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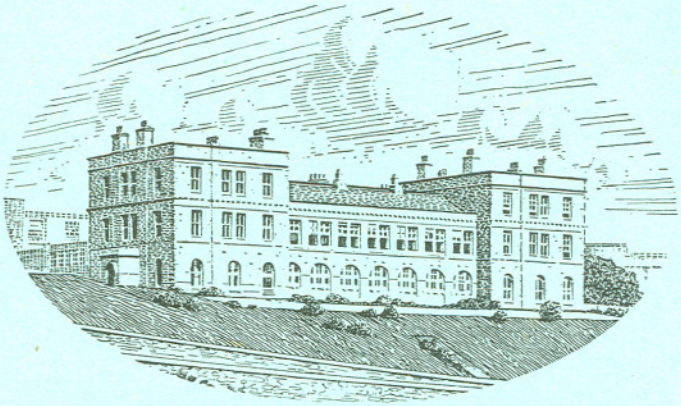

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PLANKTON PRODUCTION BETWEEN THE YORKSHIRE COAST AND THE DOGGER BANK, 1933–1939

By R. S. Wimpenny

Ministry of Agriculture and Fisheries

(Text-fig. 1)

Between March 1933 and June 1939[1] a series of vertical hauls with a plankton net has been made at a line of six stations 12 miles apart, the first lying off Flamborough Head and the last on the south-west patch of the Dogger Bank. This line was usually visited at monthly intervals, the net used being of the Hensen type fitted with bolting silk of 60 meshes to the inch and hauled to the surface by the counter-weight device introduced by Buchanan-Wollaston (1911). Hensen (1887) worked out a filtration coefficient for his net, and when this was applied to the dimensions of the one in use and the depth through which the vertical hauls were made, it was possible to express the catch in numbers per cubic metre of sea water. It was also possible to give the individual catches by weight, and it may not be without interest to observe, before passing on to deal with numbers, that the dry weights taken in 1936 varied between 0·2600 g. per m.^{3} in August and 0·0015 in February.

Although the net method of estimating plankton has often been decried as unreliable, Hensen net results have always given a consistent picture of relative plankton densities in the North Sea. Confidence arising from this consistency has not been lessened by a comparison of the net and sedimentation methods which has been made in respect of the May 1938 samples.

The sedimentation method consists in counting the entire deposit of microplankton which has settled on the floor of a glass cell containing a known volume of sea water. The counting is done by the use of Utermöhl's reversed microscope. This method has been shown to be superior to that of centrifuging and gives the most complete direct estimation at present known (Nielsen, 1933). The two sets of observations for May are shown on p. 2, the numbers being per cubic metre for the Hensen net and per litre for the sedimentation samples.

It will be seen that, while the sedimentation method reveals several thousand times the number of organisms per unit of volume, both methods agree in showing the stations of greater abundance at the ends of the line, although they disagree in showing the stations of greatest abundance at opposite ends.

[1] The observations actually began in June 1932, but, owing to war conditions, the writer has not been able to examine the data from this earlier period.

TABLE I

Stations ...	1	2	3	4	5	6
Hensen net:						
All organisms	33,011	127	434	6,968	3,628	57,972
Diatoms	32,376	76	285	2,590	1,191	49,066
Sedimentation:						
All organisms	156,819	3,925	16,865	6,667	10,100	24,533
Larger diatoms	10,969	1,117	1,565	3,050	1,633	8,633

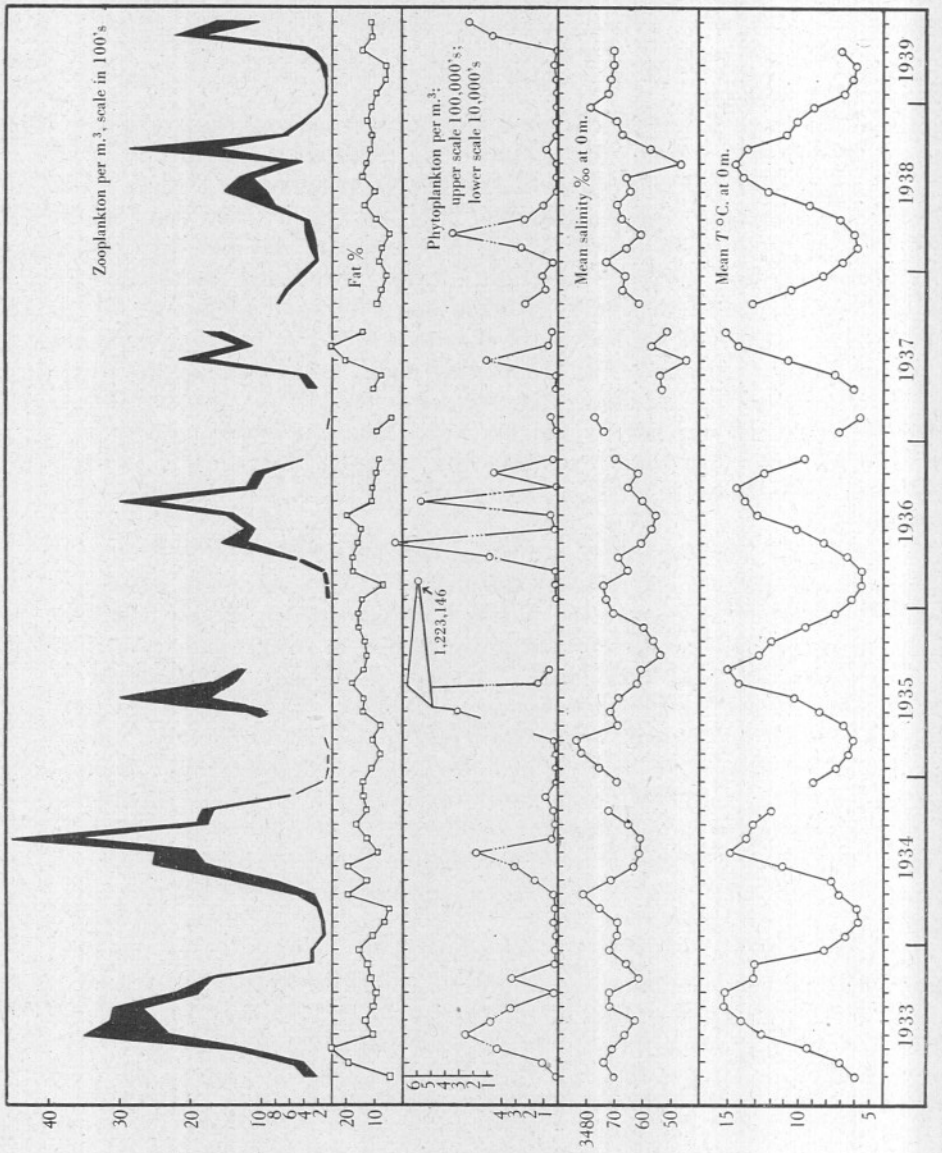

Fig. 1. Mean monthly values at six stations between Flamborough Head and the Dogger Bank for zooplankton, plankton-fat, phytoplankton, salinity and temperature.

The average catches per cubic metre, taking all the Flamborough line stations together, have been plotted at their monthly intervals in respect of zooplankton and phytoplankton in Fig. 1. On the same figure are also shown the average percentage fat contents of dried net samples taken as duplicates of those used for enumeration.

The phytoplankton shown in the figure reached its highest values in 1935 and 1936, but otherwise it gives no indication of any special trend during the period and generally rises to a climax each year between May and June, often followed by a secondary maximum later in the year. The year 1938 was exceptional, however, in that the maximum occurred in March. In 1936 the early maximum was succeeded by successively diminishing peaks in August and October.

In contrast to the phytoplankton, the zooplankton decreased through the period until 1937, after which it showed slight signs of a revival. Although during each year the zooplankton population appears to have built itself up on the corresponding phytoplankton maximum, the size of the stock so supported has little or no relation to the size of the phytoplankton standing crop revealed in the different years. The graph of the zooplankton has been split into upper and lower halves, the former showing the proportion of eggs and larvae. This representation suggests that reproduction must have been vigorous in 1933, 1934 and 1935, but that it sank to a minimum in 1936 and 1937, recovering again in 1938 and 1939.

The average for the six fat percentages taken each month and followed through the period shows a general downward trend. The annual cycle usually gives higher values in the first half of the year, and it seems likely that the fat percentage rises prior to the vigorous reproduction resulting in the zooplankton maxima.

Of the non-vital phenomena likely to form an explanatory background to the changes just described, salinity is probably the best index of certain relevant water movements now to be outlined. The stations from which the samples were taken lie across a submarine channel between Flamborough Head and the Dogger Bank. Down this channel the residual current system of the North Sea produces a south-going flow of water of higher salinity than that which it is about to enter. In this neighbourhood, it may be added, the south-going current is joining the western periphery of a circulation that usually flows in an anti-clockwise direction and is called the South-west Dogger Bank Swirl. The immediate origin of the south-going current is to be sought in oceanic water running into the northern entrance to the North Sea. It has been suggested elsewhere (Savage & Wimpenny, 1936) that an unusually strong incursion of oceanic water into the southern North Sea from the north also implies the convection of an increased supply of nutrient salts essential for diatom growth and this supply may form the foundation for especially abundant plankton production. Conditions of this sort are thought to have obtained in 1921 and 1933.

Fig. 1 shows the course taken by the surface salinities of the Flamborough area for the period under review. Each year there appears to have been an impulse of water originating from the north. In the early part of the time, the salter water from the north reached the peak of its influence about April, but it tended to become earlier thereafter and by 1938 it occurred in January, the peak of the next maximum coming again in December of the same year instead of early the next year, as had previously been the case. There are, therefore, indications of a periodicity in the time of arrival of this water, the duration of which is less than a year. Considering next the salinities for the whole period shown in the figure, it is also to be observed that there is a progressive lowering in the values up to 1937, indicating a slackening in the strength of the northern current and its fertile influence. During 1938 and 1939 a reversal of this process appears to have begun.

With regard to the minimum in 1937, it should be mentioned that observations taken over a wider area in October of the same year, which are being published elsewhere, revealed that the anti-clockwise direction of the South-west Dogger Bank Swirl had been reversed, the northern current entering the eastern periphery. A similar reversal has already been recorded for 1927 (Savage & Hardy, 1935), and here it should be noted that, lying midway between 1921 and 1933, the northern influx might also be expected to have been low in 1927.

The surface temperatures for the period are also plotted in Fig. 1, but, beyond pointing out that 1936 is revealed as notably different from the other years in the lowness of both winter and summer values, no further comment need be made here.

The decrease and slight increase of salinities, during the period discussed, correspond so well with the sequence of abundance for the zooplankton that a significant relation suggests itself. Although at first sight this seems to be denied by the fact that no comparable sequence is shown by the phytoplankton, it is to be argued that the standing crop of phytoplankton is not necessarily a measure of its own production when the amounts eaten by zooplankton and the rate of growth are unknown. Indeed, the fact that a greater zooplankton population was supported in the earlier part of the period, whilst the standing crop of phytoplankton remained much the same at the close, implies a greater plankton production at the beginning. Given relations of this sort between the two plankton communities, it is even possible that the standing crop of phytoplankton may at times be in inverse relation to the zooplankton it supports and also to its own growth rate and the total production of plankton.

In connexion with this latter suggestion it may be noted that the results from very extensive samplings of the North Sea with the Hardy Continuous Recorder have led Lucas (1941) to conclude that the phytoplankton throughout the southern North Sea increased between 1932–3 and 1935–7 but that since 1935–7 there had been a decrease—a state of affairs the opposite to that shown by the zooplankton dealt with in this account.

It is, of course, possible that the zooplankton in the Flamborough neighbourhood has been behaving independently of the phytoplankton environment to be found in this area and has been responding to antecedent conditions which may be disclosed by the subsequent publication of data from a wider field. Moreover, in view of the degree of segregation and stability known to be associated with the diatom patches in the South-west Dogger Bank Swirl area, it is quite possible that the whole plankton of the Flamborough area may show a measure of independence in its fluctuations when compared with the North Sea as a whole. Nevertheless, I want to stress that the present observations and those made with the Hardy Continuous Recorder would be reconciled if it were considered that in the earlier part of the period the zooplankton of the North Sea had eaten down a more productive phytoplankton than became available for its support towards 1937. As the zooplankton stock became reduced, it may be conceived to have permitted potentially weaker diatom flowerings to have assumed higher population densities and so have gradually resulted in the greater phytoplankton abundance indicated by Lucas.

In the northern North Sea salinities have revealed signs of predominating Atlantic influence from 1931, normal conditions not returning until 1939 (Fishery Board for Scotland, 1932–9), and, at the southern entrance, Carruthers's latest work on residual currents revealed by Lucas (1941) indicates a hold-up or reversal of the current entering from the Channel between 1931 and 1938 after which the flow towards the North Sea was resumed.

Outside the North Sea, Kemp (1938), quoting the work of Ford, Atkins, Cooper, and F. S. Russell, has pointed out that the herring fishery at Plymouth, the amount of winter phosphate and the numbers of young fish have all declined sharply in the Plymouth area since 1931. Here there is no apparent relation with the temperature and salinity, and Kemp considers this likely to be due to ignorance of the constitution and origin of the water masses which enter the Channel from time to time.

In the Arctic (Scherhag, 1937) an increase in temperature has taken place in recent years which has resulted in a great spread of the cod fishery.

The changes just mentioned deserve relation to those dealt with here, especially with a view to the determination of any periodicities in plankton production that may be forecast with advantage to the commercial fisheries; it is hoped that post-war observations will allow this aim to be realized.

My thanks are due to Dr E. S. Russell, Director of Fisheries Research, and Lt.-Commander J. R. Lumby of the Fisheries Laboratory, Lowestoft, for their helpful comments on the matter in this note.

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THE LARVAL STAGES OF *PORTUMNUS* (CRUSTACEA BRACHYURA) WITH NOTES ON SOME OTHER GENERA

By Marie V. Lebour, D.Sc.

Naturalist at the Plymouth Laboratory

(Text-figs. 1–5)

Two species of *Portumnus* occur in the Plymouth area, *P. biguttatus* (Risso) and *P. latipes* (Pennant). *P. biguttatus* was the only species recorded when the old fauna list of Plymouth was published (1904), but since then it is known that *P. latipes* is very common in certain sandy areas (see *Plymouth Marine Fauna*, 1931), far commoner than *P. biguttatus*.

P. biguttatus is rare and has not been seen since 1906. It was first found by W. Garstang and R. Todd on Drake's Island in Plymouth Sound, burrowing in fine gravel (1905), and two specimens, ♂ and ♀, are recorded from a sandy patch from the north-east corner of Drake's Island. A female in berry was recorded from the same locality by R. Todd, and L. R. Crawshay dredged one in Cawsand Bay in 1906. Apparently the eggs were not hatched out and the zoea of this species is unknown. In August 1902 R. Gurney obtained a megalopa in the plankton and from it secured the first crab stage. He describes the megalopa as being intensely blue. The cast skin of the megalopa and the crab obtained from it (Fig. 3 *a–c*), which he kindly handed to me, are described in my paper of 1928 (Lebour, 1928*c*, p. 518, pl. viii, figs. 1–3). There is no reason to doubt the accuracy of the determination, especially because, as shown below, corresponding stages of *P. latipes* as well as the zoeae are now known and are very distinct, differing considerably from those of *P. biguttatus*.

Portumnus latipes occurs commonly at low water and below, burrowing in sandy beaches on the Cornish coast. It is found in abundance in Whitsand Bay, but the berried female has only lately been captured and the eggs hatched out. The crabs live at a depth of about four to six inches when the sand is uncovered by the tide; but they probably swim about just above the surface or are covered lightly by the sand when the tide is up, for they can be caught by skimming a shrimping net along the sand in the water. Very small crabs can be obtained in this way, probably only a few stages from the megalopa.

In 1928 an unidentified zoea from the plankton was provisionally attributed to *Pirimela denticulata*? (Lebour, 1928*c*, pp. 518–21, pl. i, fig. 9; pl. vii, fig. 6; pl. viii, figs. 4–6). I have since hatched out the larva of *Pirimela* which agrees in essentials with the descriptions by Kinahan (1857*b*, 1862) and Cano (1892*a*). The discovery that this unidentified zoea is really that of *Portumnus latipes*

is due to Mr F. Hinrichs of the Staatliche Biologische Anstalt in Heligoland, who, in 1935, wrote to inform me that some years previously (1911, 1912) he had hatched out the larvae of this species, procured all the zoeal stages from the plankton, and also studied the megalopa and young stages, and that these agreed with my description of the queried *Pirimela*. Since he has not published anything on the subject and it is important that the life histories of these crabs should be correctly known, it now seems a suitable opportunity to put them on record and correct the previous erroneous supposition.

Portumnus latipes in berry was obtained on 20 June 1940, from Whitsand Bay. It was dug out of the sand with a fork at low spring tide just above low water, about four inches down. These crabs are frequently found in similar situations by the fishermen digging for sand-eels (*Ammodytes*) which they use for baiting their long lines set on the beach. They informed me that they always kill the crabs as they eat the bait. Besides sand-eels, nereids and amphipods are commonly dug up in the same habitat. When kept in captivity the adult crabs ate pieces of mussel and *Nereis*. When placed in sand they dig themselves in with all the walking legs, but when disturbed they can swim easily. When dug up on the beach they burrow deeply as they are uncovered, but they also escape by running quickly along the sandy beach.

The female, in good condition, carried a large mass of eggs, greenish brown due to black chromatophores and yellowish yolk. The eggs were nearly ready to hatch with a small amount of yolk. The chromatophores were bordered with yellow. The berried female was placed in a plunger jar and the eggs hatched on 23 June. The eggs measured 0·32 mm. across (Fig. 1*a*) and the pre-zoea obtained from them measured 1·12 mm. in length without the long spines (Fig. 1*b*). The pre-zoeal skin was so extremely thin that it was impossible to make out the details of the spines. There are four zoeal stages as in *Carcinus maenas*, and the zoea resembles that species in many ways, especially in the arrangement of chromatophores and in having no lateral spines on the carapace. The body is clear and transparent but there are numerous nearly black chromatophores edged with yellow and there is a pinkish tinge all round. A very conspicuous series of dark chromatophores extends laterally along the body as in *Carcinus*. The rostral and dorsal spines are, however, considerably longer. There are chromatophores on the dorsal spine, in front of the eyes, on the thorax, mandible and first and second maxillipedes, on each abdominal somite ventro-laterally and on the telson. The last (fourth) zoea has already been described as *Pirimela* (?) (Lebour, 1928*c*, p. 520, pl. i, fig. 9), and the megalopa and two crab stages reared from it (p. 520, pl. vii, fig. 6; pl. viii, figs. 4, 5). As very young crabs, about stages four and five after the megalopa, were caught in June, and as these almost certainly must be from spring larvae, it follows that the breeding season must be a fairly long one, extending from spring to autumn, for the last zoeae and megalopae were found in the plankton from July to October. The usual breeding season, however, appears to be in the summer months.

The first zoea (Fig. 1 *c*, *e*) measured 1·6 mm. from the tip of the dorsal spine to the tip of the rostral spine, the length of the body being *ca.* 1·3 mm. Both spines are slightly curved. There are no lateral carapace spines. The antennules and antennae are like those of all Portunids. The antennal exopodite is about half the length of the spinous process, with one long and one very short spine at the tip. The second abdominal somite has a lateral hook each side,

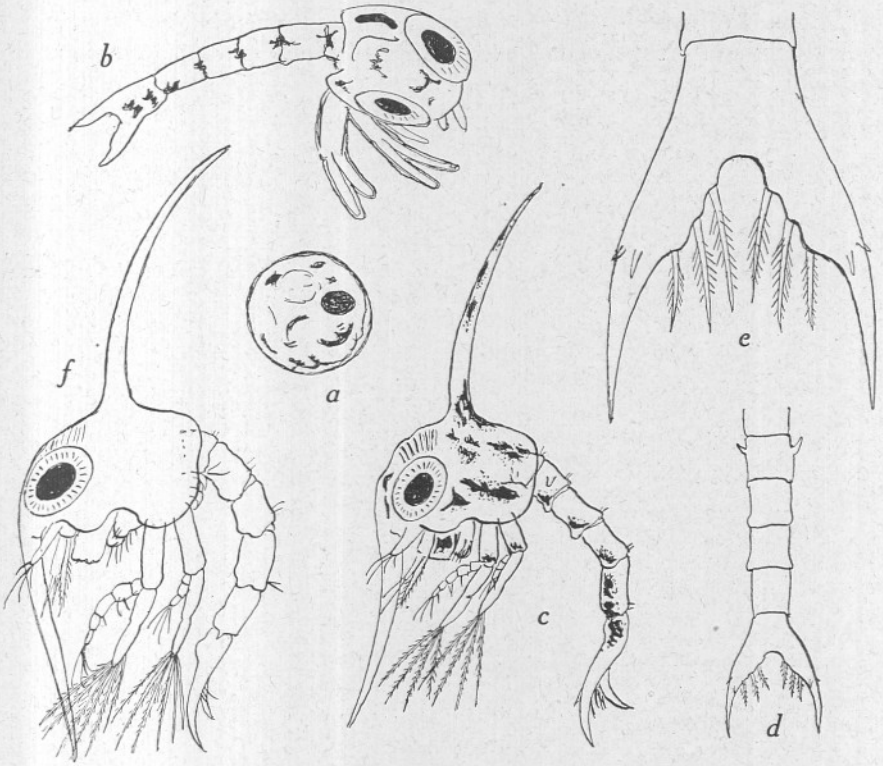

Fig. 1. *Portumnus latipes*. *a*, egg, 0·32 mm. across; *b*, pre-zoea from egg, 1·12 mm. long; *c*, first zoea from pre-zoea, 1·28 mm. from spine to spine; *d*, abdomen and telson of same; *e*, telson of same; *f*, second zoea from first from pre-zoea, 1·8 mm. from spine to spine.

but there are no lateral spines on any of the somites. The telson has two lateral spines instead of the usual three of the Portunid, the outer spine being very small and disappearing in the later stages, leaving only one as in *Carcinus*. Hinrichs obtained second, third and fourth zoeae from the plankton in Heligoland. The first zoea was hatched from the egg in a plunger jar; the second zoea moulted from the first in a bowl; the fourth (and last) zoea was obtained in the plankton.

The second zoea (Fig. 1*f*) measured 1·8 mm. from spine to spine, the length of the body being *ca.* 1·6 mm. In essentials it is like the first, but there are

six setae on the ends of the maxillipedes and only one lateral spine on each side of the telson. The third zoea was not seen, but Hinrichs found it in the plankton in Heligoland.

The fourth zoea (last) (Fig. 2) was obtained several times from the Plymouth plankton. The length from spine to spine was 3·6 mm., the body length 3·2 mm. There were ten setae on the maxillipedes and the pleopods were long and without setae. It is much more elongated than the corresponding stage of *Carcinus* and is not so darkly coloured, dark chromatophores being mixed with yellow and pinkish red. The last zoea moulted in the laboratory to the megalopa.

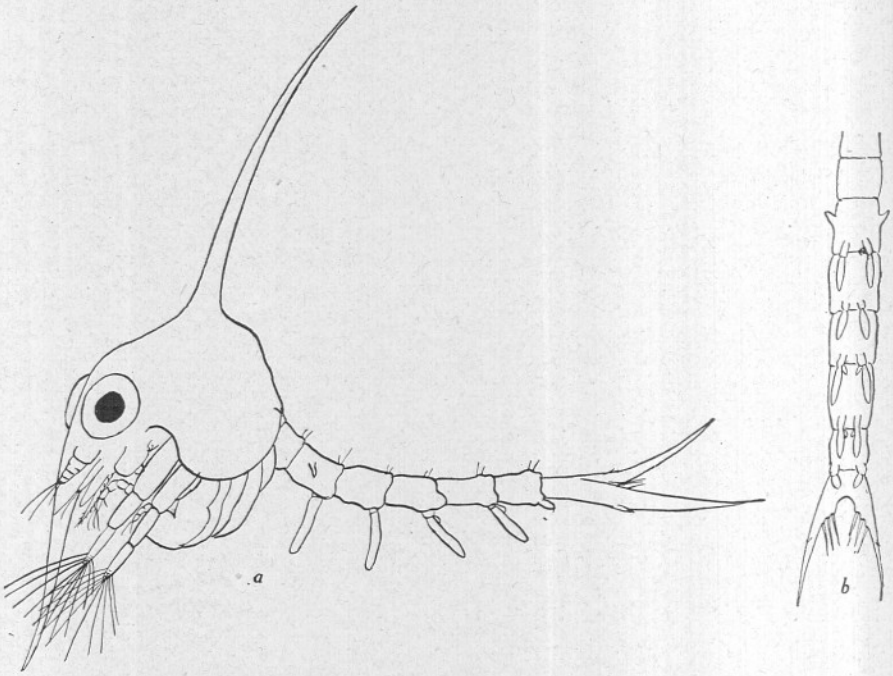

Fig. 2. *Portumnus latipes*. *a*, fourth (last) zoea from plankton, 3·6 mm. from spine to spine; *b*, abdomen of cast fourth stage.

The megalopa (Fig. 3*d*) measured 2 mm. from the tip of the rostral spine to the end of the carapace. Unlike any known Portunid it has a dorsal spine and thus resembles *Cancer* and *Atelecyclus*. It is coloured in much the same way as the last zoea and has long dark chromatophores on each side of the carapace in the same position as in *Carcinus*. The rostrum is pointed and sticks out horizontally, the dorsal spine being curved. The carapace is broad with inconspicuous protuberances. There are seven setae on the last pleopods. There is a large hook on the ischium of the first leg, but no hooks on the other legs. The presence of the dorsal spine and the absence of hooks on the legs

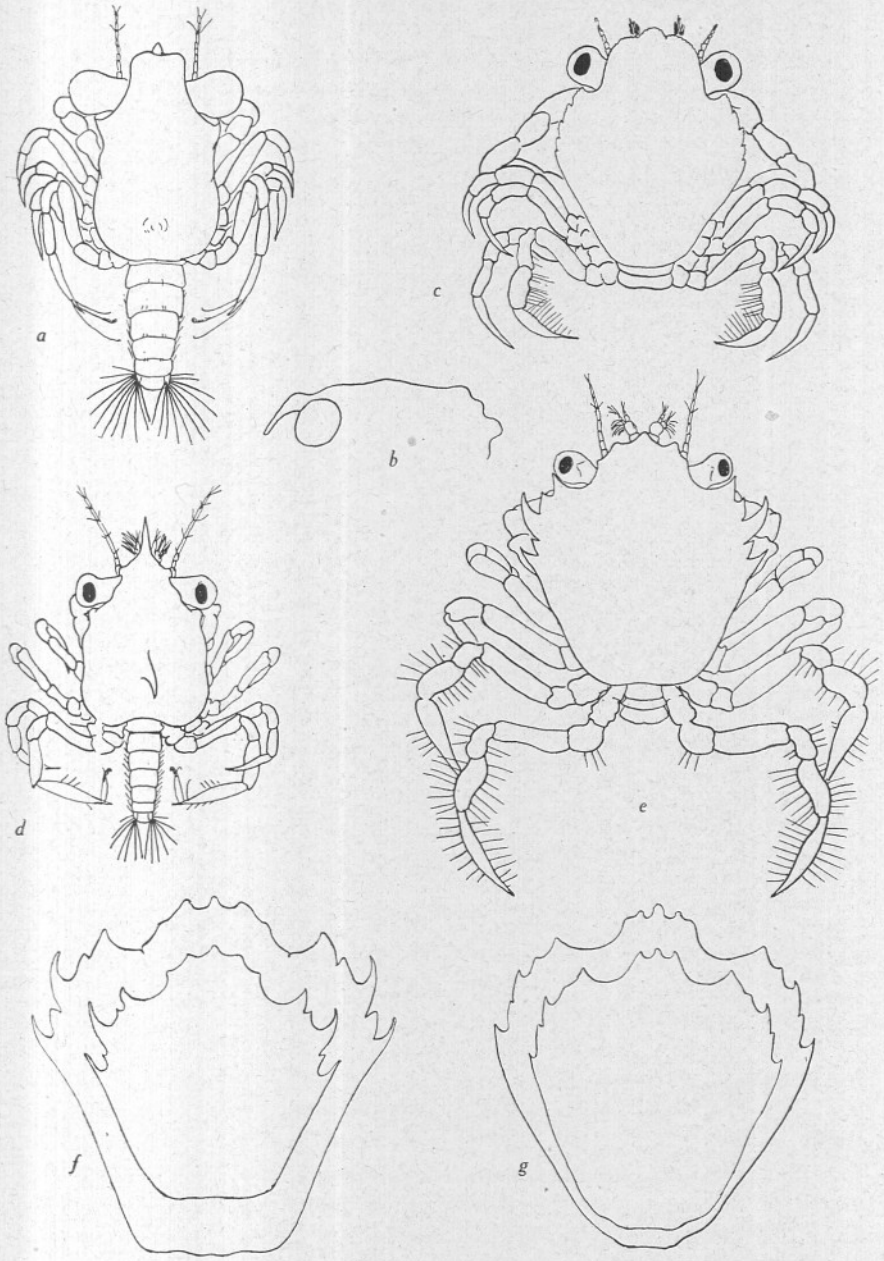

Fig. 3. *Portumnus latipes* and *P. biguttatus*. *a–c*, *P. biguttatus*: *a*, megalopa, cast skin, carapace 2·2 mm. long; *b*, carapace of same, side view; *c*, first young crab stage from megalopa, length of carapace 2·3 mm; *d–g*, *P. latipes*: *d*, megalopa from last zoea, carapace 2 mm. long; *e*, first young crab from same, carapace 2·4 mm. long; *f*, carapace of first and second crab stages (first from megalopa, carapace 2·4 mm. long, second from first, carapace 3·52 mm. long); *g*, carapace of *ca.* fifth and *ca.* sixth young crab stages consecutive moults), 8·5 and 10 mm. across greatest width.

other than the first (usually present in the Portunidae) are characters which set this megalopa apart from all the other British Portunidae. The megalopa moulted to the first crab stage.

The first crab stage (Fig. 3 *e*, *f*) obtained from the megalopa is striking in having the last pair of legs with paddles bearing swimming setae on both sides, like *Portunus*, whereas the adult *Portumnus* bears these on one side only except for a small row at the proximal end of the outer side. This last character of the first crab stage was regarded in the previous paper as an indication that it

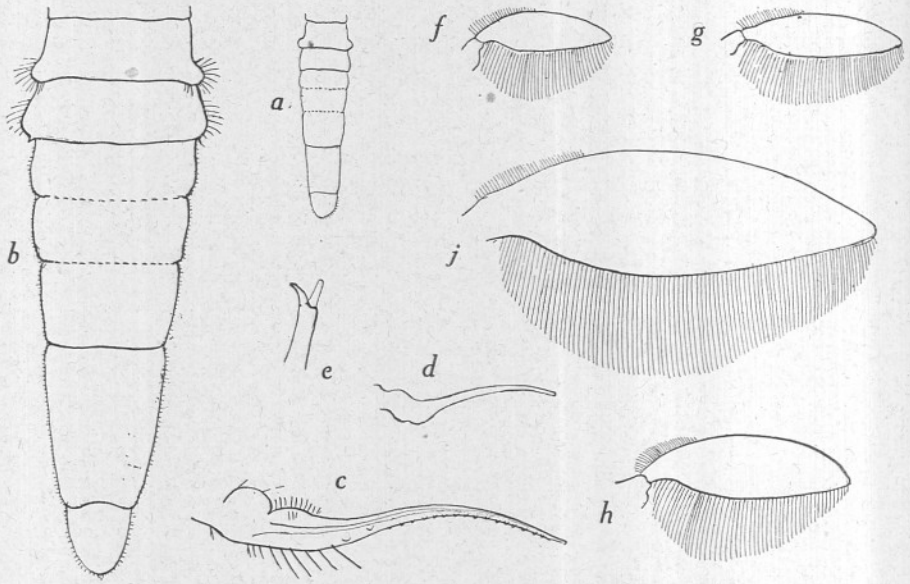

Fig. 4. *Portumnus latipes*. *a*, abdomen of cast, *ca*. fifth crab stage; *b*, abdomen of adult ♂; *c*, first pleopod of *ca*. fifth crab stage, ♂; *d*, second pleopod of same; *e*, tip of second pleopod of adult ♂; *f*, paddle of last leg of *ca*. fifth crab stage; *g*, paddle of the next stage (moulted); *h*, paddle of the next stage (moulted); *j*, paddle of adult.

did not belong to *Portumnus* (Lebour, 1928, p. 421). A study of a series of stages, however, shows that the setae on one side dwindle and finally almost disappear (Fig. 4 *f–j*).

