cambridge.* (**Council**, 1895–1912, 1918–23; representing Royal Society, 1925–44; **Vice-President**, 1934→)
1932 Harris, Prof. J. E., Ph.D., *Department of Zoology, The University, Bristol.* (**Council**, 1946→)
1946 Harris, T. R., 31 *All Saints Road, Wyke Regis, Weymouth, Dorset*
1939 Harrison, R. J., M.R.C.S., L.R.C.P., *Vinicombe, The Woodlands, Farnborough, Kent*
1947 Harrow Lower School Biology Department, *Lower School of John Lyon, Harrow, Middlesex*
1929 Hart, T. J., D.Sc., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1934 Hartley, P. H. T., *Edward Gray Institute of Field Ornithology*, 91 *Banbury Road, Oxford*
1924 Harvey, H. W., Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon*
1933 Harvey, L. A., *Department of Zoology, University College of the South West, Exeter, Devon.* (**Council**, 1940–43)
1939 Hayes, Dr F. R., *Dalhousie University, Halifax, N.S., Canada*
1939 Hayes, Mrs F. R., *Dalhousie University, Halifax, N.S., Canada*
1948 Hedley, Ronald H., *Armstrong House, Meadowfield, Durham*
1931 Henderson, G. T. D., D.S.C., Ph.D., *Oceanographic Laboratory*, 23 *Sandport Street, Leith, Edinburgh* 6
1939 Henry, Dr Herbert G. M., *Doune Cottage, Macduff, Banffshire*
1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W.* 1
1939 Herklots, G. A. C., Ph.D., *Vanners, Chobham, Surrey*
1939 Hewer, H. R., Assistant Professor, *Department of Zoology, Imperial College of Science, London, S.W.* 7
1926 Hickling, C. F., Sc.D., *Colonial Office, Sanctuary Buildings, Great Smith Street, London, S.W.* 1. (**Council**, 1947→)
1926 Hill, Prof. A. V., C.H., O.B.E., Sc.D., F.R.S., 16 *Bishopswood Road, Highgate, London, N.* 6. (**Council**, 1925–29, 1930–33, 1934–37, 1938–41, 1942–43; representing Royal Society, 1944→; **Vice-President**, 1948→)
1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*
1947 Hill, M. N., 6 *St Eligius Street, Cambridge*

1919 Hillier, W. T., M.R.C.S., 73 *Francis Road, Edgbaston, Birmingham*
*1921 Hindle, E., Sc.D., F.R.S., *Zoological Society of London, Regent's Park, London, N.W.* 8. (**Council**, 1946→)
1937 Hinton, M. A. C., F.R.S., 23 *Polworth Road, Streatham, London, S.W.* 16
1926 Hobson, Prof. A. D., *King's College, Newcastle-upon-Tyne* 1, *Northumberland*
1948 Hockley, A. R., *University College, Southampton*
1939 Hodgkin, A. L., F.R.S., *Trinity College, Cambridge*
1945 Hodson, W., *Rhodena, Penare Avenue, Prestatyn, Flints*
1947 Hollowday, E. D., F.R.M.S., 45 *Manor Road, Aylesbury, Bucks*
1948 Holme, N. A., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1946 Holmes, E. J., *Education Offices, Cobourg Street, Plymouth, Devon*
1939 Holmes, W., D.Phil., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1948 Holsgrove, H. E., 67 *Bridwell Road, Weston Mill Estate, Devonport*
1933 Horne, F. R., *National Institute of Agricultural Botany, Huntingdon Road, Cambridge*
1948 Howe, Surg. Lt.-Cdr. (D) D. C., R.N., *H.M.S. "Victorious" c/o G.P.O., London*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C.* 1
1948 Human, A. H., C.B.E., 32 *Victoria Street, London, S.W.* 1
1928 Hunt, O. D., *Corrofell, Newton Ferrers, S. Devon.* (**Council**, 1944–47, 1948→)
1947 Hunter, W. Russell, *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
*1947 Hurrell, H. G., J.P., *Moorgate, Wrangaton, S. Devon*
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
1912 Huxley, Julian S., D.Sc., F.R.S., *UNESCO*, 19 *Avenue Kleber, Paris* 16, *France.* (**Council**, 1920–25)

1946 Iceland: *Átvinnudeild Háskólans* (*Fiskideild*), *Reykjavik*
1945 Imperial Chemical Industries Ltd, *Nobel House*, 2 *Buckingham Gate, London, S.W.* 1

1945 Jefferies, H. S., 6 *Forester Road, Bath*
1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
*1921 Jenkin, Mrs W., *Westhide, Hereford*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*
*1947 John, C. C., D.Sc., *The Aquarium, Trivandrum, S. India*
1934 John, D. Dilwyn, D.Sc., *National Museum of Wales, Cardiff*
*1947 Johnson, D. S., 10 *St John's Road, Cambridge*
1944 Johnson, Dr F. R., *Osu Fisheries Station, P.O. Box* 630, *Accra, Gold Coast Colony*
1948 Jones, C. Burdon, *Department of Zoology, University College of N. Wales, Bangor*
1948 Jones, J. D., *c/o The Secretariat, Mauritius* (*ref. P/*891), *Mauritius*
1946 Jones, L. W. G., 28 *Dale Gardens, Mutley, Plymouth, Devon*
1946 Jones, N. S., *Marine Biological Station, Port Erin, Isle of Man*
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*