The first crab stage obtained from the megalopa of *P. biguttatus* (Fig. 3*c*) has no hairs on one side of the paddle and it seems that we probably have a series in the Portunidae from *Portunus* through *Portumnus latipes* and *P. biguttatus* to *Carcinus* which has no swimming paddles. Unfortunately the megalopa of *Portumnus biguttatus* was not noticed in detail before moulting, and it is impossible to be sure whether a dorsal spine was present on the carapace or not. There is an indication near the centre that a prominence, now more or less collapsed, was present and may have been a spine (Fig. 3 *a*, *b*). The first

young stage is very different in the two species, and the differences in both megalopa and crab, as well as in the adult, may warrant a separation into different genera. In the early crab stages of *P. latipes* the shape of the carapace is different from that of the adult, being broader in proportion to the length, and the lateral teeth are much more pointed and hook-like. Young stages, probably about the fifth, are much more like the adult (Fig. 3 *f*, *g*). The abdomen of a male in this stage is like the adult (Fig. 4 *a*, *b*), having segments 3–5 fused with only an indication of a suture between 3 and 4, and 4 and 5. The male pleopods of *P. latipes* are interesting, for in the adult the second pleopod is bifurcate whilst in *Carcinus* it is simple (although similar in other respects) (Fig. 4 *c–e*). In the early stages up to about stage 5 there is no bifurcation. The affinity with *Carcinus* is apparent in many ways throughout the life history.

Some notes on the feeding of the young *Portumnus latipes* may be given. A last zoea was obtained in the inshore plankton on 9 September 1943, which moulted during the night to the megalopa. It was kept in a glass finger bowl until it moulted to the first crab stage on 23 September, and lived until 3 October when it died without further moult. During this time the water was frequently changed and a variety of food offered. All the Plymouth crabs previously reared readily ate pieces of mussel, *Mytilus edulis*, and both megalopa and crabs moulted, but this megalopa, although it occasionally ate mussel, did not like it and it was obviously not a congenial food. Various other invertebrates were tried, many of which were eaten. The following is a list:

9. 9. 43. Newly moulted megalopa ate many dead, but newly killed, *Oikopleura*.

10. 9. 43. The megalopa ate a moribund *Calanus*, *Pseudocalanus* and *Upogebia* larva, picking out the flesh and rejecting most of the cuticle of the copepods but eating practically the whole of the *Upogebia*. The food was held in the chelae and eaten either when swimming or when resting on the bottom of the bowl.

13. 9. 43. The megalopa ate a moribund *Upogebia* larva.

16. 9. 43. The megalopa ate a piece of the mantle of a *Teredo*. It was noticed that the large hook on the ischium of the first leg helps in holding the food fast while the crab swims. It also ate a moribund *Processa* larva.

23. 9. 43. The megalopa moulted to the first young crab which ate two dead *Autolytus* sp., but did not eat pieces of mussel (foot and mantle) which were present. In a few days, however, it ate some of the mussel. The crab always dances round the food as though testing and smelling it before grasping it.

24. 9. 43. The young crab ate muscles of a newly killed *Crangon vulgaris*, preferring it to mussel.

28. 9. 43. The young crab ate muscles of *Crangon*, a young cockle taken from its shell, and a moribund *Macropodia* zoea. The crab was at first almost colourless, but now has a brownish yellow colour.

29. 9. 43. The young crab ate a moribund pagurid larva and a moribund *Macropodia* larva. The cuticle of both was rejected.

30. 9. 43. The young crab ate a young cockle removed from its shell.

From these observations it appears that the natural food of the megalopa and young crab is small crustacea, mollusca and worms, but that it probably

does not catch them alive for in no case when live material was offered was it eaten. Worms, molluscs and copepods could easily be obtained, whilst the megalopa would probably catch the dead plankton. It has already been shown that the adult eats dead fish and worms.

The Zoea of *Pirimela denticulata* Montagu

A female in berry from Wembury was kept in a plunger jar and the eggs hatched out. The eggs when ready to hatch measured 0·4 mm. across. The pre-zoea obtained from the egg (Fig. 5*a*) is very like *Portunus*, but it was

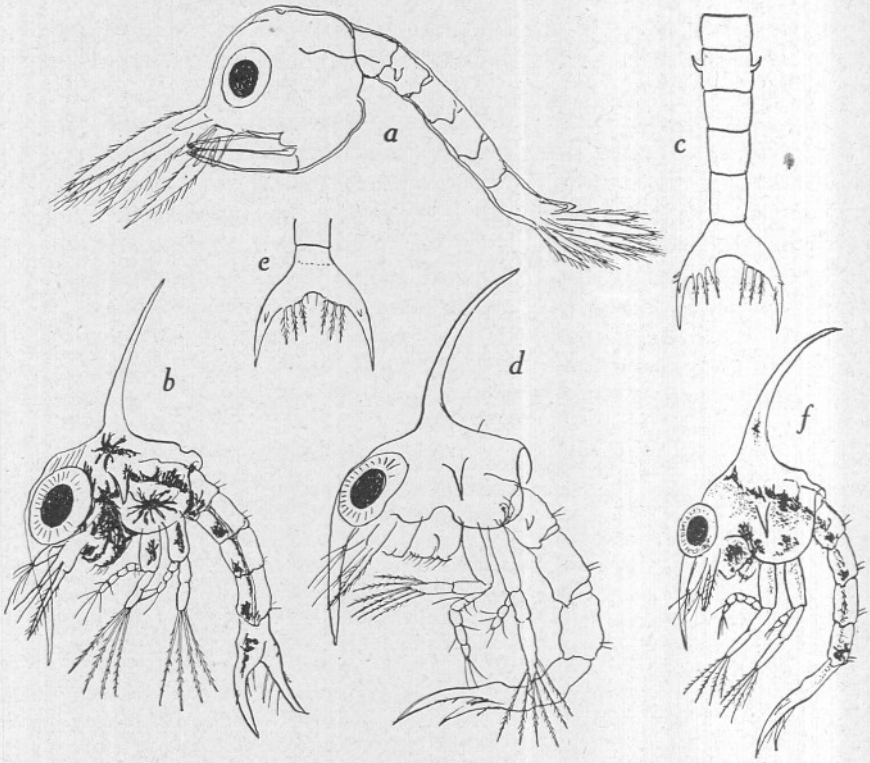

Fig. 5. *Pirimela denticulata* and *Polybius henslowi*. *a–e*, *Pirimela denticulata*: *a*, pre-zoea from egg, 1·8 mm. long; *b*, first zoea from pre-zoea, 1·3 mm. from spine to spine; *c*, abdomen and telson of same; *d*, second zoea from first, 1·3 mm. from spine to spine; *e*, telson of same; *f*, *Polybius henslowi*, first zoea from pre-zoea, 1·4 mm. long.

unfortunately impossible to ascertain whether there were three or four large spines on the antennal exopodite, the number distinguishing *Portunus* and *Cancer*.

The first zoea (Fig. 5 *b*, *c*) from the pre-zoea is pale greenish with thick very dark brown chromatophores along the thorax and abdomen, on the carapace, in the mouth region and on the bases of the maxillipedes. The zoea,

which agrees with the description by Kinahan (1856–59) who hatched out the species, is like *Portunus*, with lateral spines on the carapace and three external spines on the telson. A pair of lateral hooks is present on the second abdominal somite. The first zoea measured 1·4 mm. in length and 1·34 mm. from spine to spine. This moulted to the second zoea.

The second zoea (Fig. 5 *d–e*), from the first, measured 2 mm. long and 1·3 mm. from spine to spine. Thus whilst the body is larger the spine measurement is the same as that of the first zoea. The colouring is the same. There are six setae at the tips of the exopodites of the maxillipedes and faint rudiments of the third maxillipede and legs. There is only one lateral spine remaining on the telson, but there is an extra pair inside the fork. There is a faint line showing beneath the cuticle where the division of the fifth and sixth abdominal somites occurs.

No further stages were obtained, therefore it is not known how many zoeal stages there are. Cano (1891) figures the megalopa, which has a pointed rostrum and no dorsal spine, the first leg having a large hook on the ischium. He also figures a second megalopa stage and a first young crab stage which he attributes to *Pirimela*. None of the British crabs has two megalopa stages, indeed it is very unusual for there to be two (see Gurney, 1942, p. 37). It is possible that Cano may have had an older megalopa really in the first and only stage. As his specimens were taken in the plankton we cannot be sure that they belong to *Pirimela*. As far as we know from its larval stages *Pirimela* is probably related to *Portunus* and *Cancer*, perhaps more nearly to *Cancer*.

Polybius henslowi Leach

Polybius henslowi Leach (Fig. 5 *f*) is rare in the Plymouth area, being occasionally taken in the deeper waters. The first zoea has already been described from specimens obtained by Todd and hatched by him from the egg (Lebour, 1928*c*, p. 516, pl. iv, fig. 6). A female in berry was obtained from outside waters (17. 12. 31) and the eggs hatched out in a plunger jar. This is the first time that colour notes are available. The eggs ready to hatch measured 0·36 mm. across. The pre-zoea from the egg measured 1·12 mm. in length with conspicuous orange and black chromatophores. The pre-zoeal skin was too fragile for complete examination of the spines. The first zoea from the pre-zoea is transparent with a slight yellowish green tinge and dark brown chromatophores accompanied by yellow and orange on the dorsal spine about one-third of the way up, on the eye (yellow and orange), carapace, abdomen and mouthparts (dark brown, orange and yellow), the dark chromatophores forming a line along each side of the carapace and along almost the whole length of the abdomen. No further stages were available.

All literature is to be found in R. Gurney's *Bibliography of the Larvae of Decapod Crustacea*, Ray Society, 1939 and *Larvae of Decapod Crustacea*, Ray Society, 1942.

STRUCTURE AND FUNCTION OF THE GUT IN *SPADELLA CEPHALOPTERA* AND *SAGITTA SETOSA*

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(Text-figs. 1–14)

CONTENTS

INTRODUCTION

Beyond observations on the mode of feeding and type of food, little is known about nutrition and digestion in the Chaetognatha. This research represents an attempt to fill this gap in our knowledge. Originally it had been intended to work solely on *Sagitta*, but the greater ease with which *Spadella cephaloptera* was obtained and could be kept resulted in attention being largely transferred to this species.

The work was carried out at the suggestion and under the direction of Prof. C. M. Yonge, who has condensed and prepared the manuscript for

the press. The observations on living animals were made at the Plymouth Laboratory and the author is indebted to the Director and members of the staff, in particular Mr F. S. Russell, F.R.S., for interest and help. Thanks are also due to Dr J. A. Kitching for profitable suggestions and to Miss M. W. Jepps for help in identifying the ciliate parasite mentioned in the last section of this paper.

SPADELLA CEPHALOPTERA

Spadella cephaloptera is a bottom-living Chaetognath. It fixes itself to a suitable substratum by adhesive papillae on the ventral surface of the body (Fig. 1, *ap*). It was rarely seen to swim but makes occasional rapid movements from one point of attachment to another. John (1933) found it on

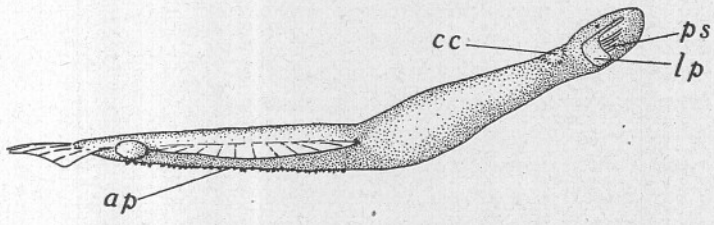

Fig. 1. *Spadella cephaloptera*, lateral aspect of living specimen showing normal resting position. × 18. *ap*, adhesive papillae; *cc*, corona ciliata; *lp*, lateral plate; *ps*, prehensile spines.

the eastern shore of Plymouth Sound attached to weed and resting on mud in tidal pools. He quotes other workers who found it in similar environments.

The material for the present work was obtained from certain tanks at the Plymouth Laboratory. *Spadella* was reported to be infecting the tanks in 1911, and from this source John (1933) obtained much of his material in 1930. It was not, however, as abundant during 1937–8 as it was reported to have been a few years previously.

The animals were stored in finger-bowls and transferred to watch-glasses for close examination.

Morphology of the Alimentary Canal

Living animals were examined and drawn under the binocular microscope, the gut being clearly visible through the transparent body wall. They readily fed on small copepods while under observation.

For general histological work Bouin's fixative was used, except for the head where it caused considerable contraction. Flemming-without-acetic fixed the head well and penetrated adequately when the animal was cut transversely behind the anus. Sections were cut transversely and longitudinally at 4 μ. Most of the staining was done with Mallory's triple stain, the slides being first treated with corrosive sublimate, followed by Lugol's solution and 'hypo'. This gave excellent results. Good results were also

obtained using Delafield's haematoxylin followed by erythrosin, and Heidenhain's haematoxylin followed by Biebrich scarlet. For the investigation of fat, material was fixed in Flemming-without-acetic and stained lightly with erythrosin. An unsuccessful attempt was made to detect glycogen, fixing with Carnoy and staining with Lugol's solution and also Best's carmine. Animals fed on copepods covered with iron saccharate were fixed in alcoholic ammonium sulphide and Bouin's fluid (Yonge, 1931), but iron could not be detected in sections. Material was fixed with food in the oesophagus and in the posterior region of the gut, and at $\frac{3}{4}$, 2, 5, 8 and 10 hr. and later periods after feeding.

Anatomy. The alimentary canal is divided into three regions: oesophagus, intestine and rectum (Fig. 2). The oesophagus runs obliquely over the bicornis muscle and then backwards through the head. When the animal is not feeding the mouth opening is laterally compressed, forming a narrow slit on the antero-ventral surface of the head. This slit occurs at the base of a groove, the 'vestibule' (John, 1933), the walls of which form thick lateral lips (Fig. 4, *ll*). The groove extends beyond the mouth anteriorly as a deep depression. John (1933) has described the lateral plates (Fig. 2, *lp*) lying in the dorsal region of the head supporting teeth at their anterior ends; and the prehensile spines (*ps*) on either side of the head, covered by the hood when the animal is not feeding.

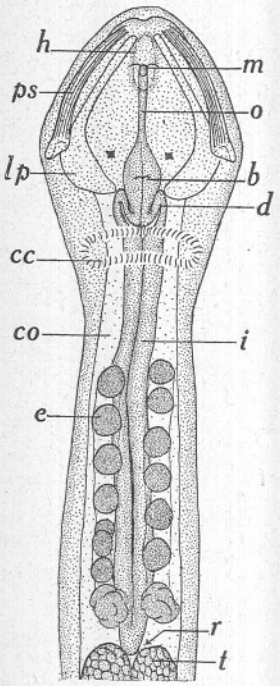

Fig. 2. *Spadella cephaloptera*, anterior half viewed from dorsal aspect. ×25. *b*, bulb; *co*, coelom; *d*, diverticulum; *e*, eggs in ovary; *h*, edge of hood (on ventral surface); *i*, intestine; *m*, mouth; *o*, oesophagus; *r*, rectum; *t*, testis. Other lettering as before.

In the region of the bicornis muscle the oesophagus is pear-shaped in transverse section, with the expanded region dorsal. It then becomes laterally compressed, expanding posteriorly to form a conspicuous bulb (Fig. 2, *b*). Beyond the bulb the oesophagus is laterally flattened and narrows rapidly as it leads into the intestine. As the latter is extended forwards on either side of the oesophagus as short diverticula (Fig. 2, *d*), the posterior half of the oesophagus forms a valve or nozzle which may prevent regurgitation from the intestine (see Fig. 2). When the oesophagus contains food it may be greatly distended, causing great displacement of the head musculature.

The intestine runs straight through the body and, apart from the lateral diverticula already mentioned, is without morphological differentiation (Fig. 2). The diverticula themselves are obliterated during the passage of food. In transverse section the intestine is circular or slightly elliptical and the lumen

narrow, especially in the anterior region. When the gut contains food its wall is greatly distended, obliterating much of the coelomic cavity.

The rectum is a short tube leading out of the postero-ventral region of the intestine (Fig. 3, *r*) and ending at the anus. Although narrow in the resting condition (Fig. 8), it is capable of accommodating the entire skeleton of a copepod during defaecation.

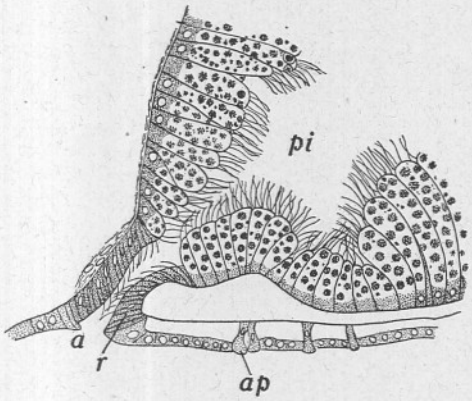

Fig. 3. *Spadella cephaloptera*, longitudinal, semi-diagrammatic section through posterior region of gut. × 50. *a*, anus; *pi*, posterior intestine. Other lettering as before.

Histology. The epithelium on the ventral surface of the head is covered by a thick hyaline cuticle staining yellow or bluish with Mallory's triple stain and black with Heidenhain's haematoxylin. This cuticle lines the groove anterior to the mouth and covers the lateral lips which are formed by a thickening of the general epidermis (Fig. 4).

The epithelium of the oesophagus is composed of two types of cell, granular and vacuolated cells. The former are more abundant (Fig. 4, *grc*). They are columnar in form and packed distally with a granular material which is also found free in the lumen (Figs. 4, 5, *s*). This secretion is not mucus but consists of granules which stain with Heidenhain's haematoxylin and a matrix which takes cytoplasmic stains. These two constituents seem to be inversely related, and the granules may be the precursor of the matrix. When there is a copepod in the oesophagus the secretion can be seen among its appendages, and it is absent from the lumen after swallowing.

Although these granular cells appear to produce a similar secretion throughout the oesophagus, yet they differ, in different regions, in height and in the angle subtended to the basement membrane. Those forming the dorsal and lateral walls of the oesophagus immediately within the mouth are particularly tall and are directed downwards towards the mouth opening. Their secretion is very profuse and the granules frequently large. The ventral wall is composed of shorter cells similarly directed towards the mouth and in such a way that

in transverse sections the epithelium in that region appears very low. Their secretion consists of much finer granules.

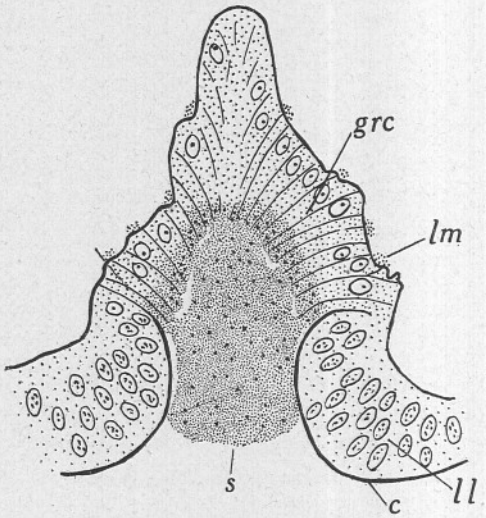

Fig. 4. *Spadella cephaloptera*, vertical section through mouth region. × 660. *c*, cuticle; *grc*, granular cells; *ll*, lateral lip; *lm*, longitudinal muscle; *s*, free secretion.

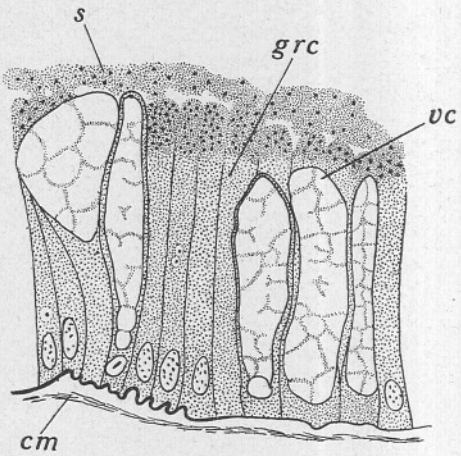

Fig. 5. *Spadella cephaloptera*, transverse section through epithelium of bulb. × 1320. *cm*, circular muscle; *vc*, vacuolated cells. Other lettering as before.

Farther back along the oesophagus the cells have a medium height but become taller again at the bulb. This region is, however, especially characterized by the presence of the vacuolated cells (Fig. 5, *vc*). The basal cytoplasm of these cells possesses similar staining reactions to that of the granular

cells, but distally each contains a large vacuole sometimes faintly subdivided by thin spherical partitions. They vary in their degree of development, sometimes occupying almost the entire wall of the bulb, the granular cells forming thin streaks among them. They are clearly secretory, but it has not been possible to obtain preparations of them during, or immediately after, secretion. Behind the bulb the granular cells alone compose the epithelium: there they are low and indistinct.

The above account of the oesophageal epithelium differs from that of John (1933). He does not describe the vacuolated cells of the bulb, and considers the granular cells to consist of two types: tall and secretory in the dorsal half, short and probably not secretory in the ventral half of the oesophagus. He figures these two types as being very sharply segregated in the lateral region. The present investigation has failed to confirm this. Although the granular cells vary in height all produced a secretion with the same staining reactions.

The oesophagus is surrounded by circular muscle, the relation of which to the cephalic muscles is described by John (1933). His account of the presence of several small bundles of longitudinal muscle occurring laterally between the circular muscle and the thick basement membrane of the epithelium has been verified. Occasionally a fine strand of connective tissue may be distinguished outside the circular muscle.

The intestinal epithelium is composed of gland cells and absorptive cells. These are not sharply segregated, but, whereas one type is distributed throughout the length of the intestine, the other is largely restricted to that region anterior to the ventral ganglion.

The gland cells may be recognized at all stages of activity by their affinity for nuclear stains. In animals which have not fed for some hours or days the cells are tall and columnar, expanded distally by large, clear vacuoles (Fig. 6, *gc*). Ten minutes after food has been taken the vacuoles present every appearance of disruption (Fig. 7 A, *gc*). Three-quarters of an hour after feeding, the cells, identified by their affinity for nuclear stains, are small and inconspicuous. Three hours after feeding they are larger (Fig. 7 B, *gc*), but possess only small vacuoles embedded in the distal parts of the cell. Proximally can be seen clear eosinophilous inclusions (*ei*) which are probably the precursors of the vacuoles. At this stage of development the gland cells appear to be ciliated, though cilia could not be found at the end of restitution.

The description just given of these vacuolated cells leaves little doubt that they secrete digestive enzymes. When actively secreting, with the vacuolar wall ruptured (Fig. 7 A), there is no evidence that the basal cytoplasm and the nuclei pass into the gut. Further, throughout this investigation no mitotic figures have been found among the cells. They therefore appear to be polyphasic according to the definition of Hirsch (1931). They are most abundant in the anterior region of the intestine and in the diverticula; at the level of the ventral ganglion and posteriorly they are rare.

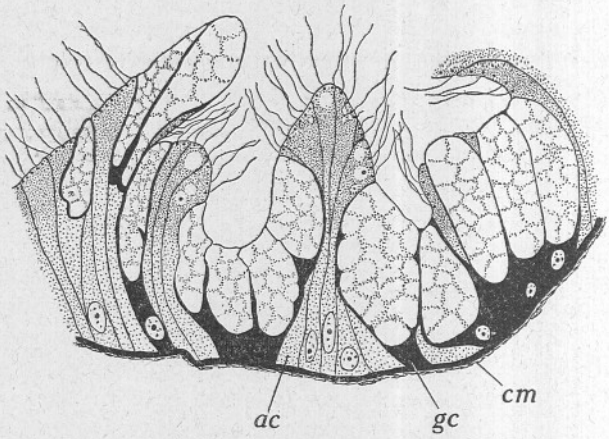

Fig. 6. *Spadella cephaloptera*, transverse section of intestine, anterior region. × 1000. *ac*, absorptive cell; *gc*, gland cell. Other lettering as before.

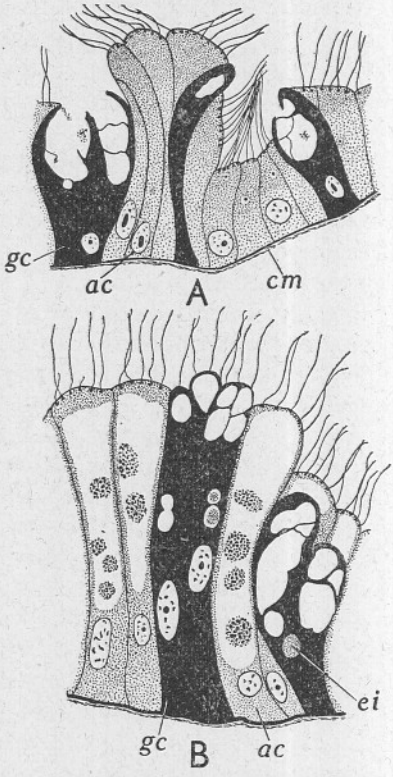

Fig. 7. *Spadella cephaloptera*, transverse sections of intestine, anterior region: A, 10 min. after feeding; B, 3 hr. after feeding. × 1000. *ei*, eosinophilous inclusion. Other lettering as before.

The absorptive cells may first be described as they appear after the animal has fed (Fig. 7 B, *ac*). The greater part of each columnar cell is occupied by a vesicle containing one or more large concretions of material which stain black with Heidenhain's haematoxylin and yellow or reddish with Mallory. The cytoplasm is largely restricted to the basal part of the cell where the nucleus is embedded; distally it merely forms a narrow wall enclosing the vesicle. This cytoplasm stains lightly with the ordinary cytoplasmic stains. In the extreme distal wall of the vesicle are the basal granules of long flagella-like cilia. These cells are invariably in the condition just described between $\frac{3}{4}$ and 5 hr. after feeding. Later, 8 and 10 hr. after feeding, the vesicle becomes subdivided into smaller, spherical vesicles each containing an inclusion. The cytoplasm round these smaller vesicles has a characteristic, finely granular, appearance and stains a bluish grey with Mallory. In animals fixed at later stages after feeding every gradation was found from the condition described above to cells containing few, small vesicles with indefinite inclusions, and finally cells the distal parts of which consist entirely of finely granular cytoplasm staining bluish grey with Mallory (Fig. 6, *ac*). Examination of material fixed with Flemming-without-acetic, up to 8 hr. after feeding, shows that the cell vesicles also contain masses of fat.

In the living animal, observed by reflected light just after feeding, large numbers of globular bodies can be seen within the intestinal epithelium.

It will be noted that these ciliated cells acquire a maximum development of vesicles with included concretions a short time after the gland cells have secreted, and that the vesicles become progressively reduced later. Of two animals sectioned a few minutes after feeding one had these cells in a non-vesicular condition while in the other the vesicles were small. It is concluded that this type of cell is absorptive in function, and the concretions described within them constitute some sort of digestive product. They gave negative tests with Best's carmine and Lugol's solution, and therefore are not glycogen. Fat has been found to occur independently of them in the vesicles. It is therefore suggested that they consist of nitrogenous material, possibly amino-acids.

The only other possible interpretation of these cells is that they are excretory. However, it is *a priori* very unlikely that this small marine animal excretes nitrogenous material in solid form, and it is almost inconceivable that such a large amount would be produced so rapidly after feeding. Further, the concretions were found to be insoluble in K_2CO_3 solution and they gave a negative Murex test (using the method of Howland, 1924).

These absorptive cells occur throughout the intestine, being least numerous in the anterior region where the epithelium is largely composed of gland cells. The possession of cilia by these cells will be discussed later.

In dividing the intestinal cells into glandular and absorptive cells, the above account agrees with that of John (1933). In that paper, however, the glandular cells are described as 'granular' and the absorptive cells as 'non-granular', the two types of cell varying in size to form longitudinal ridges throughout

the gut. In the absence of detailed figures it is not possible to correlate John's two types of cell with those described here. Further, both from observation of the living animal and from longitudinal sections, it appears that the taller epithelial cells form irregular papillae and not continuous ridges.

The ciliation of the gut is described here for the first time. Surrounding the intestine and closely applied to the basement membrane is a membrane which is continuous with the dorsal and ventral mesenteries. External to this is a very thin layer of tissue running round the intestine, presumably circular muscle. Longitudinal muscle has not been found. In the posterior region the mesenteries are absent and the intestine is supported dorsally by the transverse septum, a sheet of tissue inserted into the ventral body wall just posterior to the anus and running obliquely forwards and upwards to the dorsal body wall.

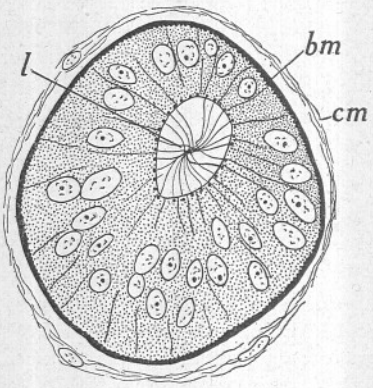

Fig. 8. *Spadella cephaloptera*, transverse section through rectum. × 1000. *bm*, basement membrane; *l*, lumen with cilia. Other lettering as before.

The epithelium of the rectum is composed of very regular columnar cells devoid of vacuoles or inclusions of any sort. They bear short cilia (Fig. 8). They are bounded by a very thick basement membrane (*bm*) which is thrown into folds and capable of considerable expansion. John (1933) mentions that the rectal epithelium appears to be ciliated. Like the intestine, the rectum is surrounded by circular muscle fibres. It is supported dorsally by the transverse septum.

Physiology of the Alimentary Canal

Feeding. As already mentioned, *S. cephaloptera* is usually found adhering to the substratum by its adhesive ventral papillae. These papillae are situated on the more posterior region of the body, to which the head and anterior region are inclined at an angle (Fig. 1). It is in this position that the animal awaits the approach of its food. When a copepod swims past, there occurs a very rapid upward and backward jerk, and at the same time the hood is thrown back and the prehensile spines extended. During this movement the animal maintains a firm grip of the substratum: it has never been seen to chase its food.

If the copepod is secured, the head of the *Spadella* remains directed almost vertically upwards during swallowing (Fig. 9 A). The prehensile spines play an important part in manipulation, turning the copepod until either head or tail is worked into the mouth opening, and then clawing it down the oesophagus. Usually the struggle is short, but may be prolonged for 10 min. or more, during which time a particularly large copepod will be turned round repeatedly, now the head and now the tail being worked into the mouth. Usually such prolonged struggles end in the prey being relinquished.

As pointed out by John (1933) the mouth becomes terminal during feeding; immediately after the prey has passed into the oesophagus it is possible to observe this (Fig. 9 B). A considerable lip, supported by the lateral plates, then extends above and beyond the mouth. This lip is presumably formed of the extended walls of the vestibule of the resting animal. The prey is apparently clasped by the prehensile spines (*ps*) against this lip, and the movements of the latter, due to the supporting lateral plates (*lp*), help to work the copepod down into the mouth. The ends of the lateral plates move repeatedly towards the mouth, gripping the prey with the teeth (*te*) which they support at their extremities.

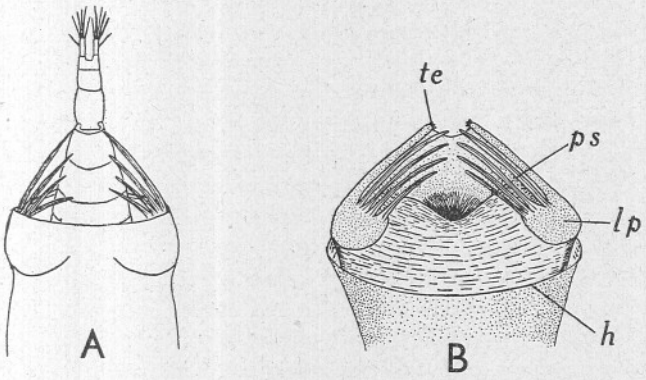

Fig. 9. *Spadella cephaloptera*, ventral view of head showing: A, prey being swallowed; B, position of mouth after swallowing. *te*, teeth. Other lettering as before.

The above account is in general agreement with that given by John (1933). The consideration given in that paper to the head muscles and their probable functions is beyond the scope of the present investigation.

Sections have shown that copepods swallowed by a *Spadella* are coated with the secretion produced by the granular cells. Application of carmine powder and manipulation with needles leaves no doubt that a sticky secretion is present in the mouth region. As the prey is clasped against the mouth region it is probably coated with secretion produced by the granular cells. By this means the appendages would be entangled and the copepod prevented from escaping. That the prey is not killed is shown by its circulating blood and gut peristalsis, which can be observed for some time after swallowing. On the other hand, a copepod which has been relinquished is unable to move away.

During this work small copepods (especially *Acartia clausi*) were used as food. No selective feeding was observed; the animal reacted in the usual way to any copepod moving past its head but failed to catch those above a certain size. As it is generally considered (cf. John, 1933) that the corona ciliata on the dorsal region of the head (Fig. 1, *cc*) is a sensory organ, it may be significant

that it appears to be copepods just above or behind the head which elicit the feeding response.

Spadella readily catches two or even three copepods in quick succession; on the other hand individuals could be starved for three or four days without apparent ill-effect. It is probable that under natural conditions the animal eats as opportunity arises, and is capable of subsisting on stored material for a long time when food is not available. The above account shows that *Spadella* possesses the characteristics of an animal adapted for seizing and swallowing active prey (Yonge, 1928).

Digestion. Yonge (1937) has put forward strong evidence in favour of the view that, primitively, digestion is an intracellular process, and that specialized animals have either retained this method in correlation with a particular type of food, or have evolved a process of extracellular digestion. Extracellular digestion usually involves the distinct processes of: (1) food conduction, usually accompanied by lubrication; (2) enzyme secretion; (3) absorption of digested material; (4) formation and conduction of faeces. Frequently, specialized regions of the gut are associated with each of these processes.

Spadella is an animal of considerable morphological specialization and digestion is extracellular. However, there has been very little specialization of the gut in relation to the constituent processes of digestion mentioned above.

Food, once inside the oesophagus, passes down to the posterior region of the intestine (Fig. 10). This movement is clearly brought about by peristalsis and may take from 2 to 8 min. The secretion of the oesophageal granular cells, the function of which during feeding has already been mentioned, may also serve for lubrication.

The intestinal gland cells are chiefly situated in the anterior region of the intestine through which the food quickly passes. Their secretion must, therefore, be passed backwards, and this is borne out by observation of peristaltic movements and of fluid globules in the gut lumen.

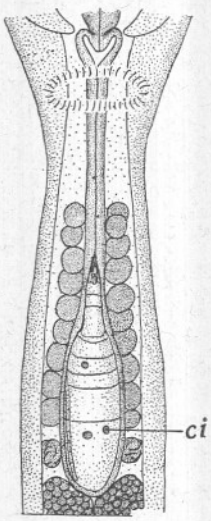

Fig. 10. *Spadella cephaloptera*, dorsal view showing copepod in the intestine. ×25. *ci*, ciliates within copepod.

Little evidence has been obtained as to the function of the vacuolated cells in the oesophageal bulb, which closely resemble the intestinal gland cells in appearance. However it was noticed that after a copepod had been swallowed, the *Spadella* almost invariably took gulps of sea water. This water passed into, and distended, the bulb and was then forcibly expelled from there into the intestine. Should the vacuolated cells be liberating a digestive secretion, this water would effectively carry it down into the intestine.

An attempt was made to estimate the *p*H of the lumen of the gut during

digestion. A copepod, to which granules of neutral red were adhering, was swallowed by a *Spadella*, and the colour of the dye, seen through the gut wall, was compared with that of standard solutions. The estimated value was approximately *p*H 6·4.

Absorptive cells occur throughout the intestine, and probably also act as storage cells. It is not uncommon for digestive and absorptive cells to occur together in the intestine (Yonge, 1937).

The rectum is concerned with defaecation, consisting of a small tube in the resting condition, and probably little more than a large pore when the faecal pellet passes out. This latter consists of the empty exoskeleton of the copepod.

The whole process of digestion, from feeding to defaecation, occupies about three or four hours.

Function of the Cilia. The presence of long flagella-like cilia, borne by the absorptive cells, and possibly by the gland cells at one phase of restitution, is somewhat surprising in an active carnivorous animal, the gut of which is capable of peristaltic movements. Nevertheless, the cilia are clearly seen in preparations and have been detected in the living animal in the following manner. An animal was decapitated and a suspension of carmine applied to the cut surface. A large piece of carmine, followed by several small particles, entered the gut and moved slowly down to the anus. This movement was unaccompanied by peristalsis.

Thus it appears that the cilia maintain a current in the gut lumen. This may be concerned with respiration or with the removal of dissolved excretory matter liberated by the intestinal cells. Neither circulation of body fluids nor excretory organs have been described in *Spadella* so it may be concluded that the intake of oxygen and excretion of katabolites takes place at the surfaces of the body. If these processes occur at the surface of the gut, then some means would be necessary to renew the water in the lumen. The cilia would provide this means.

There exists a third possible function of the cilia. Recent work has emphasized the importance of excretory organs in osmoregulation. John (1933) draws attention to the littoral habitat of *Spadella* and demonstrates that the animal can survive immersion in hypotonic sea water. In the absence of excretory organs the possibility arises that in *Spadella* the gut may be concerned in osmoregulation, acting like a large flame cell. In this connexion, animals were placed in 80 and 75 % sea water and observed carefully. The body became visibly turgid and difficulty seemed to be experienced in adhering to the glass dish. Water was repeatedly swallowed and the intestine became greatly distended. Carmine suspension applied to the anus and vaginal openings failed to reveal any currents. When these animals were examined in section the distension of the intestine and oesophagus was still seen, but the epithelial cells showed no unusual features.

It thus appears that the gut cilia are not concerned in osmoregulation. Although further investigation would be required finally to establish this

point, the above observations suggest that in *Spadella* a decrease in external osmotic pressure leads to a passage of water into the coelom until a new equilibrium is established owing to the increased turgor of the body wall.[1]

Sagitta setosa

The genus *Sagitta* has received considerably more attention than has *Spadella*. Burfield's monograph (1927) contains detailed anatomical and histological descriptions of '*S. bipunctata*'; Kuhl (1928) gives an account of the North Sea species; John (1931) has studied the anatomy of the head of '*S. bipunctata*'; and Kuhl (1932) has investigated in great detail the various movements concerned in feeding.

There has been considerable confusion in the past concerning the different species found off the British coasts. At one time they were all referred to as the species '*S. bipunctata*' but now it is established that *S. bipunctata* itself is a warm-water form not found off Britain, and that the British forms are *S. setosa*, *S. elegans*, together with the oceanic form, *S. serratodentata*, which is only occasionally driven inshore (see Russell, 1935, for the distribution of these three species). The present work concerns *S. setosa* only.

One difficulty has confronted several workers: that of keeping *Sagitta* alive and healthy in the laboratory for any length of time. During the present work it was found that only a few individuals out of any catch would survive for as long as 24 hr. Further, it was only very occasionally that *Sagitta* would feed under these conditions.

These represent very real obstacles to the interpretation of the histology of the gut, where it is so important to be able to examine material at all stages after feeding. There exists, however, another line of approach. In the first part of this paper a description has been given of the gut of *Spadella*, based on material at many stages of feeding and digestion. An attempt will now be made to interpret the gut of *Sagitta*, as examined in freshly caught animals, by a comparison with that of the closely allied *Spadella*.

Advantage was taken of the fact that *Sagitta* can be obtained in large numbers to make extracts and test for the presence of enzymes.

Morphology of the Alimentary Canal

The animals used were taken by tow-net off Plymouth and brought into the laboratory in the late afternoon. Many were already in a flaccid condition, but healthy ones were actively swimming near the surface. These were most successfully kept in shallow dishes standing in circulating water. Only active animals were fixed. These were caught by pipette, straightened out on a glass

[1] *Note on the female reproductive system.* This has been described by several workers for *Sagitta* (see Burfield, 1927). In *Spadella*, according to Vasiljev (1925), conditions are similar, but John (1933) states that the ovary opens direct into the seminal receptacle. Examination of sections has confirmed the findings of Vasiljev, the chief difference between conditions in *Spadella* and *Sagitta* being the presence in the former of a dorsal pouch in the seminal receptacle. Possibly this contains the sperm when eggs are passing down the oviduct and so occluding the main lumen of the 'samentasche'.

slide, and rapidly flooded with fixative. If they curled up during this they could readily be straightened again before fixation was complete. They were allowed to remain in a minimum amount of fixative on the slide until no tendency to curl remained, and then were removed to a larger volume of fluid if necessary. This is essentially the method of Burfield (1927). Bouin's fluid, Carnoy's fluid and Flemming-without-acetic all gave satisfactory results.

Material was embedded in paraffin wax and sectioned transversely and longitudinally at 4 μ. Satisfactory sections of the head were obtained by this method, using a very sharp knife and moving it after every few cuts. Two stain combinations were used: Mallory, preceded by corrosive sublimate, Lugol's solution and 'hypo'; and Heidenhain's haematoxylin and erythrosin. For whole mounts, borax carmine was used.

Anatomy. The account given by Burfield (1927) of the alimentary canal of '*S. bipunctata*' applies to *S. setosa* with the exception of one or two particulars. The oesophagus of *S. setosa*, after expanding to form a slight bulb behind the complex lateralis muscle, becomes laterally compressed, and passes directly into the intestine; there are no lateral diverticula. Like the most posterior portion of the oesophagus, the intestine also is laterally flattened so that the lumen is almost or entirely obliterated (Fig. 13). Especially in the anterior region the intestinal epithelium is very low, the gut appearing as little more than a thickening of the median mesentery.

Histology. Histologically, the oesophagus is divided into four regions: from the mouth to the level of the dorsal pit; from the pit to the bulb; the bulb itself; and from the bulb to the commencement of the intestine. Three types of epithelial cell can be recognized: granular cells, vacuolated cells, and compound granular cells.

Immediately within the mouth the epithelium consists of granular cells, columnar in form and packed distally with a granular secretion (Fig. 11, *grc*). This secretion also occurs free within the lumen of the gut. Stained with Heidenhain's haematoxylin and erythrosin it consists of black granules embedded in a reddish matrix. With Mallory it appears either blue or purple. The cells lining the roof and sides of the oesophagus are very tall and produce large granules, while those occurring in the ventral region are shorter and the secretion finer. Intermediate conditions occur. The dorsal wall of the oesophagus is raised as a small projection corresponding to the dorsal pit in the epidermis, and the granular cells cease abruptly at this projection.

The second region of the oesophagus is composed of the vacuolated cells (Fig. 12 A, *vc*). Apart from the nucleus within the basal cytoplasm, the entire cell is occupied by a large vacuole, sometimes subdivided by spherical partitions. Occasionally small hyaline globules staining bright red with Mallory occur within the vacuoles and possibly represent the precursors of these. In transverse section the oesophagus in this region is in the shape of an inverted pear, and the narrow ventral region consists of a low epithelium of granular cells similar to those occurring farther forward.

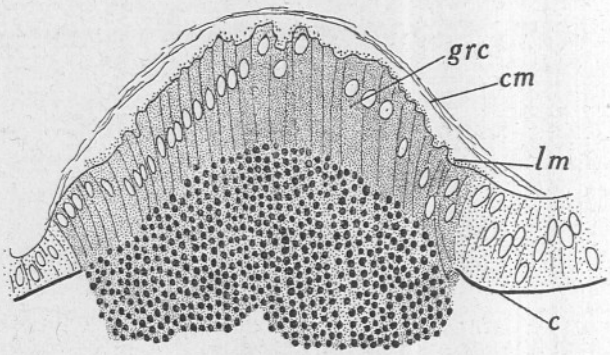

Fig. 11. *Sagitta setosa*, vertical section cutting mouth region obliquely. × 500. Lettering as before.

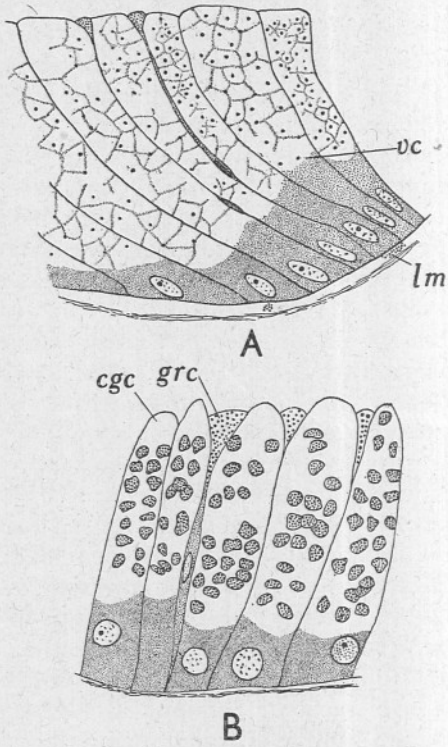

Fig. 12. *Sagitta setosa*, transverse section of oesophagus: A, in region of vacuolated cells; B, through bulb with compound granular cells. × 1000. *cgc*, compound granular cells. Other lettering as before.

The epithelium of the bulb is chiefly composed of the compound granular cells, tall columnar cells closely packed with large inclusions which themselves contain small granules (Fig. 12 B, *cgc*). These inclusions stain reddish with Mallory and take up erythrosin slightly. It should be made clear that these cells are quite distinct from the vacuolated and the granular cells already described. They take the place of the former abruptly on a level with the anterior limit of the transversus dorsalis muscle.

Among the compound granular cells occur cells similar to those described round the mouth. Here they are very narrow, occurring as thin streaks among the others (Fig. 12 B, *grc*). Distally they contain the usual granular secretion, staining blue with Mallory's triple stain and black with Heidenhain's haematoxylin. They are chiefly found in the extreme dorsal and ventral regions of the bulb. Beyond the bulb granular cells entirely replace the compound granular cells and form a rather low epithelium. They end abruptly with the beginning of the intestine.

The description given above differs from that of Burfield (1927) for '*S. bipunctata*'. He states that the epithelium consists of 'one type of cell of a narrow and high cylindrical form'. These cells, according to him, contain closely packed granules staining with eosin and being either very small, or large and containing smaller granules within them. This description would apply exactly to the epithelium of the bulb as described above. The small granules would be those in the granular cells, while the large granules clearly correspond to the 'compound granules' described above. The oesophagus of *S. setosa* thus appears to include the types of cell referred to by Burfield but to be of a more complex nature than that described by him for '*S. bipunctata*' in that it contains at least one other type of cell (the vacuolated cells) and is divided into four histologically distinct regions.

The intestine may be roughly divided histologically into anterior and posterior regions. The anterior region occupies about three-quarters of the entire intestine. The epithelium is very low, being composed of large, flattened cells (Fig. 13 A) which give to the intestine of the living animal a curious scaly appearance. It is characterized by cells containing a large vacuole with 'compound granules' (*cgc*) indistinguishable from those contained within the cells of the oesophageal bulb.

The posterior region of the intestine is composed of a very regular columnar epithelium with basal nuclei and bearing short cilia (Fig. 13 B). These may be seen when the walls of the intestine have been drawn slightly apart; otherwise their presence is indicated by a row of basal granules (Fig. 13 B, *bg*). The division between the two types of cell is not abrupt, and granular cells occur among the columnar epithelium in the posterior region (Fig. 13 B, *cgc*).

Burfield (1927) described the intestine of '*S. bipunctata*' as oval or rectangular in cross-section and figures it as consisting of a tall epithelium, while the most striking characteristic of the intestine of *S. setosa* is its lateral compression and low epithelium. On the other hand, Burfield's recognition of

two types of cell, glandular cells with granules of secretion and non-granular, occasionally ciliated, cells, would agree with the above account.

Meek (1928) describes the epithelium as forming a thin layer anteriorly where the lumen is large, and becoming vacuolated posteriorly and thus reducing the lumen. During the present investigation many healthy living *Sagitta* were examined and only when the gut contained food were the walls ever found not applied together and obliterating the lumen.

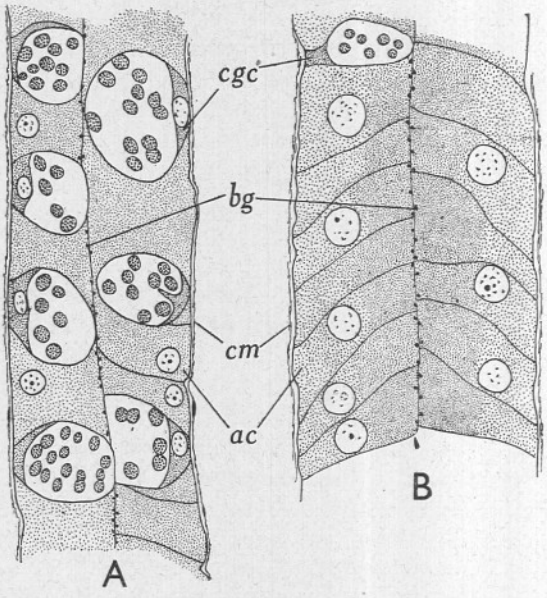

Fig. 13. *Sagitta setosa*, transverse section of intestine showing close application of lateral walls: A, in anterior; B, in posterior region. × 1000. *bg*, basal granules. Other lettering as before.

Comparison with Spadella. The resemblance between the granular cells occurring round the mouth in the two animals is very exact. It is therefore concluded that in *Sagitta* these granular cells produce a glutinous secretion which entangles and lubricates the prey. As in *Spadella* these granular cells are also scattered throughout the oesophagus.

Beyond the granular cells there occur in *Sagitta* the vacuolated cells, followed by the compound granular cells of the bulb. In *Spadella* the only other type of cell is the vacuolated cell characteristic of the bulb. The two types of cell in *Sagitta* are presumably both secretory, but no purpose would be served in speculating whether either or both correspond functionally to the vacuolated cells of *Spadella*.

In *Spadella* there occur glandular secretory cells in the anterior region of the intestine and ciliated absorptive cells throughout. It seems probable that

the flat granular cells of the anterior region of the intestine in *Sagitta* correspond to the glandular cells of *Spadella*, and the columnar ciliated cells in *Sagitta* correspond to the absorptive cells of *Spadella*.

Physiology of the Alimentary Canal

Feeding. *Sagitta* is carnivorous, feeding upon copepods, herring larvae, other *Sagitta*, etc. (Lebour, 1922, 1923). It rarely feeds in captivity. Experiments were conducted to estimate the effect of light on feeding. Of forty-seven animals kept in the dark, six fed; of twenty-seven kept in light, none fed. In so far as these data are significant, it appears that *Sagitta* feeds only under certain conditions, one of which is a low light intensity. This agrees well with the diurnal migration normally undergone (Russell, 1927). Animals were kept in a cool place under natural conditions of illumination and fixed at 3-hourly intervals throughout day and night. No periodic secretion in the gut was noted in the sections. This would imply secretion on the stimulus of food as might be expected with a predacious carnivore. After being seized, food passes steadily down to the posterior region of the intestine where digestion occurs. As shown in Fig. 14, the intestinal walls remain opposed except in the region occupied by the prey. Digestion probably takes about 5 hr. Immediately after defaecation the animal swallows water thereby distending the gut anterior to the prey. The actual passage of the faeces is not accompanied by any obvious peristalsis, but 'flickering' of cilia was detected.

Fig. 14. *Sagitta setosa*, complete animal with three copepods in posterior region of intestine, lumen of anterior region (*i*) occluded. ×7.

Digestive Enzymes. Some 1000 specimens of *S. setosa* were ground up with cleansed silver sand moistened with glycerine. The whole was diluted with 10 c.c. of 50 % glycerine, a few drops of 5 % thymol added and kept at a temperature below 4° C. until required.

Digests were carried out with a variety of carbohydrates, the glucose produced being estimated by the method of Hagedorn & Jensen as modified by Boyland (1928). With soluble starch and glycogen appreciable quantities of glucose were produced the *p*H optimum being in both cases about 6·4. No appreciable digestion of sucrose, maltose or lactose was obtained. Attempts to detect the presence of proteoclastic enzymes also gave negative results.

The very small amounts of extract obtainable with even large numbers of animals probably explain the failure of the bulk of the experiments but in the case of proteoclastic enzymes it is possible that the enzymes are not liberated in the active form until food enters the gut and so would not be

extracted. It is a fact that most of the secretory cells in the gut of *Sagitta* contain granules which are usually regarded as pre-secretion. The *p*H optimum of the sucroclastic enzyme agrees closely with the *p*H of the gut of *Spadella* as estimated colorimetrically by feeding with food coloured with neutral red. It has been shown by Yonge (1937) that the optimal *p*H of the enzymes usually corresponds closely with the *p*H of the gut.

Discussion

In respect of food, structure of the gut and physiology of digestion, *Sagitta* and *Spadella* closely resemble one another. On the other hand, they differ widely in their habits and habitat and these differences seem to be reflected in their behaviour in the laboratory. *Spadella* is a shallow-water animal found in shore pools where it will be exposed to a wide range of light intensity, salinity and temperature. It is sedentary in habit, waiting for its prey to approach within catching distance. It is, therefore, not surprising that it lives well under laboratory conditions, feeding under bright illumination and in various suspensions, e.g. iron saccharate and neutral red. *Sagitta setosa*, on the other hand, is an active member of the plankton of open waters living in a much more uniform environment. Further, in common with other members of the plankton, it is probably adapted for life at a particular light intensity maintaining this by diurnal vertical migrations (Russell, 1927). It is clearly unable to live for long or behave normally under laboratory conditions.

Note on an Apostomous Ciliate

Small ciliates were frequently observed moving actively about within copepods (*Acartia clausi*) which were being digested in the gut of *Spadella* (Fig. 10, *ci*). These were the trophont stage of an Apostomous Ciliate (probably *Vampyrophrya pelagica*). The group has been investigated in detail by Chatton & Lwoff (1935), but as *Spadella*, owing to its transparency, provides a particularly good opportunity of observing the trophont stage while within a predator, the following details are recorded.

The copepod, with encysted ciliates on its terga or pleopods, is swallowed by *Spadella* and usually reaches the posterior region of the gut in 5–7 min. By this time the ciliates have decysted and may be already inside the copepod or can be seen actively swimming among its appendages. Entrance seems to be made from the ventral, anterior, region, possibly by way of the maxillary gland. Once inside, the ciliates at first move slowly among the tissues, but, as these are gradually digested, movement becomes more rapid. Ten minutes after entering they are already appreciably larger and when the copepod 'shell' is defaecated they are greatly distended and move slowly. This movement persists for a few hours, but no attempt is made to leave the copepod.

The ciliates may also be seen in copepods eaten by *Sagitta setosa*. Considering the abundance of this species and the numbers of copepods they must eat, it will be realized that it must play a very large part in the life of

the protozoan. Chatton and Lwoff's method of pricking infested copepods so as to activate the ciliates was successfully repeated and the tomites obtained. In one experiment a copepod was only slightly damaged and lived for over an hour after the ciliate had entered its body.

Summary

Spadella cephaloptera

1. The oesophageal epithelium is composed of granular and vacuolated cells. The former produce a glutinous secretion which appears to immobilize and lubricate the prey. The function of the vacuolated cells remains undetermined.

2. The intestinal epithelium is composed of gland cells and absorptive cells. The gland cells contain large vacuoles which disrupt when food is taken, restitution taking several hours. The absorptive cells accumulate large concretions of fat and other material as digestion proceeds; later this gradually disappears.

3. The absorptive cells in the intestine are ciliated. The cilia may be concerned with respiration and excretion; there is no evidence that they are concerned with osmoregulation.

4. The rectum has a ciliated columnar epithelium.

5. The general course of feeding and digestion is discussed.

6. It is stated in a footnote that the reproductive system of *Spadella* is similar to that of *Sagitta*.

Sagitta setosa

7. The oesophagus is divided histologically as follows: (i) a region of granular cells round the mouth; (ii) a region of vacuolated cells; (iii) a region of compound granular cells; (iv) a second region of granular cells. The granular cells produce a profuse secretion with probably the same function as the glutinous secretion in *Spadella*.

8. The intestinal epithelium is composed of compound granular cells and simple columnar cells. By comparison with the intestine of *Spadella* the former are regarded as enzyme-secreting cells and the latter as absorptive.

9. Extracts of many whole *Sagitta* digest soluble starch and glycogen with an optimum at *p*H 6·4.

10. In captivity *Sagitta* feeds more readily in the dark than in the light.

11. The frequent occurrence of an apostomous ciliate (probably *Vampyrophrya pelagica*) in copepods eaten by Chaetognaths is noted and certain observations recorded.

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METHODS OF SURVEYING *LAMINARIA* BEDS

By V. J. Chapman

(This survey was carried out whilst the author was temporarily attached to the Marine Biological Association)

(Plates I–IV and Text-figs. 1–15)

CONTENTS

Introduction

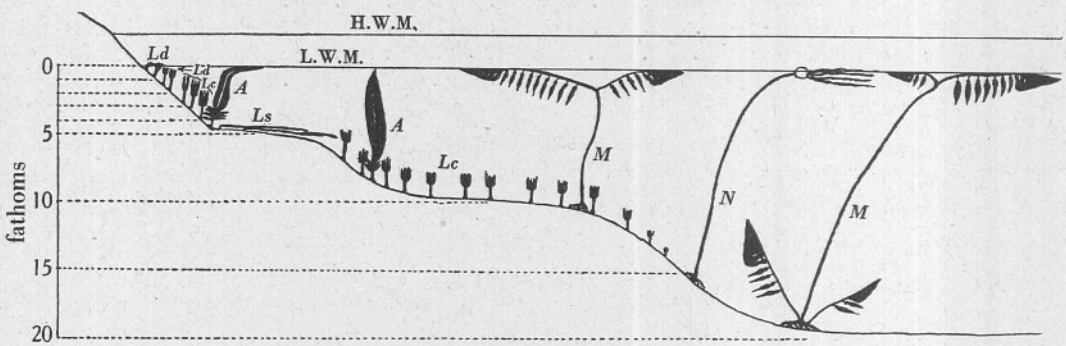
Prior to 1914 commercial interest had been aroused in America by the large beds of *Macrocystis*, *Nereocystis* and *Alaria* (collectively known as kelp)[1] which extend along the Pacific coast from Alaska to Lower California. Between 1910 and 1912 these beds were surveyed with a view to ascertaining the total area covered and the tonnage available. The survey was carried out by a number of workers and was described by Cameron (1913) and Cameron, Crandall, Rigg & Frye (1915). The methods used by these workers involved the use of a boat, a launch or steamboat, which proceeded along or around the beds, the positions being fixed at intervals. The percentage cover of any bed was usually estimated by eye. Some of these beds were cut between 1914 and 1918, but after the war the industry using this particular raw material gradually ceased to operate. I have been informed that some time after 1930 the firm which possessed the option on the majority of the beds arranged for an aerial photographic survey which was duly carried out. A description of the technique employed on this occasion, together with the results, was apparently not published as a *sequitur* to the earlier work.

The purpose of the present paper is to provide a description of the methods employed in surveying *Laminaria* beds around the coast of Great Britain. No estimate will be made in this paper of the actual tonnage available: this information, together with a discussion of other problems, has been reserved for a later date.

It must be appreciated that there is a considerable difference in habit between the weeds surveyed on the Pacific coast of America and those growing

[1] The use of this term for the living weed is not correct, as it properly refers to the burnt weed.

around Great Britain. The American *Macrocystis* and *Nereocystis* are both giant denizens of the deeper waters off-shore, often occurring down to 20 or 30 fathoms. Even when rooted at this depth the fronds may reach to the surface and thus provide an easy means of delineating the extent of the beds. The third species, *Alaria fistulosa*, is somewhat smaller and grows nearer the shore. In Great Britain only one species has its fronds commonly exposed and then only at low water of spring tides. This species is *Laminaria digitata*, which forms a belt that ranges in width depending upon the slope of the shore, just below mean low-water mark and extending out to a depth of 1 or 2 fathoms. Below that depth, if conditions are favourable, it is replaced by another species, *L. cloustoni*, which in places may extend down to depths of 13 or 14 fathoms but which generally disappears at about 10 fathoms below mean low-water mark. Neither species usually grows to much more than about 10 ft.



Text-fig. 1. The vertical distribution of the British and American brown seaweeds that form large beds and which have been surveyed. They are shown in this composite diagram in relation to each other and to high and low water. *A*, *Alaria*; *Lc*, *Laminaria cloustoni*; *Ld*, *L. digitata*; *Ls*, *L. saccharina*; *M*, *Macrocystis*; *N*, *Nereocystis*.

in length (average length about 7 ft.), and consequently while *L. digitata* may be exposed on occasion it is extremely rare for the fronds of *L. cloustoni* to be visible at the surface. The surveyor is therefore faced with the problem of surveying areas of vegetation which are not visible on the surface of the water as they are in America. He has to search for and map something which he may not even be able to see beneath the surface of the water. There is a third species around Great Britain which also has to be considered. This is the leafy *L. saccharina* which generally occupies areas where the substrate is composed of shingle or small stones because neither substrate is sufficiently stable to bear a population of the two stout erect species. It may also occur in sandy bays where the plants are probably attached to stones partially buried in the sand. The fronds of this species may extend up to about 14 ft. in length, whilst the stipe is short and relatively weak. As a result a large expanse of weakly supported frond is exposed to the subsurface currents and in such places it lies on the sea floor and never floats at or near the surface. *Macro-*

cystis and *Nereocystis* would also behave somewhat similarly were it not for the fact that both genera possess large gas-filled vesicles which aid flotation. Some of these giant Pacific seaweeds exist in other parts of the world, but so far as is known no attempt has been made to survey them accurately. Text-fig. 1 illustrates the habit of the Pacific and British species mentioned in relation to each other and to the surface of the water.