1946 Jones, Prof. R. V., C.B., C.B.E., D.Phil., F.Inst.P., *Department of Natural Philosophy, Marischal College, Aberdeen*
1947 Jörgensen, C. Barker, *Slettevej* 8, *Copenhagen Söborg, Denmark*
1923 Judge, J. J., *Virginia House, Palace Street, Plymouth, Devon*

1948 Katterns, L. B., 115 *Feltham Hill Road, Ashford, Middlesex*
1945 Katz, Max, 1915E, *Spruce Street, Seattle* 22, *Washington, U.S.A.*
1940 Keilin, Prof. D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council**, 1940–43)
1946 Kelley, Major D. F., *Gulmarg, Elmsleigh Park, Paignton, Devon*
1946 Kenya: The Game Warden, *Game Department, P.O. Box* 241, *Nairobi*
1928 King, Mrs A. Redman, *Weetwood Hall, Leeds, Yorks*
1947 Kingsbridge Modern Secondary School, *Kingsbridge, S. Devon*
1927 Kirtisinghe, P., *Department of Zoology, University of Ceylon, Colombo* 3, *Ceylon*
1930 Kitching, J. A., O.B.E., Ph.D., *Department of Zoology, The University, Bristol*
1939 Knight, Miss Margery, D.Sc., *University Hall for Women Students, Holly Road, Fairfield, Liverpool.* (**Council**, 1943–46)
1945 Knowles, F. G. W., D.Phil., *Marlborough College, Marlborough, Wilts*
1938 Kollmann, Prof. M., *Bibliothèque de la Faculté des Sciences*, 40 *Allées Léon Gambetta, Marseille, France*
1948 Kow, Tham Ah, *c/o Fisheries Department, 4th Floor, Fullerton Building, Singapore*

*1925 Lebour, Miss M. V., D.Sc., *Kean Hill, Cawsand, near Plymouth, Devon*
1947 Lechane, J. D. B., 14 *Wyndham Street East, Plymouth, Devon*
1935 Le Mare, D. W., *Fisheries Department, Federation of Malaya and Singapore, Penang, Malaya*
1948 Letts, J. K., 183 *Windmill Lane, Greenford, Middlesex*
1948 Lloyd, A. T., *Wynona, Beacon Park Road, Plymouth, Devon*
1948 Lovegrove, T., 2 *Athenaeum Place, The Hoe, Plymouth, Devon*
1926 Lowndes, A. G., Sc.D., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1931 Lucas, C. E., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1930 Lumley, Adrian, *Sunnyside, Castle Gardens, Torquay, Devon*
1938 Lysaght, Miss A. M., Ph.D., 6 *Cumberland Gardens, London, W.C.* 1

1938 MacDonald, R., 112 *Antrim Road, Belfast, N. Ireland*
1935 Mackenzie, Col. W., O.B.E., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt*
1929 Mackinnon, Prof. D. L., D.Sc., *Department of Zoology, King's College, Strand, London, W.C.* 2. (**Council**, 1938–42)
1937 Mackintosh, N. A., D.Sc., 7 *Hinde House, Hinde Street, London, W.* 1. (**Council**, 1946→)
1947 Macnae, William, *Department of Zoology, University of Capetown, Rondebosch, C.P., S. Africa*
*1925 Magdalen College, *Oxford*
1945 Maitland-Adams, C. W., *The Old Rectory, Hawkwell, Hockley, Essex*
*1902 Major, H. G. T., 24 *Beech House Road, Croydon, Surrey*
1948 Mansfield, A. W., Inst.-Lieut. R.N., *N.H.Q. Trincomalee, Ceylon*
*1928 Manton, S. M., Sc.D., F.R.S. (Mrs J. P. Harding), 18 *Ennerdale Road, Richmond, Surrey*