It was known from published floras and ecological papers that *Laminaria* beds existed in certain parts of Great Britain, but it was obviously desirable that this information should be checked and extended. The first operation, therefore, was to conduct a preliminary survey in order to ascertain the location of the principal beds, some of which were subsequently surveyed in more detail. The methods used in the preliminary survey differed somewhat from those utilized in the detailed survey because in the former it was only necessary to establish the existence of the beds. The present writer was assisted in both the detailed and preliminary surveys by Messrs R. H. Richens, G. E. Fogg and R. A. Lewin.

Preliminary Survey

For this survey the party was divided into two groups of two members each, one group working from a boat and the other from the shore. Localities where boats might profitably be employed were predetermined from a study of the Admiralty Charts and from a perusal of the available literature. The following methods were utilized to obtain information about the beds.

Boat and Grapnel

This is the most satisfactory method because if properly executed tangible evidence of the weed's existence is produced. In view of the great length of coastline to be covered hauls with the grapnel were usually made at intervals of 1 mile. This distance was also partly determined by the fact that both parties were scheduled to cover from 40 to 80 miles per day, and it was desirable that they should not become separated. The activities of the shore parties were limited daily more or less to 3 hr. before and after the time of low water when beds might be exposed. The best type of boat and grapnel will be discussed in detail later (p. 43), but it may be mentioned that in several places we were unable to carry out the boat programme because of unsuitable weather and sea conditions. It is impossible to use a grapnel to detect *Laminaria* in a rough sea without some risk to life and boat because so much of the work has to be carried out near the shore.

Information about Cast or Drift Weed

In many areas big casts are reported, and their regular annual occurrence can generally be regarded as indicative of the presence of beds in the immediate or near vicinity. The bed may, however, be as much as 10–15 miles away,

and local currents are responsible for depositing the weed on the distant beaches. The shore party was responsible for collecting the information about cast weed: this was obtained by actual inspection of the beaches, when the remnants of any cast could frequently be seen, or else by interrogation of the local residents. In making such inquiries it has to be remembered that *Laminaria* cast can be of two categories which occur at different times of the year. From November to March casts of old stipes with the fronds attached may be thrown up after any gale blowing in the requisite direction. The effective direction is determined by the position of the bed in relation to the run of the coast. From April to June these stem casts are replaced by casts of frond only, or 'may leaf' as it is called. Either type of cast is an indication of *Laminaria* beds.

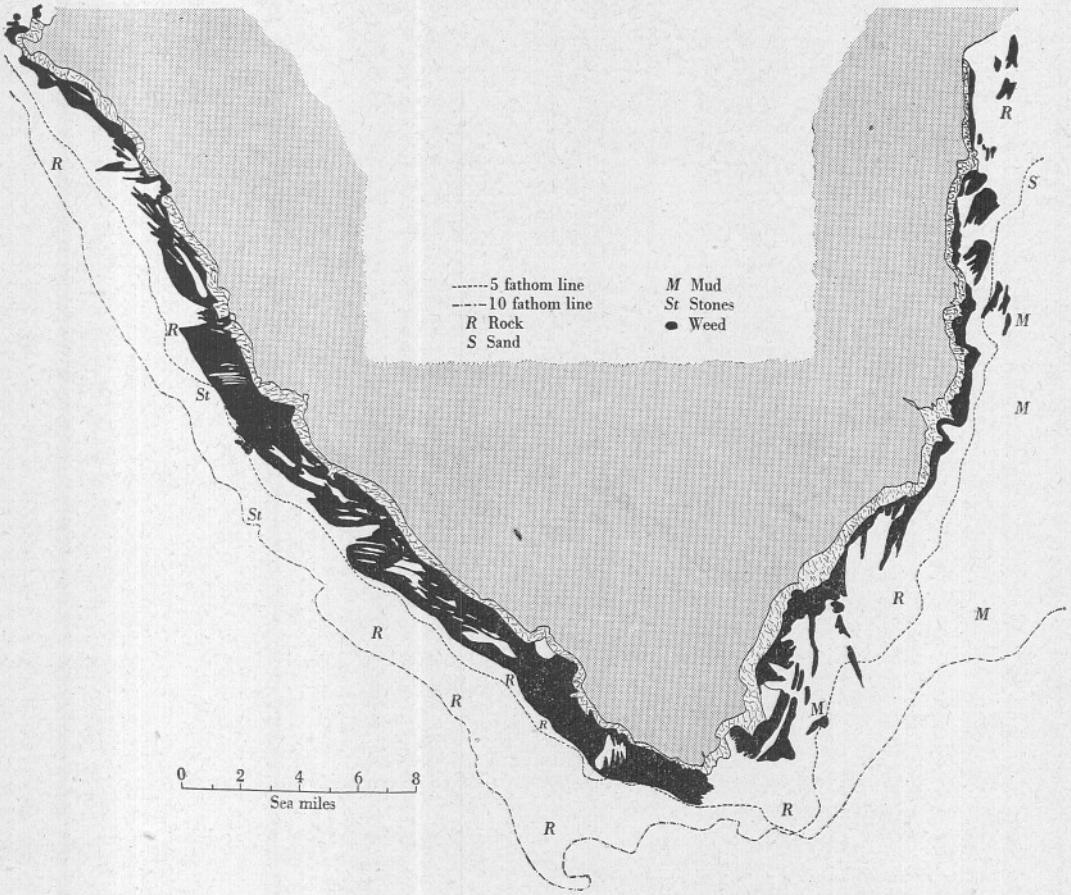
Information from Lobster Fishermen

It is a common practice for the lobster fishermen to lay their pots just along the margin of a *Laminaria* bed or in bare patches within the bed because such sites are the most profitable. It was a primary duty of the shore party to make contact with lobster fishermen in the principal towns and villages visited, and these men were usually very willing to impart their information. Indeed, it may be stated that their knowledge of the *Laminaria* beds was often extremely accurate, and they could on occasion even tell us the size of the plants in the different parts of the beds and also the location of any big bare patches. It sometimes proved difficult to translate their information on to a map because they were not familiar with maps, and they preferred to give us the information in the form of bearings on different landmarks. We had subsequently to identify the landmarks on the map or else follow their directions from a boat and then plot the positions of the beds.

Information from other Sources

Apart from the lobster fishermen there were other sources that provided fruitful information. Borough surveyors were often in a position to provide us with figures about the quantity of cast weed, especially in places where it was a nuisance and had to be removed. Farmers, if approached tactfully, could also on occasion give some data about the quantity of cast. This source could be used in those places where the cast was deposited in sufficient volume to make it worth while removing for agricultural manure. Fishermen, other than lobster fishermen, were not usually in a position to assist much, but very occasionally some useful facts could be gleaned. Fishery officers, on the other hand, proved extremely valuable, because even though they themselves could not provide any information they put us in touch with the most likely informants in their area. Other officials who could on occasion be helpful were harbour masters and coastguards. The coastguards are a fine body of men, often recruited locally, and as a consequence their knowledge was usually

reliable. Their practice of patrolling the beaches meant that they could often give us satisfactory information about the casts, whilst some members of the service were able to provide data about the location and extent of the beds.



Text-fig. 2. Map illustrating an area with an extensive rocky shelf, only a portion of which is colonized by *Laminaria*. (Reproduced by permission of the Hydrographer of the Navy.)

Visibility from Cliffs

If one stands on a cliff 100 ft. or more high with the sun behind one's back a *Laminaria* bed in the sea below shows up a deeper blue in contrast with the surrounding bare patches. It is very rarely that the seaward extent of such beds can be observed, but a good picture can be obtained of the percentage cover. This method could not be used very often because some of the coastline does not reach the required height, or the position of the sun was not favourable, or the day was, as frequently happened, completely sunless.

Admiralty Charts

These can be utilized on the justifiable assumption that *Laminaria* beds can be expected to occur in those areas where the charts indicate a rocky or stony bottom to the sea bed and where the depths are not greater than 10 fathoms. A fringe of weed will occur around most of the rocky shores of Great Britain, but there are only a few localities where the beach extends seaward as a shallow rocky shelf. These places can be detected readily on an Admiralty Chart, but it must not be regarded as a foregone conclusion that extensive weed beds will be found in such positions. In one area that we encountered, where from a study of the chart one would have expected to find an extensive bed, much of the area proved on survey to be bare (Text-fig. 2).

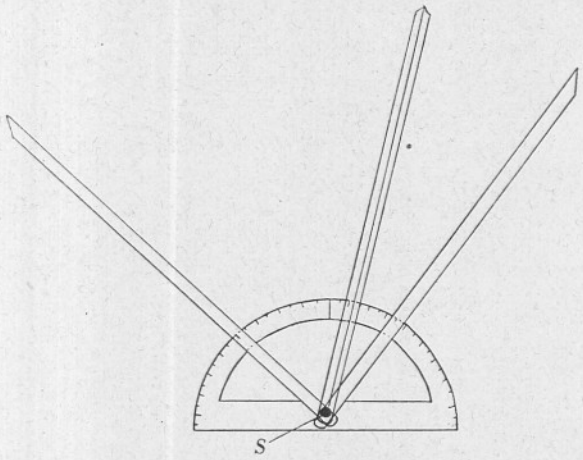
Detailed Survey

As a result of the preliminary work detailed surveys were carried out in certain places. These areas varied in size but usually they did not involve more than about 50 miles of coastline. The time taken over such a survey depended very largely upon the weather conditions and ranged from 14 to 28 days. During these detailed surveys the whole of the shore was covered on foot, and on these excursions every opportunity was taken to secure additional information by the means already outlined. Apart from these excursions, however, new methods were employed in order to render the survey as accurate as possible. At the termination of each detailed survey the outlines of the beds were plotted on 6 in. maps or on large-scale Admiralty Charts. It is not suggested that these outlines have the accuracy of a 6 in. Ordnance Survey map, but it is believed that they are as accurate as the methods employed permit. It would probably be possible to improve upon the accuracy of the mapping if the services of a deep-sea diver were available. For the immediate purpose, however, our methods proved adequate. Maps on a smaller scale are not satisfactory as they do not provide enough landmarks for plotting the readings of the box sextant.

Boat, Grapnel and Box Sextant

At selected spots the engine of the boat is put into neutral and the grapnel thrown overboard. When it reaches bottom a series of sharp tugs on the rope soon shows whether weed is present or not, although *L. saccharina* may not make itself felt immediately. Large stems of *L. cloustoni* are sometimes strong enough to anchor the boat unless it has a powerful engine. During the operations if no weed appeared to be present slow speed ahead was ordered: careful watch has to be exercised when going ahead, because should the grapnel catch on a rock it is essential to put the engine into reverse at once otherwise the rope or an arm of the grapnel may break. The bending of an arm may occur in such cases, and if this happens too frequently the arm eventually breaks, because after each mishap it requires to be hammered back into position,

if the grapnel is to remain 100% efficient. The life of the grapnel can be extended if the arms are not hammered back whilst cold, though unless spare grapnels are carried on the boat this treatment may become necessary. At the same time as the grapnel is lowered the position of the boat is established by using a box sextant to obtain the angle values between at least three points on the shore, preferably four or five. These readings have to be obtained as quickly as possible so as to discount the forward motion of the boat. It is also important that the selected points should be easily identifiable on the maps. The position of the boat is subsequently plotted on the map using the home-made station pointer[1] shown in Text-fig. 3. By means oft he screw the arms are fixed at the angles recorded for the shore points *A*, *B* and *C*; the instrument



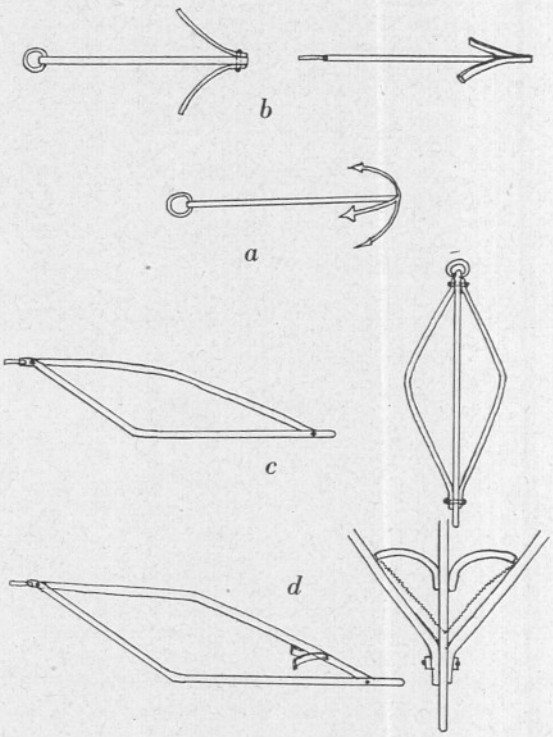
Text-fig. 3. Station-pointer used for plotting box-sextant readings. *S* is the screw retaining the three arms. The whole was made of celluloid.

is laid on the map and then gently moved about until the three arms each lie over the points to which they relate. The position of the boat is then given by the common axis of all the arms (i.e. the screw). With a little practice this method is extremely quick and accurate.

During the course of the survey we experimented with various types of grapnel which are all illustrated in Text-fig. 4. Type *a* is not satisfactory because the slippery nature of the blades and stipes of *Laminaria* makes them tend to slide over the prongs. Occasionally a small piece of frond can be brought up, but this grapnel is not sufficiently reliable for accurate surveying. Type *b* is quite good in operation so long as it is made of strong material. Most of our grapnels of this type were constructed by blacksmiths who used bars of shoeing iron, but this material is not really strong enough. The best specimen, which undoubtedly became increasingly heavy to haul in as the

[1] Professional surveyors employ more elaborate instruments.

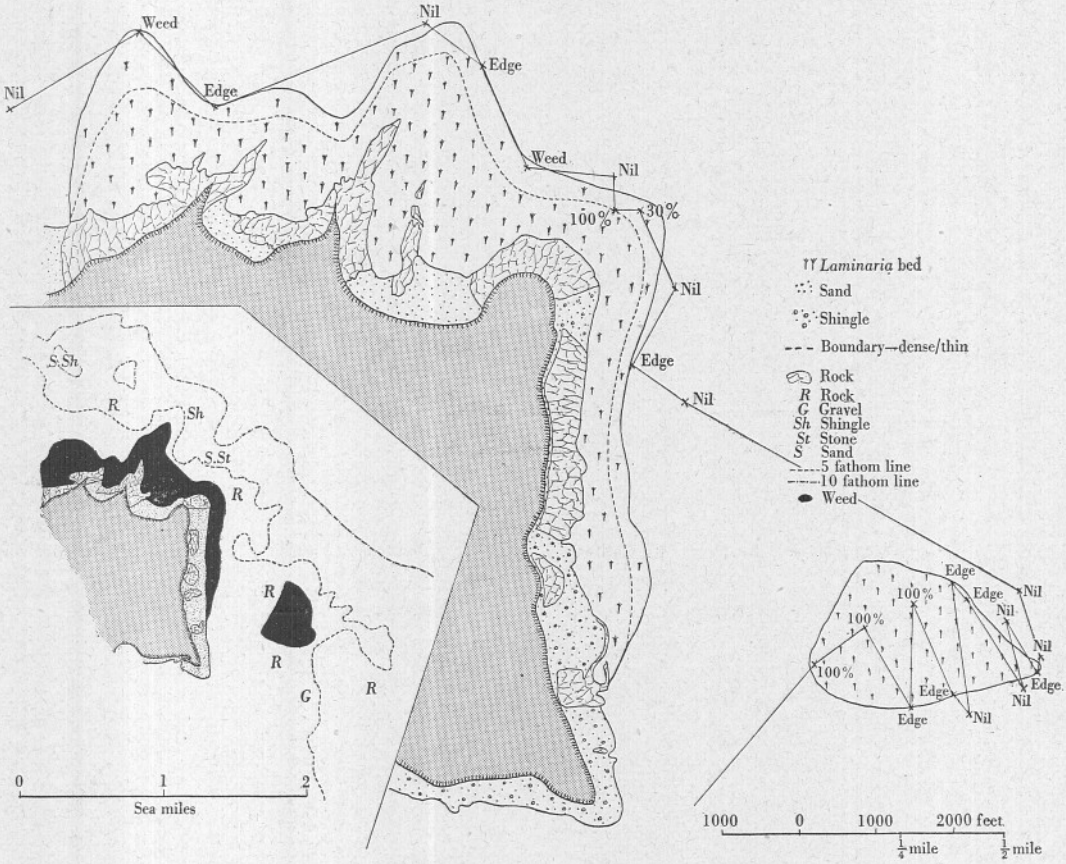
day progressed but which nevertheless possessed the longest life, had a main stem of iron $\frac{3}{4}$ in. square, whilst the two arms were of bar iron $\frac{3}{4}$ in. wide by $\frac{1}{4}$ in. thick. It is important that the arms forming the arrows should be both bolted on and welded. Bolting or welding alone did not seem to be so efficient. The two arms should be attached at an acute angle to the stem because then the stipes and fronds quickly become wedged in the crook and the grapnel need only be lowered for a short period. This type of grapnel does not always lie



Text-fig. 4. Different types of grapnel used for surveying seaweed beds.

properly on the bottom and it also tends to catch if the rock surface is irregular. Type *c* was therefore evolved in order to overcome this difficulty and it proved highly successful. Type *d* incorporated some minor modifications, and, whilst opinions were divided as to whether it was really more efficient than its predecessor, I believe that it probably represents the best solution for this type of work. The bottom side bars were made of rather heavier material than the middle upper bar in order to ensure that they reached the bottom first. The sloping portion was intended to promote the passage of the grapnel over irregularities of the sea bed. An extra notch was welded on in order to trap the *Laminaria* stipes, and two saws, which were intended to cut the stipes and

so provide almost complete plants, were fixed across the bottom. One of our aims was to secure a complete specimen at each haul so that it could be weighed and a closer approximation thus made to the total tonnage of the bed.

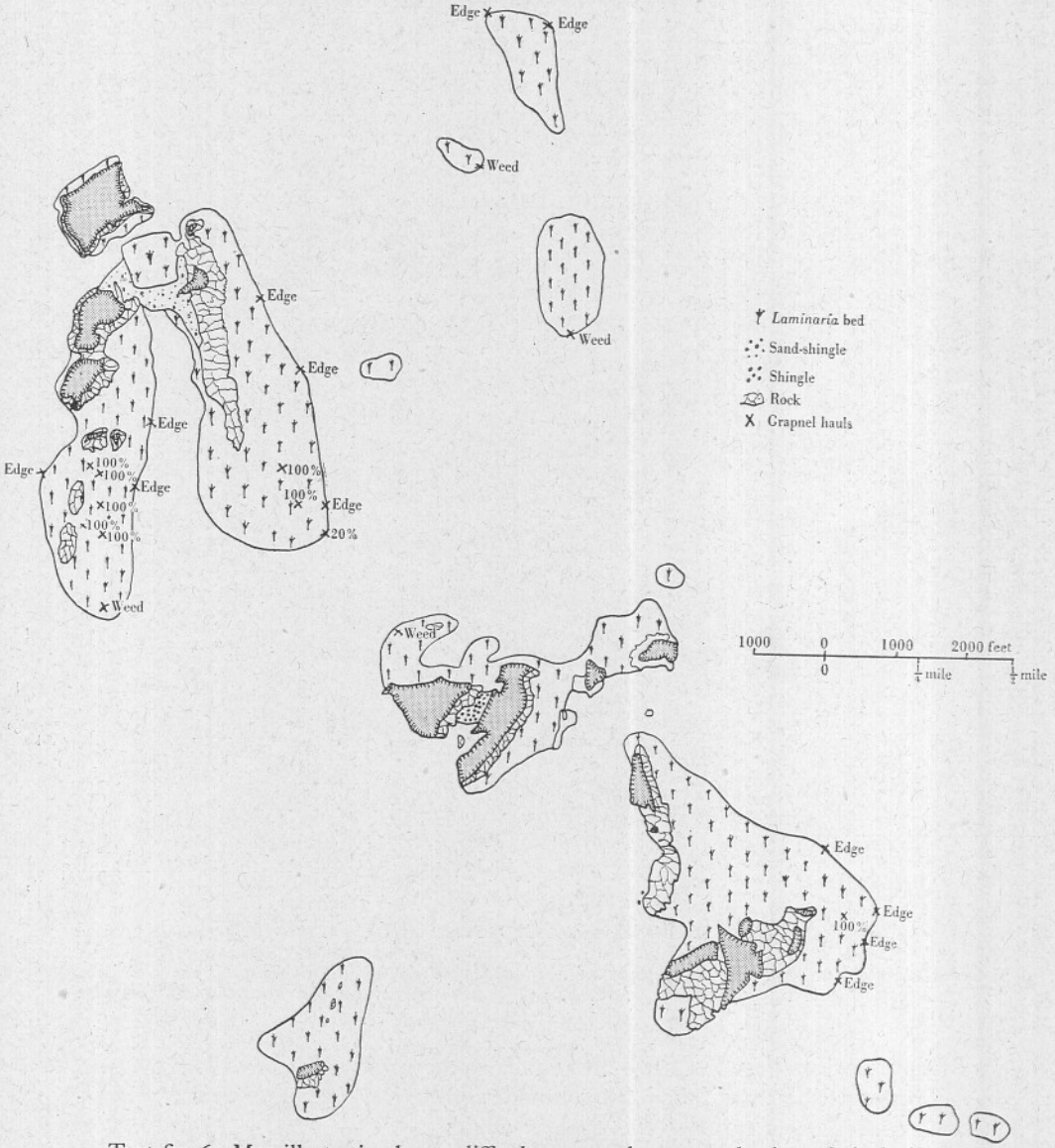


Text-fig. 5. Map illustrating how the use of a boat and grapnel can provide a plan of a weed bed. Additional assistance is also obtained from the Admiralty Chart (inset) where it was evident that the outer limit of the weed bed closely followed the 3-fathom line. (Reproduced by permission of H.M. Stationery Office and the Hydrographer of the Navy.)

Many and various were the boats that were employed on this survey, and as a result of our experience, the following points may be suggested as important in selecting a boat for this type of work:

(1) The boat must be seaworthy and of stout build. The stern is the most suitable place for conducting the grapnel operations and it should have a low free-board. A small mechanically driven winch in this part of the ship materially lightens the arduous labours of the man with the grapnel.

(2) The boat should be about 30–40 ft. long so that there is easy communication between the skipper and the man with the grapnel.



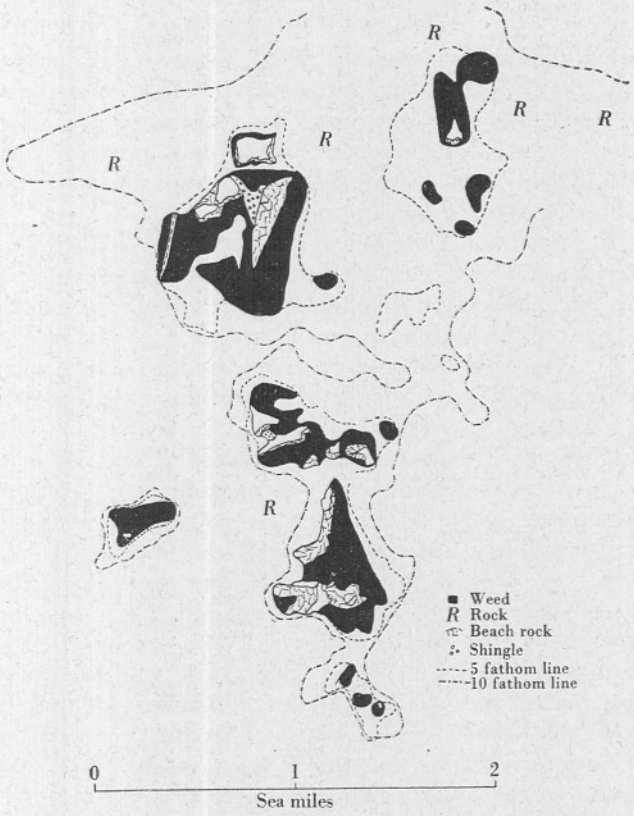
Text-fig. 6. Map illustrating how a difficult area can be surveyed using relatively few observations. (Reproduced by permission of H.M. Stationery Office.)

(3) The engine should be capable of idling for some time in neutral without stopping. It should also possess a reverse.

(4) The engine must be powerful. A 30 h.p. engine is desirable though a 20 h.p. will do in an emergency. Great speed is not an essential, but the boat should be capable of going for a long time at slow speeds.

(5) A shallow draught is an obvious requisite; it should never exceed 7 ft. and preferably should not be more than 5 ft.

(6) The boat must be very manœuvrable, as much of the work may have to be carried out close inshore.



Text-fig. 7. Admiralty Chart of the same area as Text-fig. 6 illustrating how the outer limits of the bed approximate to the 3-fathom line and hence enable the outline to be plotted. (Reproduced by permission of the Hydrographer of the Navy.)

The usual practice when surveying solely by grapnel was to traverse the area of the bed systematically unless the bed was very large; then the outer edge would be traversed systematically and additional hauls subsequently made in the centre and near the shore in order to establish percentage cover. An example of the use of this method is shown in Text-fig. 5. Text-figs. 6 and 7 illustrate the type of result that can be obtained by combining a study of an Admiralty Chart with the grapnel records. This island group was not an easy

area in which to operate, but sufficient hauls on the grapnel were obtained in order to determine the average depths to which heavy weed cover descended, and the remainder of the area was then plotted from the fathom lines on the charts. Substantial confirmation of the total result was obtained by cruising around all the islands, and as the day selected was fortunately very favourable the beds showed up to an observer on the deck of the boat and some further additional positions were fixed.

Boat and Echo-sounder

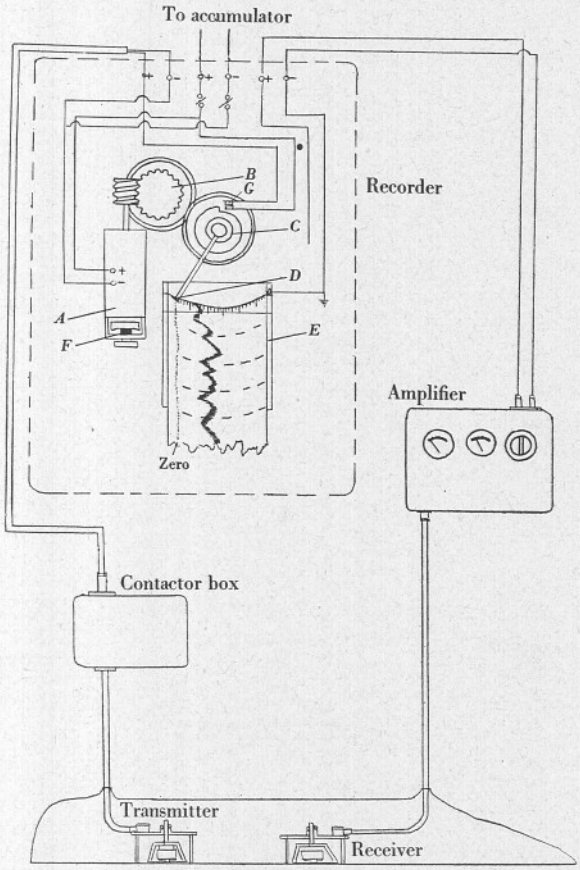
It was known that an echo-sounder fitted into a small boat had been used with great success for surveying the bottom of Lake Windermere. In the course of the Lake Survey it was noted that the presence of submerged lake weeds could be detected on the charts, and it was considered that plants of *Laminaria* would also leave a special mark on the charts so that an echo-sounder could profitably be used to indicate the beds.

The type of echo-sounder employed was the portable M.S. 12 designed by Messrs Henry Hughes and Son. The essence of the apparatus is the sending out of a short pulse of sound (which in fact is audible to the human ear) that is reflected from the sea bottom and on its return is picked up by a receiving system with an amplifier. The time required for the sound wave to travel to and from the bottom of the sea is presented by the machine in the form of a depth measurement.

The general lay-out of the apparatus is depicted in Text-fig. 8. The cam (*C*) with the stylus arm (*D*) is driven through a gear train by the electric motor (*A*). The necessary power in our apparatus was provided by a 12-volt car accumulator. It is desirable to have two of these, and in order to secure the best results the one that has been used should be recharged at the end of a day's working and the spare employed the following day. Each time the stylus arm revolves it passes over the surface of the specially prepared recording paper, a roll of which is fixed in a tank (*E*), a single roll sufficing for two or three days' intensive work. Once in every revolution the cam (*C*) operates the transmitting contacts (*G*) which cause a pulse of sound to be sent out from the transmitter. At approximately the same instant that the pulse of sound is sent out the stylus passes the zero of the scale and leaves a mark on the paper. The recording paper is treated chemically, so that when a current passes through the paper from the stylus to the plate (*E*) forming the front of the tank containing the recording roll, a brown mark is made. If a steady current is passing the stylus will leave a brown mark right across the paper, but if only a short pulse passes at a definite point during the passage of the stylus, the mark will only appear at that position.

The zero mark is made by the transmitting pulse and the amplified echo is made to supply a short pulse of current at the moment of its arrival. As the boat travels into deeper water the stylus moves farther across the paper before the echo is received. All the time the paper is moving slowly vertically downwards (at right angles to the movement of the stylus), so that

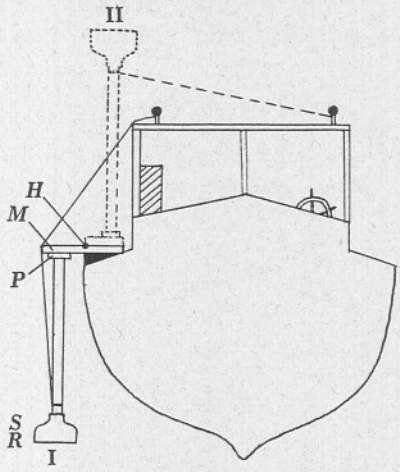
with each passage of the stylus the successive echoes form a contour of the sea bed. The chart is calibrated in feet or fathoms, and by varying the rate of the stylus different scales can be produced. Our apparatus was fitted with both a shallow and a deep scale, but as we were usually operating in waters of less



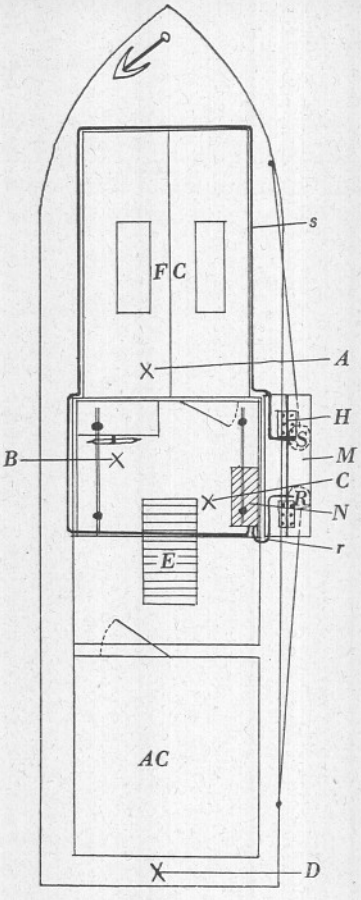
Text-fig. 8. Lay-out of echo-sounding apparatus. *A*, electric motor; *B*, interlocking wheels; *C*, driving cam; *D*, recording arm; *E*, front plate of paper tank; *F*, governor; *G*, contacts. (Reproduced by permission of Messrs Hughes and Son.)

than 10 fathoms we did not have occasion to use the deep scale. Whatever the scale it is essential that the speed be kept constant, and so the apparatus is fitted with an automatic governor (*F*).

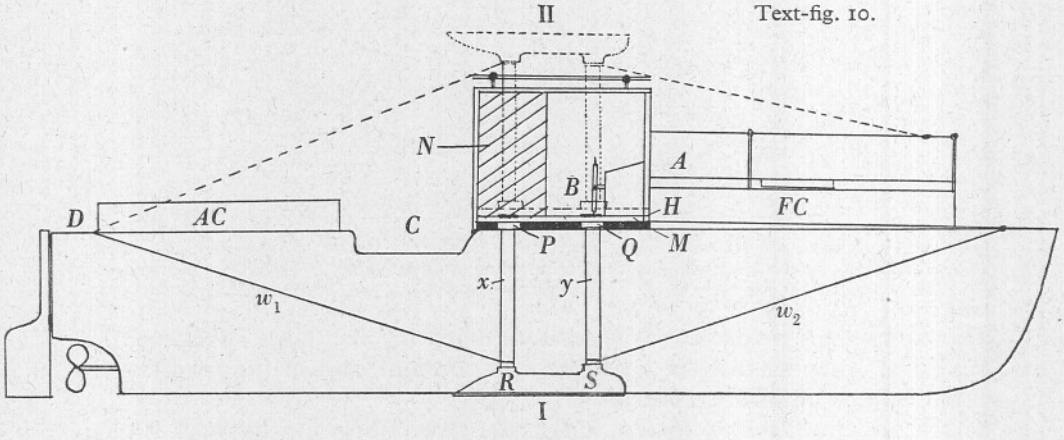
The lay-out of the equipment in the best type of boat for this work is seen in Text-figs. 9–11. The sending and receiving apparatus was contained in a streamlined torpedo-like structure (*SR*), the transmitting portion (*S*) being situated in front of the receiving portion (*R*). This structure was attached by two pipes (*x*) and (*y*) to flanges (*P*) and (*Q*) which were fastened to some stout



Text-fig. 9.



Text-fig. 10.



Text-fig. 11.

Text-fig. 9. Bow view of boat fitted with echo-sounder.

Text-fig. 10. Plan of boat fitted with echo-sounder.

Text-fig. 11. Elevation of a boat fitted with echo-sounding equipment.

I, working position; II, travelling position. *A*, man with box sextant; *B*, skipper; *C*, senior surveyor; *D*, man with grapnel; *E*, engine; *H*, hinge; *M*, plank carrying outboard equipment; *N*, recorder and amplifier; *P*, *Q*, flanges; *R*, receiver; *r*, lead to receiver; *S*, transmitter; *s*, lead to transmitter; w_1, w_2, stay wires; *x*, *y*, piping; *AC*, aft cabin; *FC*, fore cabin.

planking (*M*). This in turn was part of a superstructure firmly bolted to the boat. The outer part of this superstructure was hinged at *H* so that it could be hauled up by the stay wires (w_1 and w_2) into position II when the boat was travelling at speed to reach the working ground. It requires at least two, preferably three, men to haul the apparatus from position I to position II. When the apparatus is down in the working position I a maximum speed of 2–3 knots is the most that is desirable. At higher speeds the outboard part 'shudders', and a great strain is placed upon the superstructure. The recording part of the apparatus and the amplifier were bolted to a strong board which fitted over the side window of the deck cabin because it is important that these two parts should be protected from spray. The accumulator in use was kept on the floor beneath. It is important to keep the leads to the transmitter and receiver as widely separated as possible and so lead (*r*) from the receiver went direct to the recorder, whilst the other (*s*) to the transmitter travelled on deck round the bows of the boat.

For surveying purposes it is desirable to have a complement of five, though the work can be carried out with only four. Under normal conditions the skipper was stationed at *B* and was responsible for steering the boat and controlling the engines. The senior member of the party (in most cases the present author) was stationed at *C* and was responsible for looking after the recording machine, making notes on the record as it appeared, telling the skipper when to change course and where to go, and, by studying the record as it was produced, determining the points where grapnel hauls should be made in order to obtain confirmatory evidence. Each time the course was changed or a haul carried out the man at *C* notified another member, stationed at *A*, who was responsible for fixing the position of the boat by taking a box-sextant reading (cf. p. 43). The third member of the party was stationed at *D* and was in charge of the grapnel. If only two members of the party were out the senior man also made the readings with the box sextant because attending to the grapnel is a whole-time job. The boat also carried an engine-man-cook who occasionally gave some help with the grapnel. The success or otherwise of the echo-sounder depends very largely upon the degree of interpretation which can be given on the spot by the leader together with his estimate of the most profitable course for the boat to take. Upon his skill in interpretation also depends the number of confirmatory grapnel hauls that are necessary. It was found that in each new area to be surveyed it was a good plan to have a number of grapnel hauls during the first day and that fewer and fewer were then required on subsequent days. As we were generally relying upon another method (cf. p. 54) for plotting the shallow in-shore portions of the beds the usual practice was to locate the outer edge of the bed and then to follow it up or down the coast by 'criss-crossing' it at intervals.

It is important to be able to recognize the differences produced in the type of record by variations in the sea bottom because the echo from the weed beds will be superimposed upon that from the sea bottom.

(*a*) *Sand.* Pl. I, fig. 1, represents part of a record from a bare sand or shingle area. It is not always possible to distinguish between a sand or shingle bottom on a record.

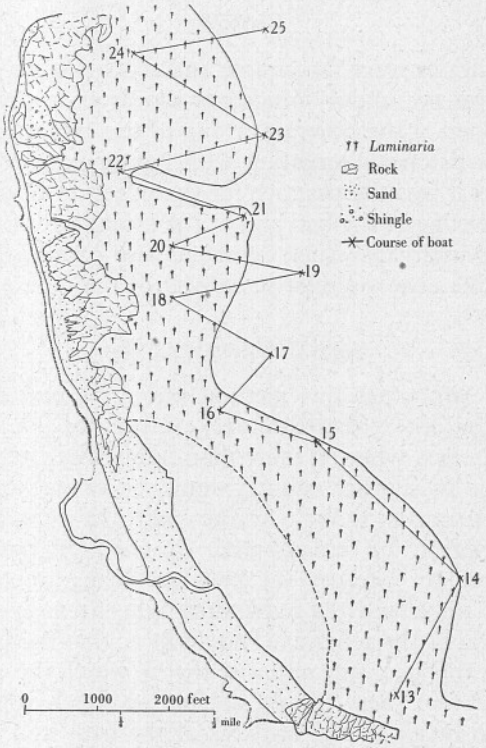
(*b*) *Rock.* Pl. I, fig. 2, illustrates rock bottom at 40 ft. where there was no weed, and it is interesting to note the extremely jagged nature of the bottom: some idea of scale is given by the fact that the distance traversed between marks 6 and 7 was 1250 ft. Pl. II, fig. 1, is a good example showing the transition from a weed bed to a bare sand area. It will be observed from these figures that the *Laminaria* appears as a slightly denser band superimposed upon the lighter record of the bottom, and that the individual plants are represented on the record as thin spikes. The thin spiky record is characteristic of *L. cloustoni* beds and each spike probably represents a single plant. The vertical width of the dense band is an indication of the height of the plants, in this case about 3–4 ft. The irregular spiky record of the bed should be compared with the smooth record obtained from the adjoining sandy bottom.

(*c*) *Boulders.* Pl. II, fig. 2, illustrates the transition from a weed bed to a practically bare patch of boulders. The large sharp irregular peaks of the *Laminaria* bed are evident on the left and the shorter and stouter peaks of the boulders on the right. The great irregularity of the peaks produced by a *L. cloustoni* bed is presumably partly due to the plants being attached at various levels on the boulders or rock and partly because they vary themselves greatly in height. Records of what were probably isolated plants are specially marked on the record. It will be noted that in this type of record, where the plants are growing on boulders, the deeper 'fuzz' obtained when they grow on a rocky bottom is not produced.

In addition to recognizing the various types of bottom a marked effect is also obtained on the chart when there is too much wave action, and for this reason we did not survey with the echo-sounder unless the sea was moderately calm. An example of the type of record produced by excessive wave action is seen in Pl. III, fig. 1, and although at first sight the record has the appearance of a *Laminaria* bed it differs from it in that the peaks are more regular in height and spacing. Soon after this record was made the boat passed over a *Laminaria* bed and the difference in the type of record can be noticed. Rolling, however, is not readily distinguishable from a boulder bottom on a chart, and hence if it is desired to have some indication of the sea floor a calm day is essential. Excessive irregular rolling would also make it very difficult to distinguish a *Laminaria* bed.

So far we have only been concerned with records of *L. cloustoni* beds which produce characteristic irregular sharp peaks. *L. digitata* normally grows too close to the shore to make it safe to venture so near, but we obtained some evidence at one place which indicated that this species gave the same type of record. The specimen chart has unfortunately faded to such an extent that it will not reproduce satisfactorily. The habit of the *L. digitata* plants would in any case lead one to expect that they would give the same type of record as

plants of *L. cloustoni*. Beds of *L. saccharina* were also encountered, and it was soon evident that their method of growth, with the frond lying extended along the sea bed, was not such as to give a reliable indication with the echo-sounder. The apparatus cannot therefore be used with any degree of certainty to detect this particular species. Pl. III, fig. 2, illustrates the type of record obtained



Text-fig. 12. Map illustrating the plotting of the record shown in Pl. III, fig. 3, on to the relevant 6 in. O.S. map. The numbered points correspond to the numbered lines on the record. (Reproduced by permission of H.M. Stationery Office.)

over a bed of *L. saccharina*, and although it shows some slight irregularities as compared with bare ground nevertheless these might well be taken for large stones. There is no dark 'fuzz' in the case of a bed of this species.

Text-fig. 12 illustrates the method of plotting the records on to a map, the relevant record being shown in Pl. III, fig. 3, and the plotted map in Text-fig. 12. These two should be compared carefully. The point on the chart where the record changes from bare ground to weed bed or vice versa between two stations is estimated by eye. Variations in the speed of the boat made it very difficult to be more accurate, but it is not believed that any appreciable error is involved.

View-box and Sextant

Sometimes it was found convenient to use a view-box in order to see if weed was present; it was, however, employed more often to ascertain the density of the cover. In such cases it was always worth while to take a reading with the box sextant in order to establish the position of the boat.

Visibility

If the sun conditions were favourable and work was proceeding in an area where the water was not unduly muddy or too deep, it was often possible for an observer stationed at the bows or on top of the cabin to see the *Laminaria* beds as deep blue patches alternating with lighter patches of sandy bottom. On such occasions it was the practice for the observer to direct the course of the boat along the edge of the bed and at the same time to take readings with the box sextant at intervals. Such occasions also proved useful for checking the behaviour of the echo-sounder in respect of the type of record.

Aerial Photography

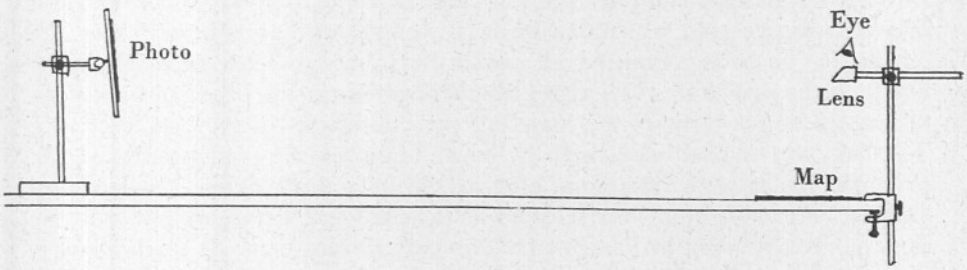
Owing to certain difficulties this method was not employed until relatively late in the investigation. It therefore only proved possible to use it in certain of the detailed surveys, where it more than fulfilled expectations. Any future preliminary survey in another country could be carried out most profitably and in the shortest time by flying over the coast. In using aerial photography certain points require to be remembered. In northern waters it is important to have bright sunlight because the beds are being photographed through varying depths of water and the maximum light intensity is essential. When taking the photographs the aeroplane should fly so that the sun is either behind or, even better, on the wing side opposite that to which the camera is attached. It is also desirable that there should not be too much wind because ripples and waves tend to break up the outlines of the beds and also there is more reflexion of light from a broken than from a calm sea. A small amount of wave action, however, is not unduly deleterious. It may not be possible to secure good photographs the day after an on-shore gale because the water is often muddy with torn-up weed. The best altitudes for securing the most satisfactory results range from 1500 to 2000 ft., although the number of photographs required at such altitudes are considerable. Quite satisfactory results can be obtained up to 4000 ft., but the degree of accuracy in the plotting decreases at altitudes above 2000 ft. In securing the photographs it is important to use an aeroplane type in which there is ready intercommunication between pilot, observer and photographer.

Two types of photograph may be secured:

(*a*) *Obliques*. Experience proved that the beds showed up best in this type of photograph (cf. Pl. IV, fig. 1), but they take somewhat longer to plot.

(*b*) *Verticals*. This type includes near verticals where the angle of deviation is not more than 5°. The beds do not always show up so well, and the depth limit to which they can be detected is apparently less than with obliques. This type of photograph, however, is very easy to plot (cf. Pl. IV, fig. 2).

Successful interpretation of the photographs depends upon a sharp line of distinction between the seaweed bed and the surrounding bare area. The best contrast is provided if the adjoining bare areas are sandy: if the sea bottom is rocky throughout but only a portion of the rocks is covered with *Laminaria* it is more difficult to interpret the photographs. It may be argued that one is really photographing the rocks rather than the beds of weed, but this is not so, because even with partially populated rocks a definite deepening in colour can be seen where a bed exists. The outline of a bed becomes sharper the shallower the water, but under good conditions a bed can be observed to a



Text-fig. 13. Apparatus for plotting verticals and near verticals. The photograph is affixed to a board on a ball bearing. The board can then be adjusted so as to compensate for any small angle of tilt.

depth of 5 or 6 fathoms. Confirmatory proof of the existence of these beds was obtained by the use of the echo-sounder and the grapnel. Cloud shadows can be mistaken for beds of weed unless great care is taken: the beds of weed can be distinguished by virtue of the sharper outline. It is desirable, however, to take photographs on cloudless days.

Vertical photographs with an angle of tilt less than 5° can be plotted by means of a simple prism and mirror apparatus. The photograph is attached to a board (Text-fig. 13) which can swivel on a ball-bearing in any direction. By this means adjustments can be made which will compensate for any small angle of tilt. Four fixed and easily identifiable points are selected and marked on the photograph and the same points are marked on the relevant map. The map is then placed in position vertically beneath the eyepiece. On looking through the eyepiece the photograph is seen superimposed upon the map. The marked points of the photograph may be made to coincide with the corresponding ones on the map by moving the board nearer to or farther from the eyepiece. If the fit is not quite perfect it can usually be made so by slightly

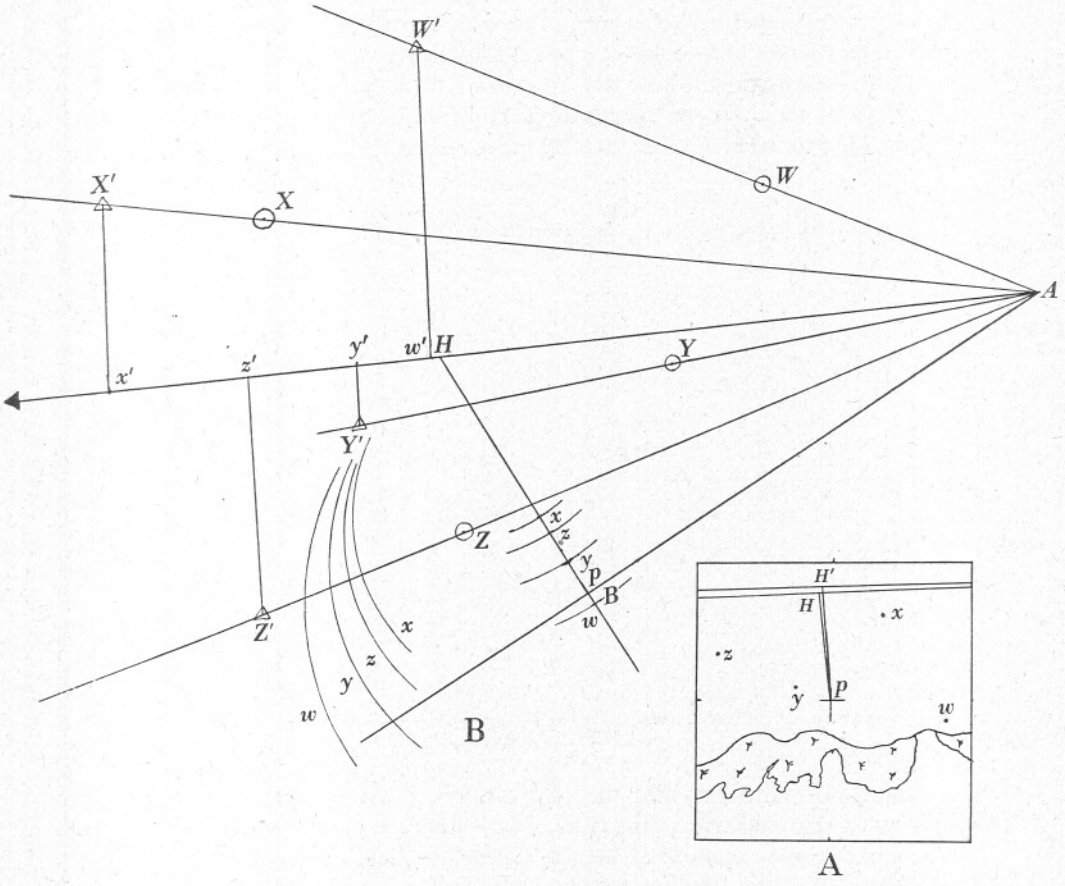
tilting the board one way or another. The distance of both map and photo from the eyepiece can also be pre-calculated from the ratio

$$\frac{\text{Distance apart of two points } AB \text{ on photo (in.)}}{\text{Distance apart of two points } AB \text{ on map (in.)}} = \frac{\text{Distance of photo from lens}}{\text{Distance of map from lens}}.$$

When the points on the photograph coincide with the same points on the map the outline of the beds can be drawn in directly on to the map. Recognition of the beds is materially assisted if they are outlined beforehand in white ink on the photograph. It is also important to select four identification points which are well scattered over the photographs and not confined to any one part.

The oblique photographs were plotted by means of a geometrical construction which is Trorey's modification of Cohn's described in any text-book on photogrammetry. Without discussing the principles involved it is perhaps worth while giving an outline of this method. It depends upon the construction of a perspective grid which can be laid over the photograph, and then the outline of the beds is transferred square by square to a corresponding grid based on the map scale. The map grid is drawn on tracing paper so that it can ultimately be placed over the map and the boundaries of the bed traced in. The beds are first outlined carefully in white ink on the photograph and the principal centre of the photograph is marked by a circle. Four scattered and easily recognizable points are selected on the photograph and marked, and the same points are identified and marked on the relevant map. If the horizon is visible on the photograph it is marked in by a straight line, but if not the photograph is firmly attached to a sheet of paper and the position of the horizon is estimated and drawn in: this is known as the 'trial' horizon. A perpendicular pH is drawn from the principal point to this trial horizon (Text-fig. 14). A sheet of kodatrace is taken, and on it is drawn a line AB the length of which is equal to the focal length of the camera lens (Text-fig. 14). At B a perpendicular pH is erected equal in length to the line joining the principal point of the photograph to the trial horizon. A, H are joined and produced. With H as centre and with a radius equal in length to a perpendicular from one of the selected points on the photograph to the trial horizon the line pH is cut at x. Then with x as centre and the same radius an arc x is drawn on the side of pH remote from A. This process is then repeated for all the remaining three selected points so that a series of four arcs (w, x, y, z) is obtained. The kodatrace is then laid over the photograph so that the line AH lies over the line pH on the photograph (the line from the principal point to the trial horizon), and the kodatrace is gently moved up until the trial horizon makes a tangent with the first arc w. Whilst in this position a prick (W) is made in the kodatrace at the selected point w in the photograph that corresponds to the arc w resting on the trial horizon. This procedure is repeated for the other three points so that now all four points have been transferred to the kodatrace (W, X, Y, Z). The point A is joined up to each of these points and the lines

are produced beyond them. The kodatrace is now removed and placed over the relevant map and moved about until the lines from A to the selected points pass over the corresponding points on the map. The point A must be on that side of the selected points from which it was evident that the photograph was

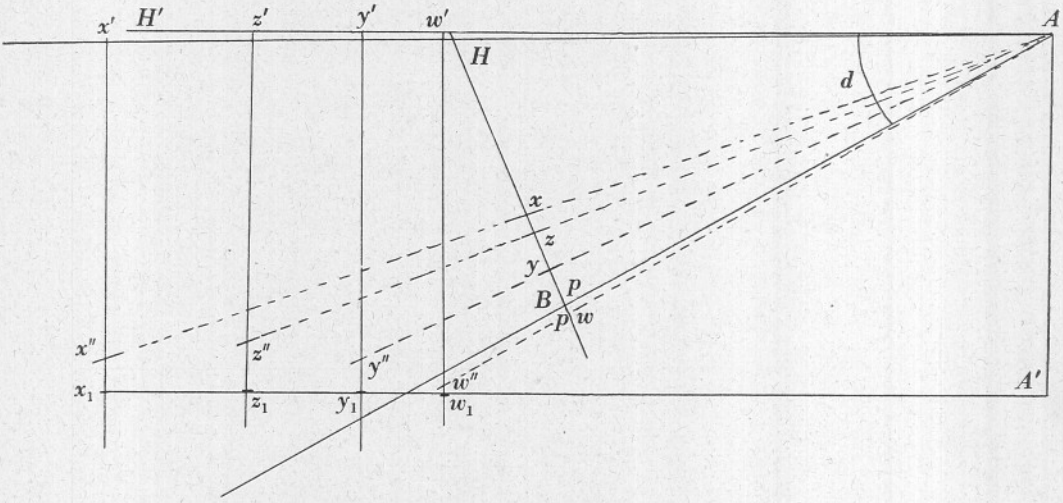


Text-fig. 14. A, photograph with principal point p, trial horizon H and true horizon H'. The four selected points are w, x, y, z. The *Laminaria* bed is also marked. B, geometrical construction on Kodatrace (cf. text for explanation).

taken. When a fit for at least three lines has been obtained, the four points on the map are pricked on to the kodatrace (X', Y', etc.) and perpendiculars are drawn from these points to the line AH produced, e.g. $X'x'$. Although it is of no immediate interest the position of A on the map marks the position on the ground immediately beneath the aircraft when the photograph was taken.

A line AB is now drawn on a large sheet of paper (Text-fig. 15), equal in length to the line AB of the kodatrace. At B a perpendicular is erected, equal in

length to pH on the kodatrace, and A is joined to H and produced. Along AH lengths are marked off equal to the distances on the kodatrace from A to the perpendiculars from the selected points (e.g. Ax'). Four points on AH produced are thus obtained, each one corresponding to one of the four selected points. From these four points perpendiculars are dropped downwards. With H as centre the new line pH is cut in the same four places as on the kodatrace, using the perpendiculars from the selected points to the trial horizon as radii. These four points on the line pH are joined to A and produced beyond the line pH until they cut the perpendiculars dropped from the four points on the line AH produced. Each line will meet a corresponding perpendicular for



Text-fig. 15. Geometrical construction to obtain altitude and angle of dip (cf. text for explanation).

the same selected point, and the spot where each is cut marks the vertical elevation of that selected point (e.g. x''). Reference is now made to the map and a correction is applied to all the points for height above sea-level, thus lowering them all by varying degrees. The map scale is used for this purpose as the figure is automatically constructed on the same scale as the map. The four corrected points (x_1, y_1, etc.) are joined up if they form a straight line and the line is produced towards A. A perpendicular AA' is drawn from A to this ground line and its length on the map scale gives the altitude of the aeroplane. If the ground line is not parallel with the line AH a new line AH' is drawn from A which is parallel with it. This line represents the true horizon and is transferred to the photograph and a new perpendicular is drawn from it to the principal point. The angle $H'Ap$ is the angle of dip of the camera lens and is measured. If the four points are not in a straight line their positions can be corrected by means of a correction triangle.

The final stage is the construction of a perspective grid to fit the photograph. One of these grids was made for every 200 ft. in altitude and for every 2° in declination of the camera lens. A family of grids was thus built up on this basis, and once the altitude and angle of dip of any photograph had been determined it was only necessary to look out the relevant grid.

The following procedure is followed in order to construct a perspective grid assuming that the map grid is to have sides 300 ft. long. A line is drawn across the top of a sheet of paper, and from a point A near the centre of the line a perpendicular AH is drawn such that

$$AH = \frac{\text{Altitude in feet}}{\text{Sides of map grid in feet}} \sec d = \frac{\text{Altitude}}{300} \times \sec d \text{ (angle of dip of the camera).}$$

At H another line is drawn at right angles to AH and parallel to the first line with H as centre; this line is divided by points each 1 in. apart. These points are joined by rays to A. Two points v and v' on opposite sides and equidistant from A on the original line are found from the formula

$$Av = Av' = f \sec d,$$

where f = focal length of camera lens. On AH a point P is marked off such that AP is equal to pH' on the photograph to be plotted (i.e. the distance from the principal point to the true horizon established by the previous construction). vP and $v'P$ are joined and produced and horizontals are then drawn using the intersections of vP and $v'P$ with the vertical rays as markers. This produces the perspective grid which is then reproduced on to kodatrace. When a photograph is plotted the point P on the grid is placed over the principal point on the photograph and the line AP adjusted so that it lies over the line joining the principal point to the true horizon. When drawing in the outlines of the bed it is necessary to draw in portions of the coast which can be laid over the corresponding portions on the map; these serve not only to orientate the drawing but also act as a check on the accuracy of the construction. If a mistake had been made in determining the altitude of the plane or angle of dip of the camera an incorrect grid will automatically have been used, and the scale of the beds, as drawn from the grid, will differ from the map scale and the guiding portions of the coastline will not coincide.

Summary

Previous methods of survey by American workers are described and the differences between the species of seaweed involved are emphasized. The small stature of the European kelps renders all methods of survey difficult and the results can only be described as the best approximations. The British survey was divided into (1) a preliminary survey in order to determine the regions with the biggest beds, and (2) a detailed survey, when some of these major

beds were mapped in detail. The primary survey was a rapid affair and the results were based on information obtained from (*a*) use of boat and grapnel, (*b*) existence of cast weed, (*c*) lobster fishermen, (*d*) coastguards, fishery officers, borough surveyors, harbour-masters, (*e*) inspection from cliffs, (*f*) a study of Admiralty Charts.

In the section on the detailed survey the different types of grapnel employed and also the method of using the box sextant are described. The use of an echo-sounder to locate weed beds is discussed and the different types of record obtained over various types of bottom or weed are noted. The use of a view-box and personal observation is also mentioned, and finally an account is given of aerial photography as a means of survey. The most suitable conditions for success are noted and also the technique of interpretation for both oblique and vertical photographs. The plotting of these two types of photograph is described in some detail.

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EXPLANATION OF PLATES I–IV

PLATE I

Fig. 1. Echo-sounding record from bare sand and *L. cloustoni*.
Fig. 2. Echo-sounding record of bare rocks.

PLATE II

Fig. 1. Echo-sounding record showing transition from bare sand to *L. cloustoni* bed.
Fig. 2. Echo-sounding record showing transition from *L. cloustoni* bed to boulders.

PLATE III

Fig. 1. Echo-sounding record showing effect of wave action compared with records from beds of *L. cloustoni* and *L. saccharina*.
Fig. 2. Echo-sounding record from *L. cloustoni* and *L. saccharina* beds.
Fig. 3. Part of the record plotted in Text-fig. 12.

PLATE IV

(Reproduced by permission of the Air Ministry)

Fig. 1. Oblique photograph of a *Laminaria* bed.
Fig. 2. Vertical photograph of the same *Laminaria* bed.

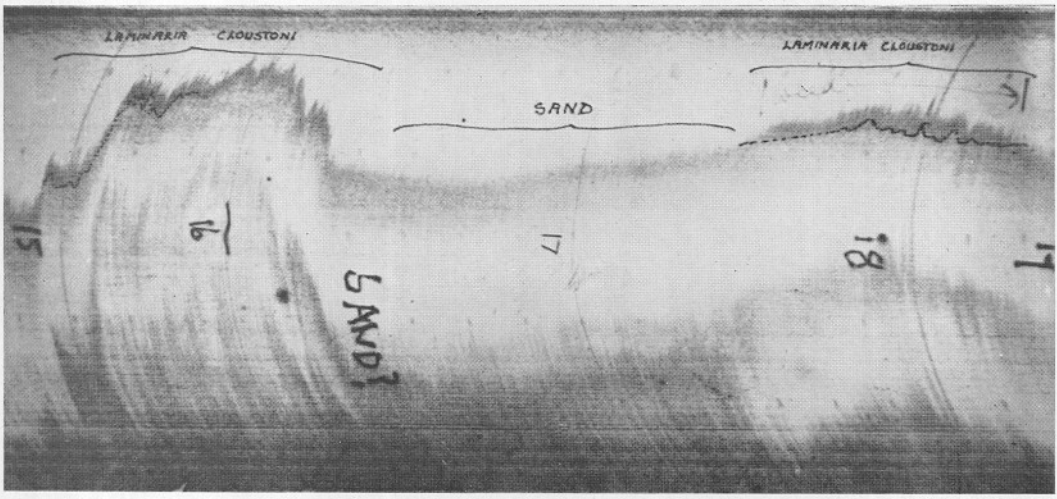

Fig. 1.

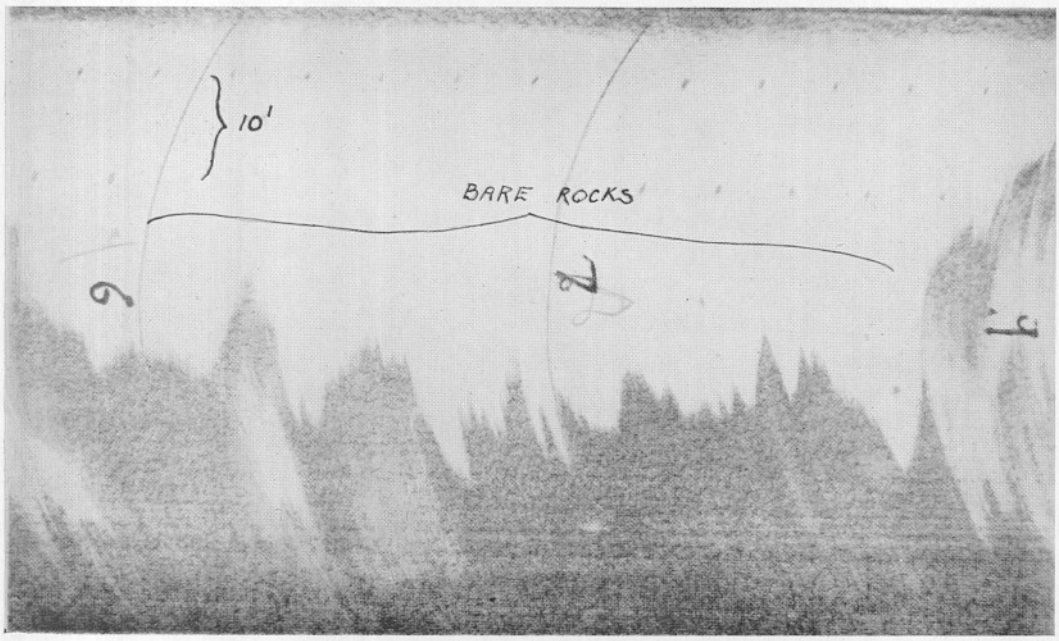

Fig. 2.