1948 Marcotte, Alexandre, D.Sc., *Faculté des Sciences, Boulevard de l'Entente, Quebec, Canada*
1948 Mardon, Jasper, *Selwyn College, Cambridge*
1939 Marr, J. W. S., 28 *Cromwell Court, Kingston Hill, Surrey*
*1947 Marshall, Miss S. M., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Matthews, L. Harrison, Sc.D., *Department of Zoology, The University, Bristol.* (**Council**, 1944–47)
1912 Maurice, H. G., C.B., 6 *St Mark's Square, Regent's Park, London, N.W.* 1. (**Council**, 1913–38, 1939–42; representing Ministry of Agriculture and Fisheries, 1927–38; representing Zoological Society, 1942→; **Vice-President**, 1948→)
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1910 McClean, Capt. W. N., 39 *Phillimore Gardens, London, W.* 8
*1929 McEwen, Mrs Lawrence, 15 *Blackett Place, Edinburgh*
1945 McGill University, *Department of Zoology, Montreal, Canada*
1948 McIntyre, A. D., 96E *King Street, Helensburg, Dumbartonshire*
*1948 Menon, M. Devidas, *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1939 Metropolitan Water Board, 177 *Rosebery Avenue, London, E.C.* 1
1947 Miami University Marine Laboratory, *Coral Gables, Florida, U.S.A.*
1923 Milford Haven Trawler Owners Association, Ltd., *Milford Haven, Pembs*
1946 Miller, Cyril J., 42 *Westbourne Road, Peverell, Plymouth, Devon*
1947 Mitchell, E. S., *Fourlanesend Boys' School, Maker, near Plymouth, Devon*
1947 Mitra, G. N., *Assistant Director of Fisheries, Cuttack (Orissa), India*
1940 Moore, Hilary, Ph.D., *Woods Hole Oceanographic Institution, Mass., U.S.A.*
1948 Morgan, C. W., 11 *Clevedon Park Avenue, Milehouse, Plymouth*
1931 Mount Desert Island Biological Laboratory, *Salisbury Cove, Maine, U.S.A.*
1938 Mowbray, Louis L., *Curator, Bermuda Government Aquarium, Flatts, Bermuda*
1942 Moynahan, Dr E. J., *Wayside, Jordans, near Beaconsfield, Bucks*

1933 Neale, Morley H., *Chaffcombe House, Chard, Somerset.* (**Council**, 1934–36, 1939–42, 1943–46, 1947→)
1934 Neale and West, *Trawler Owners, Wharf Street, Cardiff*
1939 Needham, Joseph, Sc.D., F.R.S., *Gonville and Caius College, Cambridge*
1947 Newell, G. E., Ph.D., 11 *Wave Crest, Whitstable, Kent*
1947 Newton, Prof. Lily, Ph.D., *Department of Botany, University College of Wales, Aberystwyth, Cardigan.* (**Council**, 1947→)
1930 Nicholls, A. G., Ph.D., *Marine Biological Laboratory, Cronulla, N.S.W., Australia*
1947 Nisbet, R. H., 24 *Sheldon Avenue, Highgate, London, N.* 6
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1938 Nutman, S. R., *c/o* 179 *Rustlings Road, Sheffield* 11

1934 Oakley, Dr C. L., 58 *Cumberland Road, Bromley, Kent*
1930 Olive, G. W., *Dauntsey's School, West Lavington, near Devizes, Wilts*

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1937 Omer-Cooper, J., *Zoological Department, Rhodes University College, Grahamstown, S. Africa*
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1932 Smith, J. E., Ph.D., *Department of Zoology, Downing Street, Cambridge.* (**Council**, 1943–46, 1948→)
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1929 South Africa, Fisheries Division of, *Beach Road, Sea Point, Cape Town, S. Africa*
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1903 Torquay Natural History Society, *The Museum, Torquay, Devon*
1939 Totton, A. K., M.C., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1936 Tremblay, Jean-Louis, D.Sc., *Station Biologique du Saint Laurent, Faculté des Sciences, Boulevard de l'Entente, Quebec, Canada*
*1946 Tripathi, Y. R., *c/o S. R. Tripathi, Esq., Narsinghgarh, C.I., India*
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1948 Tseng, Dr. C. K., *Botany Department, Institute of Oceanography and Limnology, National Shantung University, Tsingtao, China*
1947 Tuck, A. W., *Upriver, Potter Heigham, Norfolk*
1943 Tucker, P/O Denys W., *c/o Rockside, 25 Bonhay Road, Exeter, Devon*
1939 Tutin, T. G., *Botany Department, University College, Leicester*

1932 Ullyott, P., *Trinity College, Cambridge*

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*1946 Vevers, H. G., M.B.E., *The Laboratory, Citadel Hill, Plymouth, Devon*

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THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £23,000.

The Association is maintained by subscriptions and donations from private members, scientific societies and public bodies, and from universities and other educational institutions; a generous annual grant has been made by the Fishmongers' Company since the Association began. Practical investigations upon matters connected with sea-fishing are carried on under the direction of the Council, and from the beginning a Government Grant in aid of the maintenance of the Laboratory has been made; in recent years this grant has been greatly increased in view of the assistance which the Association has been able to render in fishery problems and in fundamental work on the environment of marine organisms. An account of the Laboratory and the scope of the work undertaken there will be found in Vol. xv (p. 735) and Vol. xxvii (p. 761) of this *Journal*.

The Laboratory is open throughout the year and its work is carried out under the supervision of a Director and with a fully qualified research staff. The names of the members of the staff will be found at the beginning of this number. Accommodation is available for British and foreign scientific workers who wish to carry out independent research in marine biology and physiology. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat and these also collect the specimens required in the Laboratory.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the Laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the Laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

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