Echo-sounding records from *Laminaria* beds.

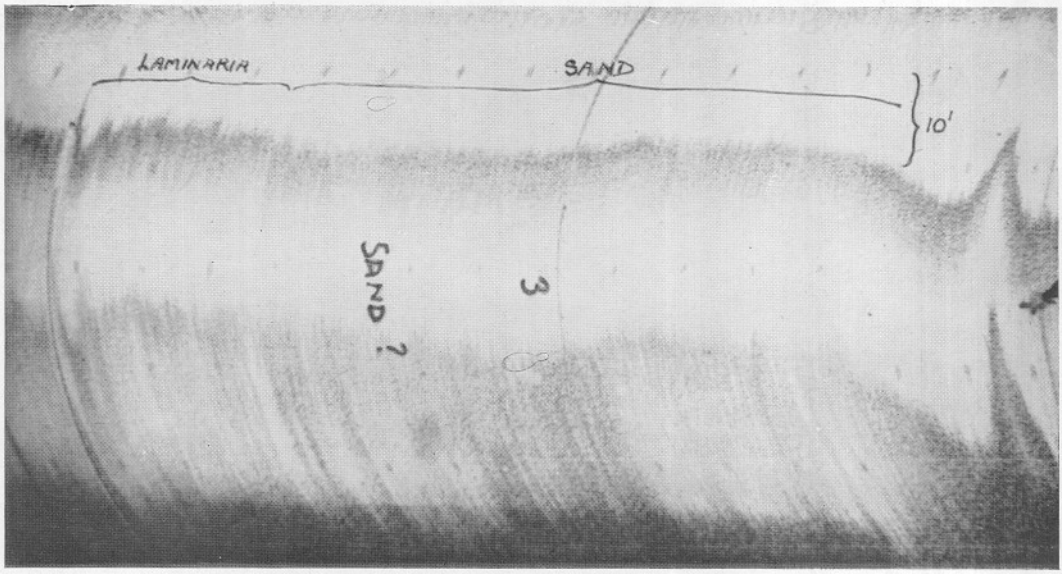

Fig. 1

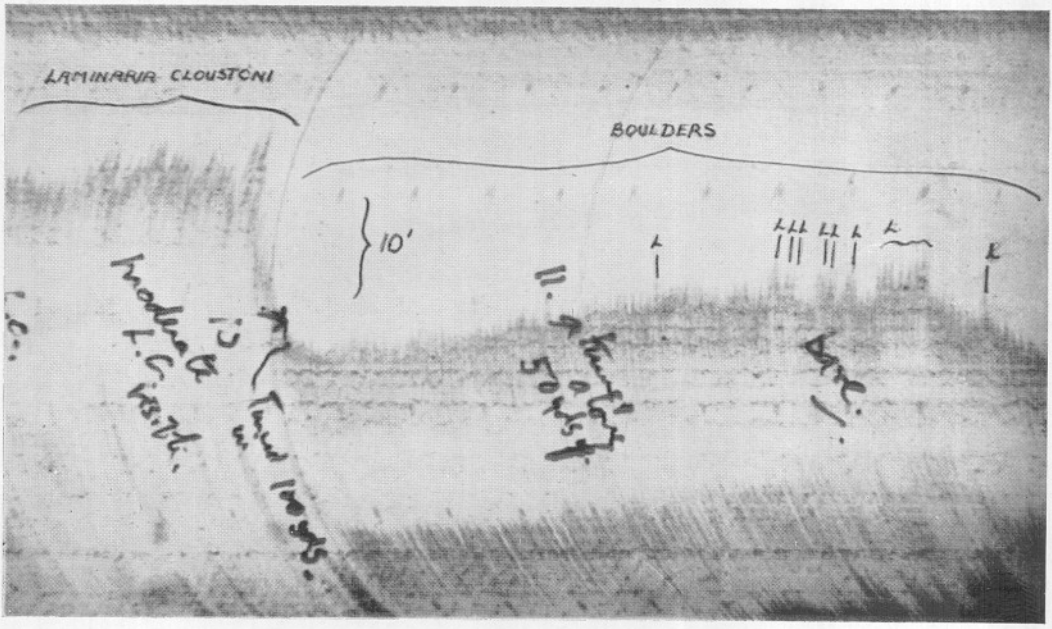

Fig. 2.

Echo-sounding records from *Laminaria* beds.

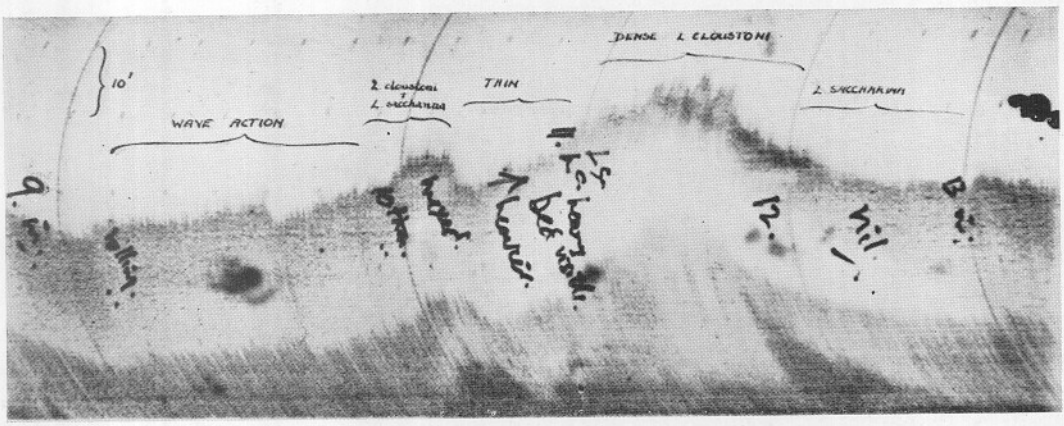

Fig. 1.

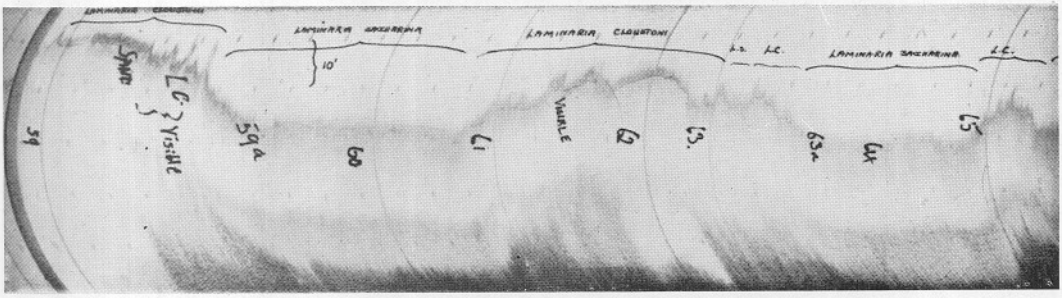

Fig. 2.

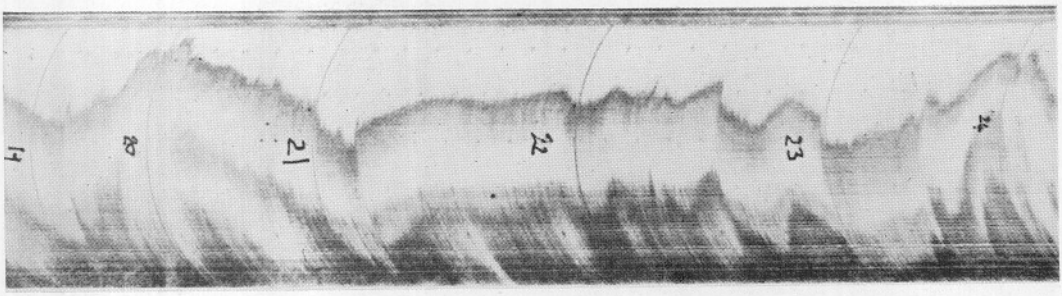

Fig. 3.

Echo-sounding records from *Laminaria* beds.

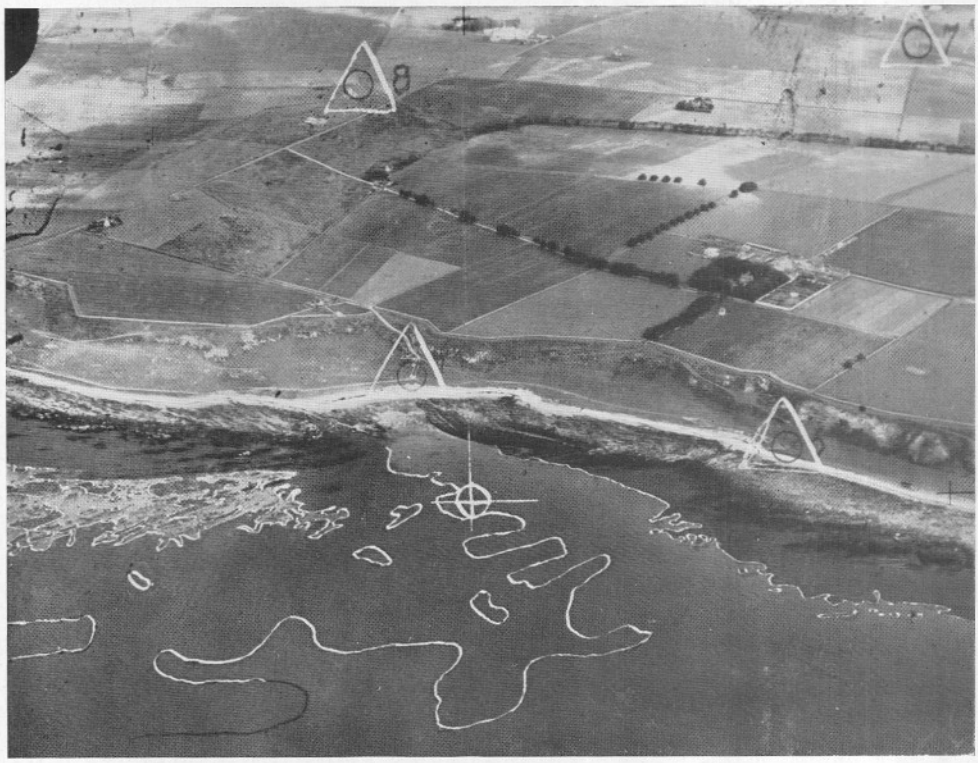

Fig. 1.

Fig. 2.

Aero-photographs of *Laminaria* beds.

NOTES ON CERTAIN ASPECTS OF THE BIOLOGY OF *CUMOPSIS GOODSIRI* (VAN BENEDEN) AND SOME OTHER CUMACEANS IN RELATION TO THEIR ENVIRONMENT

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(Text-figs. 1–7)

CONTENTS

Introduction

The results of observations on limb movements concerned with feeding, breathing, swimming, burrowing and cleaning are recorded. From the study of the habits and functional morphology of certain Cumacea, particularly *Cumopsis goodsiri* (van Beneden), the importance of some ecological factors is deduced, and the extent to which they may control the intertidal zonation of these forms is discussed.

Recent literature dealing with the habits and habitats of the Cumacea includes Dennell's (1934) account of the feeding mechanism in *Diastylis bradyi* Norman, Zimmer (1932) on the habits of *Diastylis rathkei* (Kröyer), *Iphinöe trispinosa* (Goodsir), *Lamprops fasciata* Sars, and *Pseudocuma* sp. Foxon (1936) has also described observations made on the last three forms mentioned.

I should like to thank Dr E. E. Watkin, D.Sc., for helpful criticism during the course of the work.

Distribution and Method of Collection

Within recent years several investigations have been made on the distribution of sand fauna in Great Britain, and these include a few references to *Cumopsis*. This sand-dwelling genus is, however, probably one of the most common

Cumacean forms occurring on our shores, and the scarcity of records concerning it may be due to the difficulty experienced in its collection, as the small size of the animal enables it to pass through the mesh of the standard sieves used in these researches. The specimens used in the present work were collected from the sandy beaches of Kames Bay, Millport, Buteshire; Oxwich Bay, Gower, Glamorgan; and Aberystwyth, Cardiganshire.

Sars (1879) describes *C. goodsiri* as a marked littoral form, but the collection of this species at Kames Bay, Oxwich Bay and Tenby, Pembrokeshire, showed its distribution to be confined within the neap-tide range. At Oxwich Bay and Tenby the zonation ranged from a little above M.S.L. to L.W.M.O.N.T., disappearing altogether as spring-tide levels were reached. The term 'littoral' is better applied to *Bodotria scorpioides* (Montagu), as it occurs in Aberystwyth. Here the shore is typically rocky and the intertidal zone is made up of shingle. This shingle becomes gradually finer as the L.W.M.S.T. level is approached and at this point there is a narrow strip of sand, partly exposed at L.S.T., but nearly always covered by shallow water.

The animals may either be collected from the water during swarming periods, or from the sand normally. In this investigation they were collected from the soil, and the method already described by Foxon (1936) was used. The surface inch of sand was placed in a bucket and covered with sea water. A gentle stirring of the sand disturbed the animals, and caused them to swim in the surface water, which was quickly filtered through a muslin net. At Aberystwyth *B. scorpioides* had to be collected from shallow water, where the sand was covered with a thin layer of shingle and contained a high percentage of detritus, which made the use of a muslin net impracticable. Instead the substratum was stirred, and the resulting cloudy water sieved. Only large specimens were caught in this way.

Respiration

Cumopsis goodsiri has well-developed gill chambers on either side of the thorax. Zimmer (1932) has described these chambers in *Diastylis rathkei*, and in principle his description holds for all Cumacea. Each chamber is oval in shape, with its roof, outer lateral walls, and floor formed by the branchiostegite (Fig. 1). The respiratory apparatus lying within is divided into two regions, the anterior siphonal, and the posterior gill regions. The exopodite of the first maxillipede forms the siphonal region. It is composed of a broad chitinous band whose edges curl together to form a narrow expiratory siphon, which is slightly tumose at the distal end. The latter part appears periodically outside the pseudorostral chamber. The gill region lies posteriorly, and within it are 12–15 delicate, foliaceous gills which arise from a median longitudinal hollow, on the boat-like epipodite of the first maxillipede. They graduate from large anterior to small posterior gills. In situ the floor of the epipodite lies ventrally and the gills are inclined dorsally. A thin chitinous fold arises from the floor of the epipodite in the median line and curves over laterally until

its edges come in contact with the incurving ventral portion of the branchiostegite (Fig. 1, *i*, *mf*). Together the fold of the epipodite and the incurving portion of the branchiostegite form the floor of the gill chamber. There are two openings into the latter. The anterior opening is guarded by the expiratory siphon and the posterior one by the basis of the third maxillipede. It is

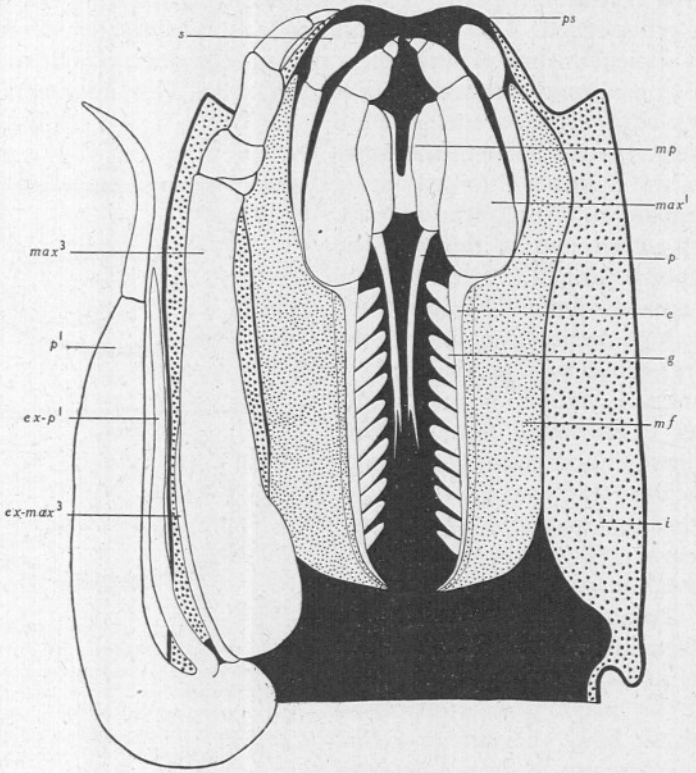

Fig. 1. A diagram of the ventral view of the thorax of *C. goodsiri* (van Beneden), showing the position of the respiratory organs. *e*, epipodite; *ex-max*³, exopodite of the 3rd maxillipede; *ex-p*¹, exopodite of the 1st peraeopod; *g*, gills; *i*, incurving part of the branchiostegite; *max*¹ *and max*³, 1st and 3rd maxillipedes; *mf*, membraneous fold of the epipodite of the 1st maxillipede; *mp*, mouth parts; *p*, maxillulary palp; *p*¹, 1st peraeopod; *ps*, pseudorostral chamber; *s*, expiratory siphon.

possible to observe the breathing mechanism by using a dilute suspension of carmine in sea water. The water enters the gill chamber posteriorly at the base of the third maxillipede, and leaves anteriorly through the expiratory siphon (Fig. 2 A, B). During respiration the third maxillipede is depressed away from the body to form a funnel through which the inspiratory current flows (Fig. 2 B) directed by the rhythmic movements of the exopodite of the third maxillipede (Fig. 1). There are two aspects of inspiration. At times the third maxillipede is depressed only slightly away from the body, so that the funnel

opening is small and the ingoing current passes slowly into the gill chamber. The only activity within the chamber is the constant movement of the maxillulary palp, which lies towards the inside of the gills (Fig. 1). This keeps up a circulation of water over the gills, and thus prevents the water inside the gill chamber from becoming stagnant. During this time no water is seen to leave through the expiratory siphon. But spasmodically inspiration becomes rapid and very pronounced. The third maxillipede is considerably depressed and there is a violent inrush of water into the gill chamber, which tilts the gill apparatus into a more vertical position (Fig. 2B). This initiates a series of movements of the gill apparatus. As fresh water enters ventrally some of the water already in the chamber is forced out by the gill apparatus dorsally through the expiratory siphon and in this way the gill chamber is flushed at intervals.

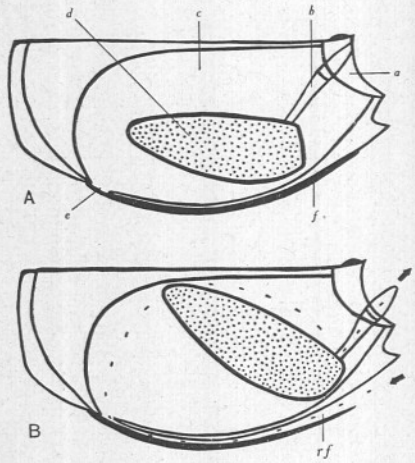

Fig. 2. Diagram of respiratory organs of *C. goodsiri*. A. At rest. B. during respiratory activity. *a*, pseudorostral chamber; *b*, expiratory siphon; *c*, gill chamber; *d*, gill apparatus; *e*, opening into the gill chamber at the base of the 3rd maxillipede; *f*, 3rd maxillipede; *rf*, respiratory funnel.

These animals live in a habitat which has a very high detritus content, and the inspiratory stream as a result carries a quantity of fine material in suspension. The latter is prevented from entering the gill chamber and causing asphyxiation by the long feathered bristles on the basis of the third maxillipede (Fig. 5A), which form a sieve over the funnel opening to filter the particles from the inspiratory current. These bristles lie normally curled inwards between the body wall and the inside of the basis, but, when the maxillipede is depressed away from the body, they uncurl so that their setules overlap to form a network over the funnel opening. This filtering process is probably important from the ecological standpoint, as the size of the particle that can be effectively filtered will depend upon the size of the holes in the mesh of the sieve. The quality of the feathering of these bristles differs in the respective species of the Cumacea. Thus *Cumopsis goodsiri* has a coarse sieve, whilst the sieves of *Bodotria scorpioides* and *Iphinöe trispinosa* are comparatively fine. The Diastylidae have very finely feathered bristles and therefore possess fine sieves. To a certain extent it is known that the species mentioned live in specific soil grades. *Cumopsis goodsiri* occurred at Oxwich Bay in greatest abundance around M.S.L. and gradually thinned out as L.W.M. and a finer soil grade were reached. At Aberystwyth *Bodotria scorpioides* inhabited fine grade sand containing abundant detritus. Watkin (1942), in a survey made at Kames Bay, found the *Cumopsis goodsiri* zone to range from M.S.L.O.N.T. to L.W.M.O.N.T.

and *Iphinöe trispinosa* from L.W.M.O.N.T. to shallow water. From an analysis of soil grade in this case it was found that *Cumopsis goodsiri* inhabited a coarser soil than *Iphinöe trispinosa*. The Diastylidae generally favour muddy soils and therefore need fine sieves. Thus, from the facts available so far along these lines, it seems that soil grade in connexion with the respiratory activities is a factor which helps to confine these species to certain zones within the intertidal area.

Feeding

The Cumacea feed on micro-organisms which occur in the soil detritus, and the manner of food collection depends upon the nature of the substratum. Mud-dwelling species filter small particles in suspension, and sand dwellers clean their food off sand grains and other small objects. *Cumopsis goodsiri* belongs to the last category.

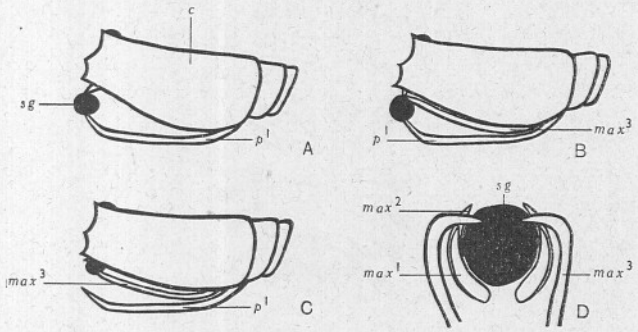

Fig. 3. Diagrammatic illustrations of some of the feeding movements of *C. goodsiri*. *c*, cephalothorax; *max*^{1} *to max*^{3}, 1st, 2nd and 3rd maxillipedes; p^1, 1st peraeopod; *sg*, sand grain.

The feeding mechanism is best observed when the animals are placed in a watch glass containing sea water, a few scattered sand grains, and bits of decaying plant matter. The objects which carry the food are picked up by the first peraeopods and passed on to the third maxillipedes. The food is then cleaned off by the first and second pairs of maxillipedes, and conveyed to the mouth by the true mouth parts, maxillae, maxillules and mandibles. The mouth with the mandibles on either side lies at the bottom of a slight depression, and all the other appendages mentioned lie one on top of the other terminating with the first peraeopods. *Cumopsis* is a selective feeder and carefully searches the substratum for food with its first peraeopods. These then pick up the grain bearing the food (Fig. 3A) and pass it to the third maxillipedes, whose endopodites flick backwards to receive it (Fig. 3 B, C). If it happens to be very heavy the first peraeopods will retain their hold as well and in this way objects almost as big as the cephalothorax are handled. The first and second maxillipedes prepare to clean the grain by arranging their endopodites into a cup-shaped hollow, into which the third maxillipedes fix the grain (Fig. 3D), and in so doing bring it in contact with the armature on the

walls of the hollow (Fig. 4). Then the first and second maxillipedes begin a saw-like movement which serves to scrape off any material clinging on to the surface of the grain. The third maxillipedes occasionally rotate the grain in the hollow to expose all its surfaces, and when it has been well cleaned it is discarded. Methods of grain disposal in other Cumacean species have been described by Zimmer (1932) and Foxon (1936). In *Pseudocuma* the grains are shot backwards over the dorsal surface of the body, in such a way that in time the grain cleaning leads to the formation of a hollow in the soil in front of the animal.

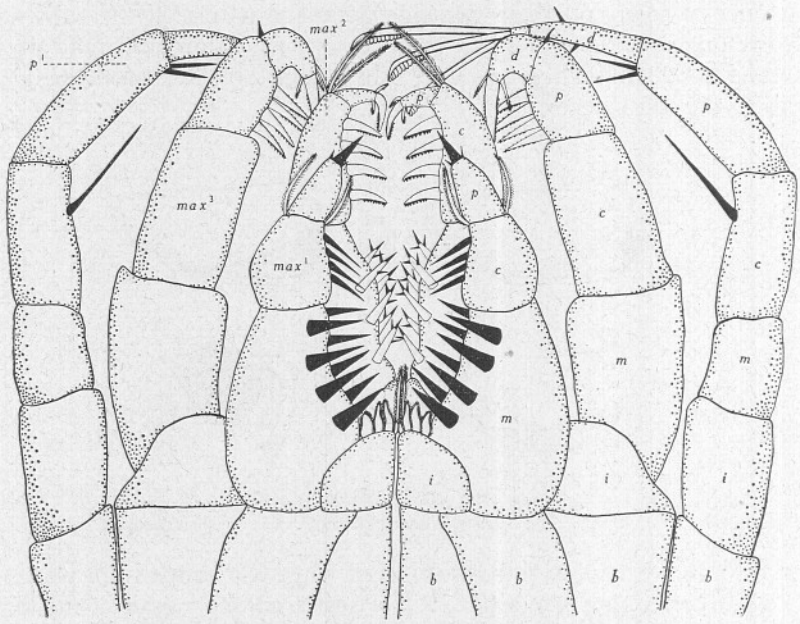

Fig. 4. Armature on the distal parts of the food-collecting limbs of *C. goodsiri*. *b*, basis; *c*, carpus; *d*, dactylus; *i*, ischium; *m*, merus; *max*¹ *to max*³, maxillipedes; *p*, propodus; p^1, 1st peraeopod.

In *Cumopsis* the third maxillipedes merely relaxed their hold on the grain, and it dropped in front of the animal. Sometimes it was shot backwards over the dorsal surface of the carapace as described above for *Pseudocuma*, but this movement was not normal and coincided with the respiratory activities. Thus often the third maxillipedes retain their hold on the grain when depressed in inspiration, but, if on returning to their position against the body wall they relaxed their hold, the grain is shot backwards over the carapace. Sometimes the grain is caught in the expiratory stream from the pseudorostral chamber as it is shot backwards and then it passes forward in front of the animal with great force. Once collected the food is passed to the mouth parts, probably along a ventral food stream. There is no positive evidence of the existence of

this food stream, but it is believed that some of the water about to pass into the respiratory funnel escapes and passes along the depression leading to the mouth, carrying with it the food scraped off the grains by the maxillipedes. The maxillae and maxillules pick up the food particles from the stream and pass them on to the mandibles to be masticated before entering the mouth. *Cumopsis* resumes feeding whenever it contacts food, while resting on the surface of the substratum, or in the initial stages of burrowing. However, certain rapid movements of the soil particles around the anterior end of the cephalothorax when the animal burrows into the soil are due to the close proximity of the grains to the expiratory stream, and not to feeding.

All the food-collecting limbs are well armed, and the function of the armature depends upon its nature and position on the respective limbs. The first peraeopod has on its dactylus four long bristles which can be spread out fan-wise to feel the substratum. These bristles have stout axes, and are slightly bent distally where they carry short combs made up of close-fitting teeth (Fig. 4). These bristles are probably tactile organs capable of locating the food, as well as being fine grasping organs. The dactylus and propodus of the third maxillipede carry bristles with short axes, which possess either one or two ventrally placed combs along their entire length. The teeth of the combs are triangular in shape and have sharp extremities (Fig. 4). These are fine grasping organs, and in this purpose they are assisted by the slightly twisted nature of the dactylus. A smaller version of the same bristle occurs on the propodus and carpus of the second maxillipede, which is used to scrape the grain in the cleaning process. Further assistance in cleaning the grain is given by the feathered bristles on the inner edges of the merus of the second maxillipede, and by the strong, smooth and sharp bristles on the inner edges of the merus and carpus of the first maxillipede (Fig. 4). These last two types line the hollow into which the grain is placed by the third maxillipedes. The maxilla comb is composed of smooth setae which lack the fine delicate setules described by Dennell for *Diastylis bradyi*, and this makes their value as a filter mechanism doubtful.

Burrowing and Swimming

The Cumacea burrow into the substratum if the soil grade is favourable. Zimmer describes how *Diastylis rathkei* refuses to burrow into sand, and in this investigation it was found that *Cumopsis* would not burrow into mud. The last four pairs of peraeopods are used in burrowing. The burrowing movements were observed by placing the animals in a dish of sea water with a few scattered sand grains to act as a stimulus. At rest the burrowing peraeopods lie close together on the ventral side of the body. Burrowing activity begins with the separation of these peraeopods in such a way that the animal appears to be standing on them, with its body lifted from the ground. This is immediately followed by a simultaneous movement of all the peraeopods. The second pair move forward and backward in an anterior to posterior direction,

and the three subsequent pairs move outward and inward in a lateral direction. In this way sand is scooped away from underneath the body and the animal sinks into the hollow thus formed. The posterior region of the thorax and the

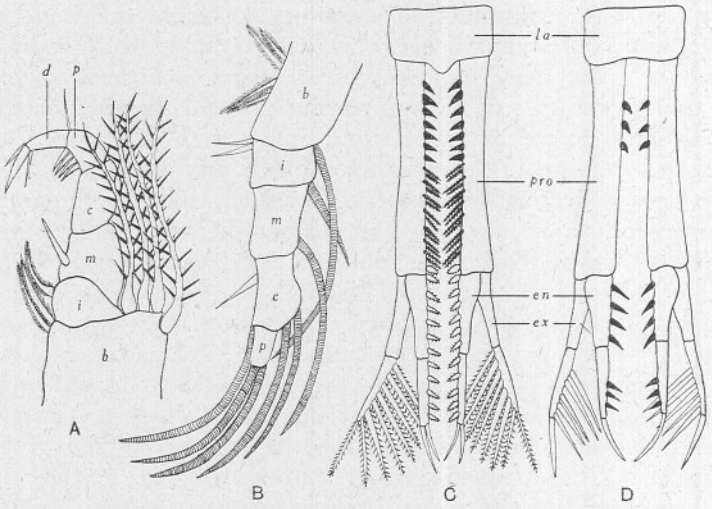

Fig. 5. A. Feathered bristles on the basis of the 3rd maxillipede. B. 2nd peraeopod. C. Uropods of male. D. Uropods of female. *en*, endopod; *ex*, exopod; *la*, last abdominal segment; *pro*, protopod. Other lettering as in Fig. 4.

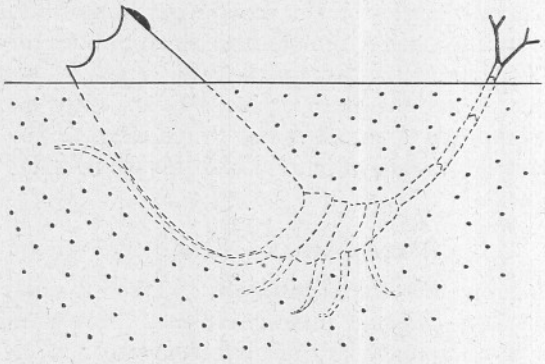

Fig. 6. Diagram to show the position of *C. goodsiri* in the soil after burrowing.

anterior region of the abdomen are buried first. The sand which has been shovelled away becomes banked up on either side of the body and after a time collapses on top of the animal. By pushing its body backwards under this cover of sand it attains almost complete burial. A part of the pseudorostrum remains exposed at one end of the tunnel, and the uropods at the opposite end (Fig. 6). In *C. goodsiri* the last three pairs of peraeopods have a very decided

curved shape, which is further emphasized by the presence of long, curved and ridged bristles (Fig. 5B). These help to scoop away the sand grains.

Though predominantly a burrower *Cumopsis* can swim actively as well. This swimming ability is made full use of in the moonlight swarms in which they are known to participate. In swimming, use is made of the exopodites of the first peraeopods and the abdomen, but both function independently. Thus the animal can swim by flexing the abdomen. The latter is brought forward underneath the cephalothorax and then violently flexed back into position. Quick repetition of this method and the consequent compression and release of water involved, pushes the animal forward in a rapid jerky manner. At other times it swims by rotating the exopodites of the first peraeopods and this is a fast even method of locomotion. In *C. goodsiri* only the exopodites of the first peraeopods are used in swimming. Foxon (1936) describes the use of the exopodites of the first peraeopods and the third maxillipedes in *Lamprops fasciata*. But a dissection of *Cumopsis* showed how the exopodites of the third maxillipedes lie wedged in between the bases of the maxillipedes and the body wall and are therefore incapable of the free movement necessary in swimming. Fully developed males also possess five pairs of pleopods on the abdomen which are sometimes used in swimming. During the investigation they were only seen to be used when the exopodites of the first peraeopods were removed. The principal methods of swimming in both adult and young stages of male and female specimens are by flexures of the abdomen and by rotation of the exopodites of the first peraeopods.

Cleaning of the Body

Cumopsis uses the uropods which are found at the end of the abdomen to clean away detritus or any other matter that may become attached to the surface of the body. The abdomen is brought forward beneath the cephalothorax, to lie near the particular part of the body in need of cleaning (Fig. 7A). Sometimes the uropods diverge on either side of the carapace (Fig. 7B). Once the uropods have taken up their position, the abdomen is drawn backward and forward, and the uropods scrape away any material adhering to the body. Each uropod consists of a protopod, an inner endopod and an outer exopod (Fig. 5 C, D). They are usually well armed, but the armature is subject to ontogenetic and sexual differences. It is best developed in the adult male and consists of smooth spines, comb-spines, comb-bristles and delicate feathered setae. The general surface of the whole uropod is rough on account of the minutely serrated character of the chitinous exoskeleton. This rough surface together with the spines and bristles scrape away the depositions on the body. The feathered setae which are found on the exopods of the male may act as filters to catch the material scraped off by the uropods, and which is later washed away in swimming. But it is possible that they have the more active function of brushing away the material loosened by the endopods. The uropod

is extremely flexible, and this flexibility is the result of an efficient joint arrangement between the segments. The junction between the protopod and last abdominal segment appears to be of the hinge-joint type, allowing only for a bending movement in the ventral direction. A similar hinge joint exists between the protopod and the endopod. But the junction between exopod and protopod is marked by a characteristic bulge, and this seems to indicate a ball-and-socket joint capable of considerable flexibility.

The uropods of the female and young male are always less heavily armed than those of the adult male. Since at all stages in the life history subsequent to leaving the brood pouch, the animal is constantly exposed to detritus and therefore in need of efficient cleaning organs, it would be expected that the

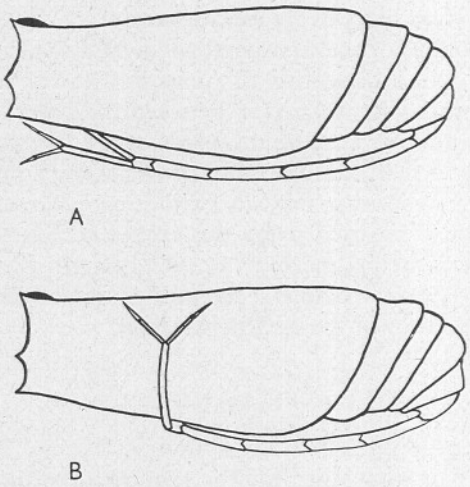

Fig. 7. Diagram of the different positions taken by the uropods during cleaning movements.

most important features of the cleaning apparatus would be present throughout ontogeny in the individuals of both sexes. In *Cumopsis* these include the general rough surface and flexibility of the uropods. The armature seems to be a later development which becomes fully developed at maturity and adds to the efficiency of the cleaning movements. Why the adult male should have uropods more heavily armed than the female is difficult to understand. The male uses the protopod combs to clean its long antennae, and the absence in the female of a counterpart to these long antennae may account for the lack of protopod combs to some extent, but these combs help to clean other parts of the body as well. From the functional standpoint the uropods should be equally armed in both sexes. It may be that the adult male shows this greater development of armature because it favours localities in the habitat which are richer in their detritus content. There is no direct evidence of this assumption, but the difficulty, when collecting, of finding adult males and females to-

gether seems to lend support to the idea. Adult females and young males are frequently collected from the same patch of soil, but adult males seem to inhabit patches of soil on their own.

SUMMARY

The breathing, feeding, swimming, burrowing and cleaning habits of *Cumopsis goodsiri* are discussed.

Cumopsis has compact respiratory chambers. The inspiratory current enters each gill chamber posteriorly at the base of the third maxillipede, and the expiratory current leaves anteriorly through the siphons which pass through the pseudorostral chamber. The inspiratory current is filtered from all suspended particles by a sieve placed at the mouth of the respiratory funnel, which is formed by the depression of the third maxillipede away from the body. The size of the spaces in the mesh of this sieve probably determines the grade of the substratum in which the animal can live.

Cumopsis feeds on micro-organisms which it cleans off sand grains and other small objects. These are collected by the first peraeopods, held in position by the third maxillipedes, and cleaned by the first and second maxillipedes. The food is then passed on to the maxillae, maxillules and mandibles and finally enters the mouth. All these appendages are suitably armed to perform their respective functions.

Use is made of the last four pairs of peraeopods in burrowing and *Cumopsis* will only burrow into a sandy substratum. Swimming is accomplished in three different ways: (*a*) by flexures of the abdomen, (*b*) by paddle-like movements of the exopodite of the first peraeopod, and (*c*) in adult males by the abdominal pleopods.

The body is cleaned by the uropods. Their general rough surface and flexibility is very important. The uropod armature seems to add efficiency to the cleaning movements in the adult animals, particularly in the males.

The size of the soil particle is vitally important in the distribution of the Cumacea. It determines whether the animals breathe properly. There is also probably a close association between the soil grade and distribution of soil micro-organisms upon which they feed. As a result they refuse to burrow into a soil grade which is unfavourable.

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ICHTHYOSPORIDIUM HOFERI (PLEHN & MULSOW, 1911), AN INTERNAL FUNGOID PARASITE OF THE MACKEREL

By Nora G. Sproston

Keddey Fletcher-Warr Student, University of London

(Text-figs. 1–44)

CONTENTS

Description of material

During his routine investigations on mackerel at Plymouth on 19 March 1940, Mr G. A. Steven drew my attention to a fish, which though externally quite normal, showed the viscera (except for the ripe ovary) to be in an advanced state of decomposition, and covered with a thick brown fluid in which were suspended numbers of yellowish granules, up to 2 mm. in diameter. Further examination showed that the brown fluid was the result of the complete necrosis of the spleen and the partial necrosis of the kidney. The blood vessels of these organs remained as dark cobweb-like strands, toughened by the hyphae and nodules of the parasite within them; dark hair-like hyphae also spread throughout the brown fluid. All the stages, so far found, of the parasite occurred in this fish. It was evident that had the fish not been caught this infection would soon have proved fatal.

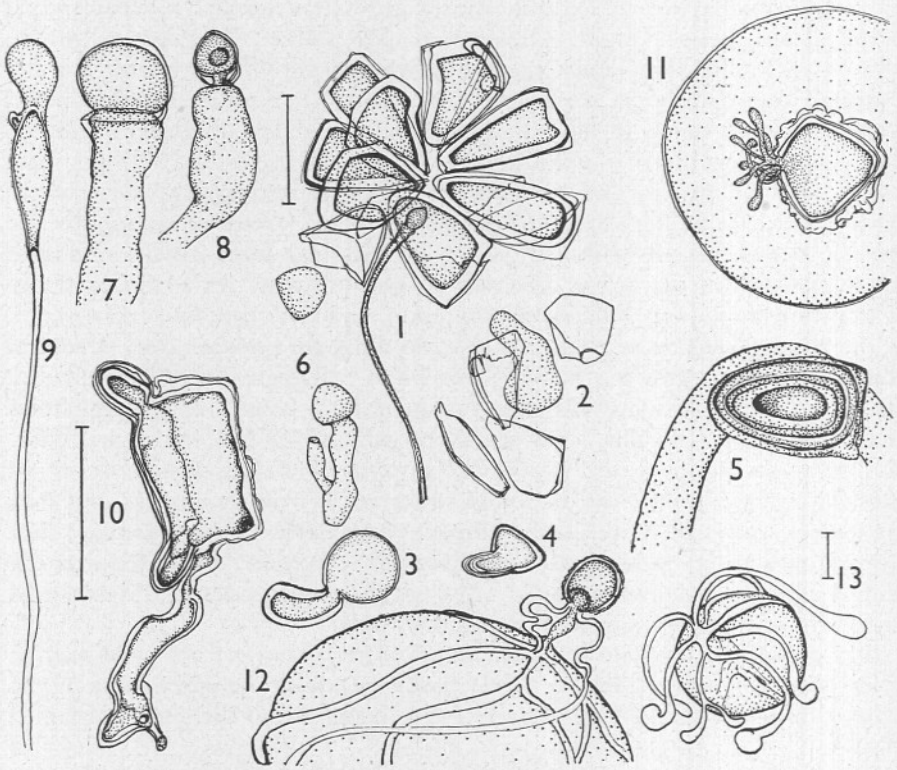
The large batches of mackerel arriving at the laboratory at frequent intervals for the fishery investigations were partly utilized in the subsequent study of the organism. Supplies became less regular in 1941 and 1942, but sufficient numbers were examined to show that the disease is a very serious one, showing no signs of abatement. There was a certain patchiness in incidence of infection; for instance, while one sample in 1941 was completely free from it, those taken from the same locality a few days previously and afterwards showed, respectively, a moderate and 100% infection. The aggregate figures for the infection rates in 1940, 1941 and 1942 were 70, 38 and 69%; in 1943 two separate lots of four fish were received from Hull in the spring, and every fish was heavily infected. There is never any external lesion or colour change, but medium to heavy grades of infection can often be detected by the soft feel of the venter during handling.

In its most characteristic form the parasite shows radiating hyphae, usually with a single dichotomy, growing from one of three types of central body. The length and thickness of the hyphae depend on the density of the infected tissue, and also on the degree of resistance put up by the tissues to histolytic action of the advancing hyphal tips. In low-grade infections there is little or no necrosis, and growth is more or less restricted within the 'granules' or 'cysts', which represent various forms of growth surrounded by a connective tissue sheath of host origin. These are usually stained yellowish or brown, with adherent flecks of black pigment if they occur in the spleen. In the autumn, when fish break shoal and come inshore to feed on small clupeoid fishes, the cysts come to have a silvery coating, which disappears again in the winter when the diet is no longer chiefly of these fishes.[1] In compact tissues, such as the heart, or between the closely packed pyloric caeca (where cysts are often abundant), instead of the cyst being stretched radially by the growth of the parasite within, it grows in columnar form, to accommodate the hyphae advancing in the direction of least pressure. In advanced stages of infection these long galleries are common, and they contain several stages of the parasite. When resistance is low the walls are broken down at several points by the out-growing hyphae; but when it is high they effectively seal off the parasites, which eventually perish, leaving behind only fat-globules and dark acicular crystals. The persistent gallery becomes horny and dark, or silvery, according to the season (see lower part of Fig. 44). Cysts of all sizes up to about 2 mm. can be found scattered all over the viscera, but they can nearly always be found in the kidney, particularly the head kidney; they are very rare in the body muscles and have not been found associated with the central nervous system or gonads. They occur on both sides of the intestinal and stomach walls and are frequent in the lumen.

It is convenient to start the description of the parasite from what may be called *chlamydospores*; these are rarely found *in situ* on the end of one of the radial hyphae as they become detached very readily from the spherical bunch

[1] This deposition of a silvery coating on parasitic cysts in fishes, when they have been feeding on other fish, is extremely common, if not universal in teleosts, though little attention seems to have been paid to it. It is assumed that it is a redeposition of crystalline guanin from the iridocytes of the skin of the food-fish, which, like some bile-pigments, is broken down with difficulty and is laid down in the body as such. Though teleosts possess the enzymes necessary for its metabolism, the subsequent excretion as urea, this process is not very efficient, as the evidence of these temporary internal deposits appears to suggest. A certain amount of guanin is, of course, always retained in the skin of mackerel and many other teleosts in the iridocytes, which provide the reflecting surfaces responsible for the silvery venter and flanks. The correlation just mentioned was first noted some years ago and is particularly striking in the John Dory; in the summer months this fish feeds actively on small fishes, and at these times the gut is packed with scintillating silvery acicular crystals which make the search for parasites exceedingly difficult. At the same time the peritoneal cysts (of tetrarhynchid cestodes, which are always present) are also silver; but as the season advances and fish disappear from the diet, the intestinal contents are bright brown and the peritoneal cysts are yellow or brownish. Several other instances could be cited which provide suggestions for a biochemical investigation of the problem.

in the necrotic fluid in which they occur (Fig. 1). Up to ten have been found in one of these bunches, but it is not possible to state the normal number produced at a time. Their shape and size are variable, but they are usually ovoid to tetragonal and from 70 to 140 μ long. The wide end bears a conical cap of a very hard hyaline substance, and this is continued as a thinner



Figs. 1–13. *Ichthyosporidium Hoferi* (Plehn & Mulsow). For description see text. The scale in all figures represents 100 μ. The scale beside Fig. 1 applies also to Figs. 2 and 6, that beside Fig. 10 also to Figs. 5, 7–9 and 11, and that above Fig. 13 also to Fig. 12.

exospore over the whole surface, except at one small area near the widest part, which appears to be a germination pore. The exospore is insoluble in all the usual reagents; it will not stain and tests for uric acid were negative. It is so hard that when crushed between two slides the latter invariably break without damaging the hyaline cap, and the rest is only divided into three or four fragments (Fig. 2 shows a crushed chlamydospore). The endospore is very thick and hyaline, apparently of a gelatinous nature; it stains with difficulty and is negative to the cellulose tests. In shed spores it

becomes lamellar (Fig. 5), and is usually protruded on germination (Figs. 4 and 3; these are drawn to a smaller scale from living material, but all other figures have their appropriate scales which have all been made equivalent to 100 μ).

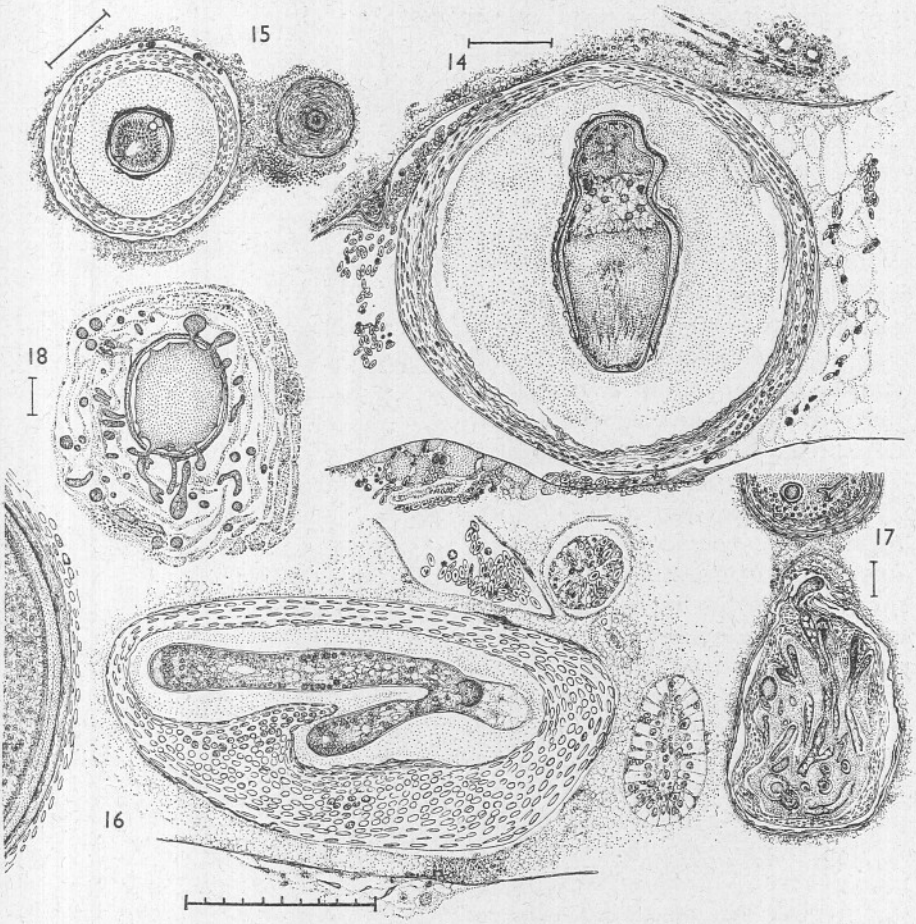
The hyphae produced immediately on germination are always much wider than those produced later, and in advanced growth the walls collapse behind the growing tips, so that in necrotic fluid or in blood vessels they become hair-like in comparison (cf. Figs. 19, 20). The primary 'macro-hyphae' may be very long (a portion of one from another spore is shown in Fig. 5); at other times they are short, and conidia-like *hyphal bodies* are abstricted very early (Fig. 6). Similar bodies, strongly reminiscent of the conidia in *Empusa* spp., are often found on the ends of long macro-hyphae (Figs. 7, 8). These macro-hyphae were particularly resistant to stains so that it was not possible to determine their nuclear state. Occasionally there is a hint of septa being produced before the abstriction of a conidium; Fig. 9 shows a long, collapsed, sister hypha to one producing chlamydospores, and in this the protoplasm in the outgrowing knob is separated from that behind by a convex wall of considerable thickness. This may either be the beginning of a conidium (as in Fig. 8) or, more probably, is the early stage of a bunch of chlamydospores which arise from a similar knob-like outgrowth at the end of an empty hypha (cf. Fig. 1). Atypical germination, where the pore is not utilized, is shown in Fig. 10 (drawn to the same scale as Fig. 5). Isolated chlamydospores are very common in advanced infections, and their presence in or near blood vessels suggests that they are dispersed by the blood or lymph streams throughout the body, coming to rest in the smaller vessels; a vascular wall, however, has not been demonstrated round all those encountered in sections. Fig. 11 shows a chlamydospore with the outer lamellae of the endospore much wrinkled, and though not shown the latter are darkly stained, probably with altered blood pigments from the necrotic kidney in which it was found; it has been enclosed by a thin connective tissue sheath forming the cyst wall and is suspended in a structureless semi-fluid. Germination is from one point in this example; but cysts in denser tissues, where pressure is probably greater, usually germinate in a radial manner, though it may be at right angles to the direction of pressure as in Fig. 16.

Fig. 15 shows two cysts from a resistant spleen; the smaller one is a hyphal body completely enclosed in a thick mass of connective tissue, and the larger one is a chlamydospore in transverse section, enclosed in a connective tissue sheath which completely fills the capillary in which it lies. The dark cells in the lumen at the top of the figure are mononuclears which are associated with fibroblasts in the formation of the capsule; wandering cells of this kind are shown on the inner side of the capsule in the upper cyst in Fig. 17. A chlamydospore just beginning to germinate is shown in longitudinal section in Fig. 14; the endospore has ruptured and the protoplasmic contents show unexplained segregations. No nuclei could be seen in the contents though

there were dark-staining chromatin-like masses of various sizes all round the periphery. At an earlier stage (Fig. 15) the nuclei are very conspicuous and are aggregated round a central vacuole, their chromatin being granular and dispersed to fill the nuclear membrane. The normal state of the nucleus is a vesicle (nearly always about 3 μ in diameter) with a darkly staining centrally placed mass of chromatin, about 0·7 μ in diameter, suspended by finely granular strands which are continuous with a similar layer lining the nuclear membrane. It is this typical nuclear picture which has been taken by some previous authors as diagnostic of *Ichthyosporidium* spp. (see Robertson, 1908, 1909; Jepps, 1937; and pp. 92–93, footnote, below). When a spore is about to germinate, and at the tips of actively growing hyphae, the central chromatin spreads to fill the vesicle and gives the superficial appearance of a larger nucleus (as in Fig. 15); but in resting stages and in some hyphal bodies the central chromatin body apparently shrinks, for it may be less than 0·5 μ in diameter on these occasions. Except for the conditions just mentioned, the nuclei are scattered throughout the protoplasm, which is also abundantly supplied with vacuoles containing fatty substances, though the latter are absent in resting stages. In spite of the very large number of sections which have been examined, fixed at different times of the day and year, no indication has ever been found of nuclear fission or fusion, so that sexual reproduction cannot be established from the present material.

The cyst containing the chlamydospore in Fig. 14 was occluding a blood vessel in the spleen, and there were many other cysts in the section but all were intact; the only abnormality in the tissue is the formation of a blood clot on the right of the cyst. Fig. 16 is from a section of a kidney, more than half of which was replaced by cysts in various stages of development, but all as yet intact; the remaining tissue is perfectly normal as is seen from the glomerulus, two renal tubules and a capillary with red cells which are included in the figure—the scale lies in a larger vessel which contained leucocytes and fibroblasts near the wall. This section passes above the spore but includes a portion of the outgrowing protoplasm and two young hyphae which show a typical distribution of nuclei and vacuoles. Other sections of the series show the spore protoplasm passing out into these and other hyphae the proximal regions of which become empty—a condition highly characteristic of nearly all stages of this organism, which is also shared by the Phycomycetes in general. On the left of Fig. 16 is a portion of a very large hyphal body from the same section; it is still within its connective tissue capsule, and beneath this is a laminated hyaline wall secreted by the hyphal body but deeply pigment-stained on the outside. Connective tissue cells in this and other capsules are much distorted, showing that they have been stretched during the growth of the parasite within the cyst; the one in the figure contained many thousands of nuclei evenly dispersed throughout its mass, and at the periphery was a layer of deeply staining chromatin-like bodies of unknown significance. Such rounded-off hyphal bodies are exceedingly

common in sections, but they vary very widely in size. It is usual for these to germinate in a radial manner, and this is shown in heart tissue of considerable density in Fig. 18; this section passes through a hyphal body which was enclosed in only a thin capsule and the hyphae have perforated it at



Figs. 14–18. *Ichthyosporidium Hoferi* (Plehn & Mulsow). For description see text. The scale in all figures represents 100 μ.

many points—they are still continuous with the central mass, the detached portions in the figure representing hyphae cut across from different levels of origin. Heart-tissue seems to be tolerant of the penetration of hyphae, for in no case was there any necrosis of the adjacent muscle fibres.

Fig. 17 shows a section of a compound cyst, or rather gallery, in a kidney; this contains chlamydospores in various stages of germination (cf. Figs. 3, 4).

It also illustrates a later stage of hyphal growth than that shown in Fig. 16, for an advancing hypha has succeeded in penetrating the connective-tissue capsule, and where it abuts on a kidney tubule the cells of the latter are disorganized, whereas those on the far side are still intact. Intrusive small lymphocytes can be seen massing towards one side of the lesion. The hyphal tips were all darkly stained due to granules of (?) secretory substances, probably connected with the histolysis of the capsule, etc. In the upper part of the same section is a portion of a quiescent gallery containing intrusive monocytes.

In extremely advanced infections of the kidney and spleen, the radial hyphae from a chlamydospore may measure over a centimetre in length; Fig. 19 is a perforated capsule with typical hyphae from a completely necrosed spleen, covered with broken-down pigment cells which appear as black flecks in low magnifications. The figure illustrates the collapse of the hyphal walls behind the outgrowing tips; some of the latter are preparing for abstriction as hyphal bodies, and others foreshadow hyphal fusions. In the more liquid part of the necrotic mass the hyphal tips tended to assume a more spherical shape (to the right of the figure) than in places where it was more solid (on the left of the figure); their minute structure was very similar to that in Fig. 16. In less extreme cases of necrosis the fate of the developing hyphae can be traced; thus in Fig. 20, which represents a whole mount of a moderately advanced stage in growth from a chlamydospore situated in a soft nodule from the wall of the stomach. To avoid further confusion in interpreting this complex colony, only about two-thirds of the radial hyphae have been drawn, and the loose connective-tissue capsule which extends throughout the area of the figure has been entirely omitted. The stippled ring round the central protoplast is the swollen, (?) gelatinous, endospore which has been perforated at several points by the outgrowing hyphae; their proximal portions are now collapsed and the protoplasm has grown out, some being

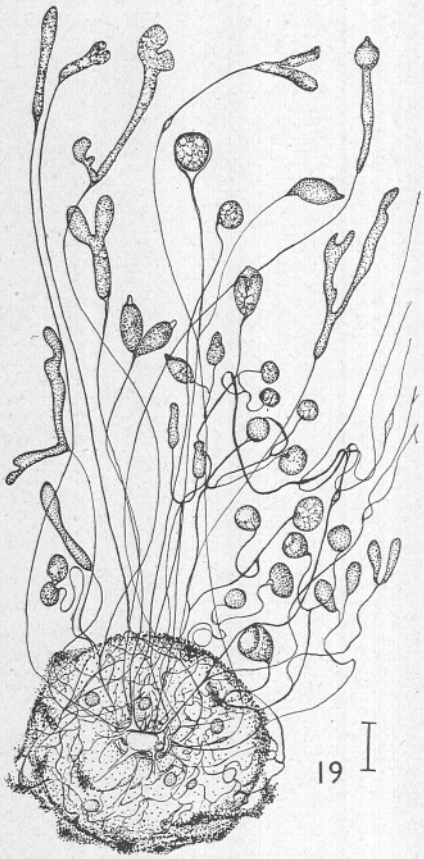


Fig. 19. *Ichthyosporidium Hoferi* (Plehn & Mulsow). The scale represents 100 μ.

abstricted as hyphal bodies which can be seen in various stages (actually lodged between the layers of connective tissue which is not depicted here). Other hyphal tips show a great variety of fusions *inter se*; at the top and to the right of the figure are conditions resembling the gametangia in siphonogamous species of Saprolegniaceae—the analogue of the antheridium being empty. The vesicular appearance of the central protoplast and its fringed lower edge is probably due to fixation and shrinkage, but other features shown are not artefacts, as they have all been seen in fresh material.

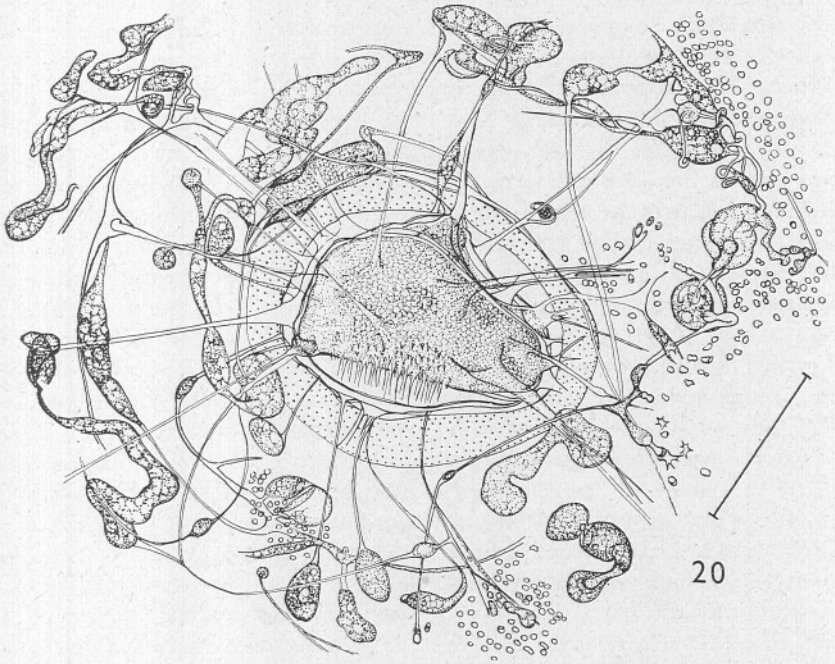


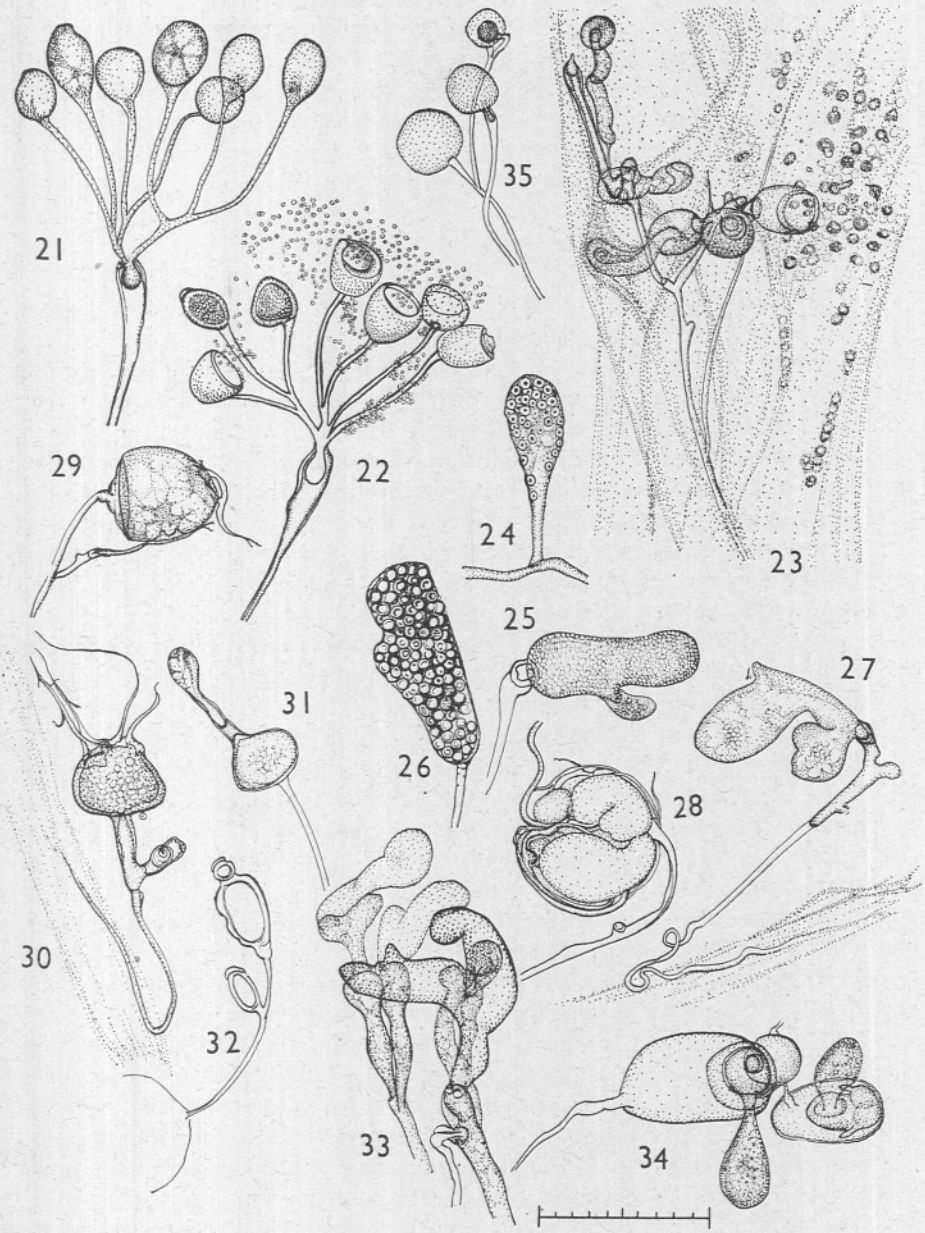
Fig. 20. *Ichthyosporidium Hoferi* (Plehn & Mulsow). The scale represents 100 μ.

At various places in Fig. 20 an unusual type of reproduction is shown; the hyphal contents break up into a single series of *endospores*, or *endo-conidia* which escape by the simple rupture of the end of the hyphal wall, and show a certain degree of amoeboid movement immediately on liberation. The fate and significance of these endo-conidia is quite unknown; they were exceedingly numerous in the region of this nodule, but though they were occasionally seen in pairs, and some double the size were met with, they were never seen to fuse or display more than the slightest change in shape and position. They stain very feebly with haematoxylin and the nuclear substance is very diffuse. Though they are of the same order of size as the small lymphocytes of the fish, they contrast markedly in general appearance—the latter having a very definitely staining large nucleus and a clear cytoplasm.

Other preparations show other types of conidia, and it is perhaps significant that all those so far found have been within, or near, rather large blood vessels, or at the side of decomposing ones. This distribution is analogous to the behaviour of certain parasitic Oomycetes such as the marine form described by Atkins (1929) in the pea-crab *Pinnotheres*. This fungus carries its sporangiophores outside the host so that the spores become dispersed in the currents of the mantle cavity of the *Mytilus* which the crab inhabits. Similarly, the sporangiophores of nearly all the Entomophthoraceae emerge from the body of the host insect, and the spores are freed into the air currents; in the body of the mackerel, however, which is a comparatively extensive micro-habitat for the fungus, the dispersal of spores from one tissue to another is effected by the sporangiophores growing into blood vessels where the blood stream acts as the dispersal agent. Fig. 21 is from a specimen taken from a mesenteric vein very soon after the fish was opened. The hypha acting as a sporangiophore is from the advanced growth of a stellate hyphal body; the protoplasm has grown towards the tip of the collapsed hypha, become rounded off and produced thinner walled branching conidiophores, each with a swollen end. After the original living material was drawn, it was placed, in its watch-glass of diluted sea-water, in a refrigerator and left overnight; next morning the specimen was drawn again (Fig. 22). The protoplasm in the sporangiophores had grown into the swollen ends and become divided into a number of spores, some of which had been discharged as minute amoeboid bodies while in others they remained packed within the 'sporangia'. Further search in fresh material yielded similar growths in veins, differing from each other slightly, both in the shape of the 'sporangia' and in the pattern of branching (cf. Fig. 23; the fine stippling in this and other figures represents the more or less disorganized vascular tissue). The greatest difference, however, is in the size of the spores which were always much larger in the material *in situ*; the latter is undoubtedly the truer picture, the small size of the refrigerator-produced spores being most probably due to the hypertonicity of the sea-water, owing to interim evaporation, causing shrinkage. There is no reason to suppose that these spores are different from the endoconidia shown in Fig. 20, notwithstanding their different mode of origin.

Clavate sporangia are not infrequent; Fig. 24 shows an example in an early stage where the nuclear vesicles appear to have swollen and the protoplasm become segregated round them (deep focusing showed a central vacuole in the sporangium). Fig. 25 is at a still earlier stage, but that shown in Fig. 26 was unusual: the contained 'spores' appeared to be slightly concave and discoid; they were highly refringent, and may have been undergoing a form of fatty degeneration, as it is otherwise unknown to find fat droplets in reproductive bodies in this mackerel parasite.

A more usual development of the hyphal tips is not the direct production of sporangia, but the participation in some form of hyphal fusion; this may take place between unequal branches of a single dichotomy, or between the



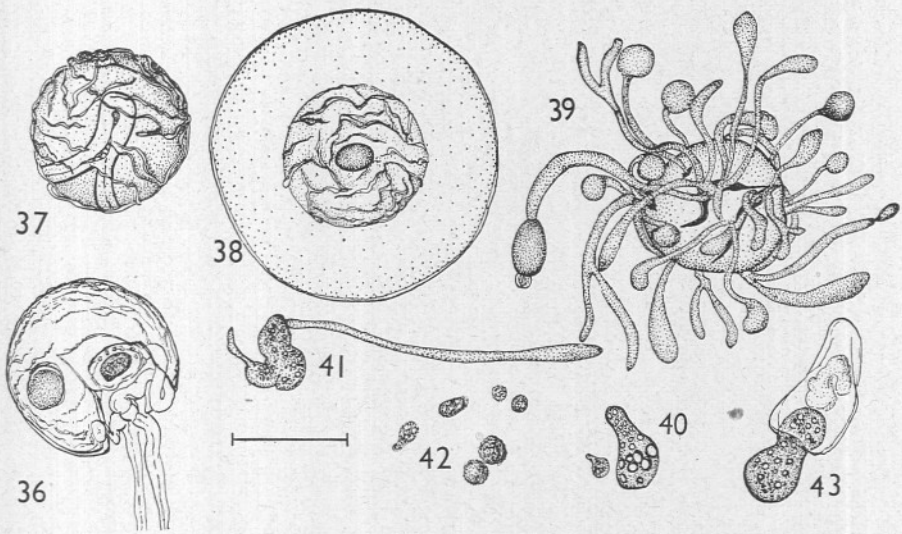
Figs. 21–35. *Ichthyosporidium Hoferi* (Plehn & Mulsow). For description see text. The scale represents 100 μ and applies to all the figures.

ends of sister hyphae (precursors of such fusions are seen in Figs. 19, 20 and 27). Such a fusion may be followed by further outgrowths and renewed fusions (Figs. 33, 34). On the other hand, the fusion may be unilateral, and the hypha receiving the protoplasm may become transformed into a sporangium-like body as in Figs. 20, 29, 30 and 35. In the material shown in Fig. 29 the entry of the protoplasm from the subsidiary hyphae was seen, though no association of nuclei could be detected. It is to be noted that in none of the forms was there any structure resembling a columella, which superficial resemblance to the Mucorales might suggest (cf. Figs. 21, 22, 23 and 29).

Hyphal bodies abstricted, simply, from the ends of hyphae (as in Figs. 6, 7, 8, 19, 20, 31, 33, 34, 35 and 39), either proceed at once to round off and grow hyphae (as in Fig. 41) or become spherical and consolidate, loosing the fatty vacuoles and secreting a wall from which the protoplasm later contracts. These spores from hyphal bodies are very common and of variable size; they may become centres of radial germination in the tissues at any size, but there is apparently a resting period during which the nuclei multiply and considerable growth in girth takes place (cf. the sector of a large example in Fig. 16). Quite frequently the encysted hyphal body divides and one or more of the enclosed spherules may divide again, a new cyst wall being secreted at each division so that compound spherules are formed containing one or more orders of smaller spherules. The sizes of these encysted hyphal bodies range from about 50μ to over a millimetre in diameter—the larger spheres are usually in the region of 250–570μ across. It is evident that they are moved about the host by the blood stream, and in this they agree with the hyphal bodies of the Entomophthoraceae, in the bodies of insects, as shown by Speare (1922), Sawyer (1933) and others. The germination of the hyphal bodies in insects is very similar to those in the mackerel; Speare (1922, fig. 13) has shown that it is sometimes radial, though the resulting hyphae are not usually dichotomously branched in the examples from insects.

There is some reason to believe that spores produced from hyphal fusions, about to be described, are the chief means of dispersal of the fungus throughout its macro-habitat, as distinct from the foregoing types of reproductive body which are sufficient for dispersal in the micro-habitat (viz. the body of the fish). Fig. 27 illustrates a phase of hyphal development which appears to precede fusion; but just as frequently it takes place between the tips of neighbouring hyphae, which coil round each other prior to actual fusion, in a manner not easy to illustrate. Fig. 28 shows an example of this intimate coiling of branches of the same hypha, the smaller one having broken away in the process, leaving a scar on the now empty 'sporangiophore'; and this also shows the shrivelled remains of other neighbouring hyphae which invariably participate in this type of fusion (both Figs. 27 and 28 were taken from the same blood-vessel colony in a necrosed spleen). Later stages of these 'spores from hyphal fusion' are seen in Figs. 36–38. In course of time

the contents consolidate and recede from the hardening wall, which is always wrinkled, the 'wrinkles' representing the remains of the ancillary hyphae which contributed to the later stages of the hyphal fusion. This outer wall usually becomes stained brownish from the necrotic mass in which it comes to lie; in addition there is almost always a Y-shaped area visible just below the outer wrinkled wall (Figs. 13, 37 and 44). This is the site of the primary fusion of the parent hyphae, their lumen often retaining an axial thread of dark (?) protoplasm or other residual matter. Fig. 36 was taken from an old stock 'culture' and the outer 'spore' wall has been partly dissected away to show the disposition of the parent hyphae and two large consolidated masses



Figs. 36–43. *Ichthyosporidium Hoferi* (Plehn & Mulsow). For description see text. The scale represents 100 μ and applies to all the figures.

each with a separate wall, which were found within. If nuclear fusion had been seen this body would be analogous to a zygospore, but such names are unwarranted in the present instance. Sometimes these 'spores from hyphal fusions' are found in the gut contents in the bare state (Fig. 37), or are enclosed with a structureless granular fluid in a thin capsule of host origin (Fig. 38). In both states they have been kept for over three months, mostly in the refrigerator, and have afterwards germinated (Fig. 39).

Germination can be induced, sometimes very rapidly, and sometimes taking several hours, by removing refrigerator material to tap water or dilute saline at room temperature. It very frequently takes place from a single point and the rather wide hyphae tend to envelop the old 'spore' or 'cyst' (Fig. 13), or an adjacent one (Fig. 12, taken directly from necrosed viscera); or it may be more luxuriant and the hyphae emerge from several points of rupture of

the cyst (Fig. 39). Though the latter figure was taken from an old stock 'culture', it differs in no respect, except the darker colour of the hyphae, from abundant examples in freshly caught fish; at least two hyphal bodies or 'conidia' can be seen becoming abstricted.

Hanging-drop and other cultures in various media were all unsuccessful owing to the overgrowth of contaminants from the original material. Various experiments involving the sterilization of different types of resting 'spores'

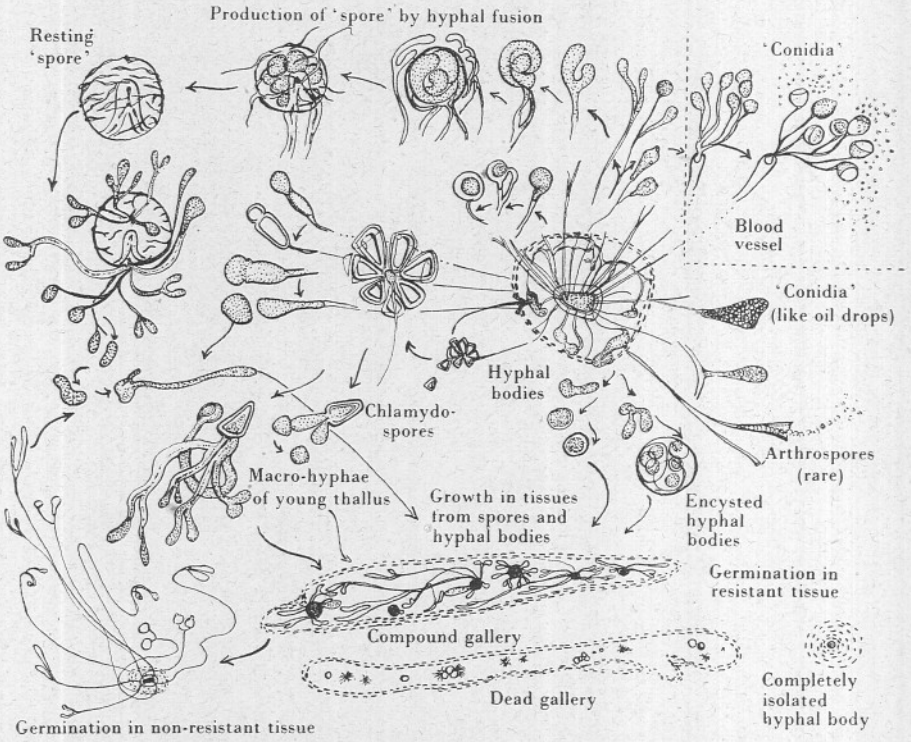


Fig. 44. Diagram of the sequence of growth forms in the life cycle of *Ichthyosporidium Hoferi* in mackerel. The broken lines represent connective tissue of the host (see text).

were also disappointing. The best results were obtained by making thin covered smears directly from the necrotic mass from a badly infected fish; in this way stellate germination has been seen at various stages in several of these 'spores from hyphal fusions', and other stages have been followed in the subsequent rounding off and germination of abstricted hyphal bodies (Figs. 40, 41). Fig. 42 represents endoconidia at various stages of growth in the stock culture fluid, though their ultimate fate could not be ascertained.

An attempt has been made to summarize the forms of growth of this fungus in the mackerel, and some of their probable relationships *inter se*

(Fig. 44); but at present I do not consider I shall be justified in selecting a series of forms for a 'normal life cycle'. Improved culture methods, when fresh fish become obtainable, will probably throw more light on the significance of the various forms described here.

Summary of Previous Work on Similar Organisms

There are several records in the literature of organisms very similar to some of the growth stages met with in the mackerel, both from freshwater and marine fishes; but this is the first time such a wealth of forms has been described from a single host species, and some of the forms are new. There is much to be learnt about the influence of other hosts on the growth of this parasite, and until it can be proved that other records from continental and American fishes represent distinct species, all these forms will be regarded, provisionally, as conspecific.

Caullery & Mesnil (1905) created the genus *Ichthyosporidium*, with *I. gasterophilum* as the type species, for organisms from the viscera of *Motella mustela* and *Liparis vulgaris*, from Wimereux. Their figures and descriptions refer to structures very similar to detached hyphal bodies in mackerel. Their fig. 106 shows a short bifid structure with rounded ends, similar to some shown in Fig. 19 herein, but without the long empty hypha; in other figures they show simple ovoid or globose bodies without a thickened wall. Plasmotomy was found to take place and bi- and uninucleate forms were common; no motile stages were discovered, but nuclear division was found to occur and was simultaneous for all nuclei in the syncytium. With these data it is not surprising that the authors classified it as a Haplosporidian (fam. Bertramiidae); they described a very similar 'species', *I. phymogenes*, from *Crenilabrus melops* from the same place.

Robertson (1908, 1909) found similar rounded and lobed forms, sometimes showing plasmotomy, also a simplified simultaneous mitotic division, and 'trophic' forms within a thick cyst, the outer layers of host origin, and the inner closely adherent to the syncytium of the parasite. All these bodies occurred in the tissues of various visceral organs of a flounder from Millport, Scotland (collected 1906), and in a sea trout from Ross-shire; she also notes that similar forms were found by her in a haddock from Aberdeen. It is now evident that her descriptions referred to stages in the growth of hyphal bodies; but in the light of Caullery & Mesnil's work she identified her organisms with the genus *Ichthyosporidium*, without naming the species. Recently, however, on examination of the present material from the mackerel, she has indicated her agreement that the two forms are in all probability identical, and have fungoid rather than protozoan affinities (personal communication).

Johnstone (1906) found that plaice from the hatchery tanks and ponds at Port Erin showed heavy infections of the liver and kidney with a fungoid organism which he considered to be near to the genus *Conidiobolus* (Entomophthoraceae), his identification being based on the presence of 'mycelium

and conidiophores' and of double-walled 'resting spores'. The figures which he gives agree with mine from the mackerel (Figs. 21, 23 and 43—though as he found 'resting spores' only isolated in sections it is not possible to tell if he had chlamydospores or thick-walled resting hyphal bodies, but they were probably the former). He was led to make his identification partly by the large numbers of dead and dying beetles and other insects in the ponds, which were assumed, without evidence, to be the vectors of the parasite. Superficial lesions were present on nearly all the plaice and were thought to provide routes of entry for the fungus. In later investigations at the same place, Riddell & Alexander (1911) showed that the bacterial disease responsible for the skin lesions precedes the occurrence of the fungus, though they added nothing to our knowledge of the latter.

Laveran & Pettit (1910) found what are apparently hyphal bodies in the trout, and identified the organism with that (partly described, but not named) from the same fish by Hofer (1893, 1904 and 1906) and others, implicated as the cause of 'Taumelkrankheiten' when cysts occur in the central nervous system and affect the co-ordination of movement in the fish. They accepted it provisionally as the haplosporidian of Caullery & Mesnil, but noted that there were indications of its having plant affinities. Plehn & Mulsow (1911) again found the parasite in salmonids, and as in Laveran & Pettit's material it was attacking the viscera, and they were the first to grow it in cultures. Their tissue sections containing the parasite agree very well with mine of the primary germination of chlamydospores and walled hyphal bodies from the mackerel; they also found encysted spherules [hyphal bodies], and they used these as the inoculum. In bouillon they obtained a profuse growth of hyphae, which to judge from their fig. 4 is more profuse and branched than any so far recorded from a fish; on solid media the spherules germinated from a single fissure producing bunched hyphae with clubbed and globose ends, very much like that shown in Fig. 39 herein. Some of the latter germinating spherules figured by Plehn & Mulsow correspond, apparently, with the 'spores from hyphal fusion' from the mackerel, since they show long wavy wrinkles over their surface suggesting the withered ancillary hyphae described here. From the results of culture they concluded that it was a fungus belonging to the Phycomycetes, and near to the Chytrids; they reported neither hyphal fusions nor sexual reproduction. In transferring this and allied organisms to the Fungi, they created a new genus, *Ichthyophonus*, and named the forms occurring in salmonids *I. Hoferi*.

Pettit (1913) re-examined the organism from several trout in aquaria and reported cysts [hyphal bodies] up to 200 μ in diameter with a double capsule; he found a simplified mitosis, though the nuclei are stated to be only 2 μ across. He also found 'spherules' 15 μ in diameter with fat droplets and a large nucleus, free in the intestinal contents, some time before the disease showed itself in the organs. He suggested that the infection may have come from small gadoids used as food (these were infected with *Lentospora* (Myxo-

sporidia)); no stage was found in the aquarium or in the water supply to the fish farm. Warming of the water was suggested as a prophylactic, to avoid undue lowering of the resistance of the trout in cold weather when the disease became a menace. The spleen showed infiltration of 'altered haemoglobin' and necrosis (p. 1001), and other pathological changes are described. He accepts the identity of Hofer's, Robertson's, Laveran & Pettit's and Plehn & Mulsow's organisms with the one he describes, but corrects the nomenclature to *Ichthyosporidium Hoferi* (Plehn & Mulsow), since the new generic name was not justified.

Neresheimer & Clodi (1914) were able to describe a complete life cycle of this organism causing 'Taumelkrankheit' in salmonids, and to show how amoeboid spores, from the clavate hyphal tips, can be liberated into the tissues; they also describe hyphal bodies in the tissues with a similar reaction-tissue capsule to that found in mackerel, but the other forms of 'sporangia' and chlamydospores were not found by them; moreover the hyphae in the tissues were always short and wide. They were successful, however, in showing that few-nucleate forms penetrate the gut wall and that infection is direct from fish to fish without the intervention of an intermediate host. They follow the nomenclature of Plehn & Mulsow and consider the parasite to be a fungus.

Léger & Hesse (1923) found a similar infection confined to the intestine of wild trout in the Alps; but here again the tissue forms appear to have been simple rounded hyphal bodies of various sizes, the nuclei increasing in number by a simplified mitosis, the spherical syncytium ultimately dividing into eight secondary masses, each of which, when dispersed by the rupture of the thin cyst, was capable of repeating the cycle. Nothing of this kind has been found in the mackerel; the readily observed mitosis and the production of equal sized bodies of a fixed number has not been described in forms of this parasite in marine fishes; moreover, they describe uninuclear masses found by others in the trout intestine. The simplicity of the forms occurring in the trout may be realized since these authors remark on the close similarity to the other grave disease of salmonids—Calkins' (1900) *Lymphosporidium truttae*, an undoubted protozoon. They name their form *Ichthyophonus intestinalis*, on account of its restriction to the intestinal wall and lumen. In 1924 Léger described a new species, *Ichthyophonus lotae* from the intestine of the freshwater *Lota*. Later Léger (1927, 1929*a*, *b*) reports the results of culturing the organism from trout and other cases of the disease from these fish and he shows that it has all the characters of *Basidiobolus* in culture; the hyphae are divided into cells with a single, comparatively large, nucleus and there is typical zygospore formation. In spite of his figures being quite unlike any of the forms hitherto described as congeneric with *Ichthyophonus Hoferi*, he groups all the forms found by him in the alimentary canal of trout into the species *I. intestinalis*, and maintains that they are congeneric with *I. Hoferi*. He states that he would be justified in including them in *Basidiobolus*; but his intentions are not clear, for he also uses the following

combinations without comment: '*Ichthyophonus* (*Basidiobolus*) *intestinalis*' (1929*a*, p. 82, in legend to fig. 4) and '*Basidiobolus* (*Ichthyophonus*) *intestinalis* Léger & Hesse' (1929*a*, p. 83). His accounts, however, do not furnish conclusive evidence that the undoubted *Basidiobolus* sp. (Entomophthoraceae) of the cultures is the same as the organism producing the disease in trout; if this is true, then it must be named *B. intestinalis* (Léger & Hesse, 1923) Léger, 1929, and not regarded as congeneric with *Ichthyophonus Hoferi*.

A form with very short wide hyphae and thick-walled 'spores' (occurring only scattered in the tissues), has been described in the herring from North American Atlantic waters by Cox (1916, a brief description without classification), Daniel (1933*a*, *b*), and in more detail, by Fish (1934); the latter author finds *Pomobolus pseudoharengus* to be an occasional host when it frequents the same waters as infected herring. He also confirms the findings of the same parasite in *Pseudopleuronectes americanus* by Ellis (1930*a*, *b*), which Fish shows becomes infected by eating diseased herring. Cross-infection by cysts [? hyphal bodies] from herring to the flounder was established experimentally. All these American forms are clearly conspecific, but they differ consistently from the forms from the eastern hemisphere in the regular occurrence of a linear plasmotomy in the short hyphae, forming a row of few-nucleate rounded bodies issuing from a cornucopia-like expansion at the end of the ruptured hypha. The nearest parallel to this found in the mackerel is the rare condition of the 'endo-conidia' formation, by the fragmentation of hyphal contents producing minute (? uni-nucleate) bodies (see Fig. 20 herein); but the relatively large rounded bodies figured by Daniel (1933*a*, figs. 6, 7, 8, 9 and 15) and by Fish (1934, pl. 1, figs. 1, 5) have no counterpart in the mackerel. There is thus a suggestion that the American forms belong to a distinct species, though the differences might equally well be due to the influence of a different host on the growth of the same parasite. Moreover, in the herring, the American authors point out that in advanced stages the muscles are infected, and pus-sacs develop which eventually perforate the skin; the incipient external lesions being indicated by black spots, due to the diseased skin failing to reflect light. In mackerel the body musculature has never been involved to this extent by the parasite in question, and even the skin and gills of fish *in extremis* show no signs of disease.

In view of its abundance during the period of investigation (1940–3), it is curious that the disease in mackerel had only been recorded from a single fish previously. This specimen was collected in July 1912 off Walney Island (Irish Sea), and the description published by Johnstone (1913), is equivalent to a moderately advanced infection. He described only three growth forms: large [hyphal] bodies in the kidney enclosed in capsules of connective tissue, and smaller [hyphal] bodies in the liver, which showed their own capsule in addition to that of host origin. Some of these bodies had short branched hyphal outgrowths invading the tissues; and lastly, there were some thick-walled germinating 'spores' with short wide hyphae. Small cysts, often

compound and well encapsuled in connective-tissue, were found on the peritoneum, particularly in the region of the pyloric caeca. He considers the organism to be 'very closely allied to the species of Plehn & Mulsow, if it is not identical' (p. 32), and says that it is 'rather different' from a 'closely similar condition' described by him in plaice and attributed (1906) to Entomophthorinae, near to *Conidiobolus*. The latter parasite was again found by him in *Pleuronectes platessa* from Port Erin in 1916, and briefly described later (1920) without being named; it showed a fairly restricted growth of hyphae in the wall of the intestine, and partial necrosis had occurred. He also figures a rugose body with outgrowing clavate hyphae ('mycelium with sporangium-like bodies', p. 24) from the liver. He does not deny its identity with the mackerel parasite, as he is stated to do by Fish (1934, p. 3), nor is there any evidence for so doing; proofs either of identity or of distinctness are both lacking.

In the same paper (1920, pp. 25, 27, figs. 3 and 4) Johnstone describes elongated capsules containing a degenerate homogeneous substance; they are conspicuous in the musculature of the hake by their dark colour, and he identifies them as degenerate cestode larvae, though they show no sign of calcareous corpuscles or hooklets, and no terminal enlargement, as is common with pleurocercoid cysts, even when degenerate. Such bodies have been described before, and Williamson (1913, pp. 8–9, pl. 3, figs. 56, 60, 69, 70 and 73) referred to them as the 'columnar disease' of cod, or 'the brown parasite', because of the stained outer wall; they were common between the body muscles, some being empty and others 'of a hard cheesy consistency'. He also described similar 'columns' in connexion with *Dokus adus*, the 'intra-capillary parasite' of *Gadus aeglefinus*, and thought to represent its final stage in the fish; they often had a very friable wall, exactly like the 'dead galleries' found in mackerel. It is most likely, therefore, that all these bodies represent the remains of a similar infection to that of the mackerel. In the latter fish, cestode cysts are always abundant, but it is quite easy to distinguish them from the simple tubular inter-muscular galleries of the fungus (both these are also frequent between the packed mass of pyloric caeca).

Williamson's description of *Dokus adus* (1913, pp. 4–7, pls. 1–8) is rather confused, as he was uncertain whether it was a plant or an animal, though he inclined to the latter, since the out-growing hyphae were described as larvae leaving the cyst; yet he detected no movement of any phase. His figures, however, show clearly enough that he was dealing with a parasite morphologically identical with the fungus of the mackerel. He calls it an intra-capillary parasite and his figures of small blood vessels distended with cysts, of bile-stained masses in the necrosed viscera surrounding the spore-like bodies, which give rise to radiating hyphae with bifid clavate ends, all have exact counterparts in the present material. He describes long tubes between the muscles containing out-growing hyphae, and rugose spores ['spores from hyphal fusions'] are also figured. He does not show the thick-walled chlamydo-

spores, the branched conidiophores, nor the various forms of hyphal fusion, nor some other growth forms found in the mackerel. He admits that it is in many respects similar to Johnstone's *Conidiobolus*-like fungus from plaice.

In a separate part of the same paper (1913, p. 12, pl. 2, figs. 39, 46 and 50), Williamson describes what appears to be the same fungus from the kidney of *Brosmius brosme* and of *Gadus callarias*—the growth of the former being especially typical. The disease in the haddock is apparently common enough to have earned the local names of 'spotted haddock', 'greasers' and 'smelly haddock'; there is no external sign of the trouble, but in gadoids, like clupeoids, the muscles become infected, and stained areas round the cysts are visible to the naked eye so that the fish have to be condemned as human food.

Quite recently, what may be the same parasite, has been found to be of economic importance by Fischthal (1944, pp. 35–6) on the north-east coast of the United States, where it occurs as cysts, parallel to the muscle fibres of *Zoarces anguillaris*; clusters of cysts may form a brownish concretion, or actively growing 'trophozoites' may cause a hyaline degeneration of the muscles. The fish is marketed in fillets which have to be examined against a strong light so that infected ones can be discarded. No mention is made of the viscera being attacked, nor of marked necrosis, but an aggregate infection rate of about 7% is recorded between March and August 1943. The morphology is not described beyond the mention that cysts, 11–23 μ in diameter contain ovoid spores 4–7 μ long. The larger cysts are 3–5 mm. long and 0·3–1·2 mm. wide. It was described as a sporozoan, and placed in the genus *Ichthyosporidium*.

Discussion and Conclusions

The absence of a plasmodial stage in the life history excludes the present organism from Myxomycetes, and this and its capability of forming an organized thallus, from the Haplosporidia; for though the minute 'endoconidia' are apparently amoeboid and naked, no regular vegetative stage has been found without a wall surrounding the syncytium. In the type species *Ichthyosporidium gasterophilum* Caullery & Mesnil (1905, fig. 106) the original figure is apparently from a bifid hyphal body, recently abstricted from its parent hypha (such hyphae, however, are not mentioned) as the protoplasm is seen receding from a clearly drawn wall, corresponding to the proximal region. The parasite from *Motella mustela*, described under this name by Alexeieff (1914), is evidently quite a different organism, probably much more closely related to *Amoebidium* (see Chatton, 1906), for the prevailing phase is a binucleate amoeba-like body without a distinct wall, and uninucleate spores are another characteristic. He places this organism in a new suborder of 'Mycetozoa-Haplomycetozoae (fam. Haplosporididae)'. Debaisieux (1916) in reviewing *Coelomycidium*, *Blastulidium*, *Amoebidium* and Alexeieff's *Ichthyosporidium gasterophilum*, places these genera in the family Coelosporidiidae which he considers to be near to the Chytrids. Debaisieux does

not examine the validity of Alexeieff's *I. gasterophilum*; but it is clearly not synonymous with *I. Hoferi* as is suggested by the latter author.

The presence of an aseptate thallus, with well-developed non-cellulose walls, places the organism in Phycomycetes. The mode of development of the branched 'conidiophores' from the ends of hyphae (see Figs. 21, 22) is reminiscent of some Chytrids, such as *Urophlyctis*, as Prof. Bennet-Clark has pointed out (personal communication); though unlike the majority of this group, flagellate spores are unknown. (The spores are amoeboid in Protomycetaceae, but there is no great development of hyphae in any of the members at all comparable with that in *Ichthyosporidium* in mackerel.) In the present accepted classification the only possible position for this genus is in Entomophthorales (Zygomycetes), in which flagellate spores are absent, and most other characters are in agreement. The types of fusion of the ends of vegetative hyphae are externally similar in *Ichthyosporidium* to those of several widely different members of the Phycomycetes; forms resembling the gametangia of *Syncephalus nodosa* (cf. Fig. 20), *Pythium de Baryanum* (Figs. 20, 34 and 35), and siphonogamous species of Saprolegniaceae (see Figs. 20, 29) have been found in mackerel.[1] The similarity may only be superficial, since no nuclear fusions have been seen. Among the Mucorales, *Mortierella* is without a columella at the base of the sporangium, and there is some further agreement here, for after hyphal fusion the zygospore becomes covered with a layer of vegetative hyphae analogous to the condition in the 'spores from hyphal fusion' in mackerel (see upper figures in Fig. 44, and Ou, 1940). Nevertheless, the participation of these ancillary hyphae may also be compared with the development of haustoria on the zygospores of the Entomophthoraceae (see figures in Thaxter, 1888). Like the condition in Zygomycetes (in contradistinction to that in Oomycetes) the protoplasmic division in the clavate sporangia is probably centripetal. The dome-shaped conidia [or hyphal bodies] developed on the ends of some of the hyphae are in most respects similar to those of *Empusa* and its allies, except that they are apparently not shot off with such violence; in *Massospora cicadina* Peck,

[1] Though there is no question of close relationship to the present parasite, it is to be noted that adaptation to true internal parasitism has been achieved in several genera of the Phycomycetes; *Mucor* sp. and *Rhizopus equinus* Constantin & Lucet, 1903, for instance, were demonstrated, both naturally and experimentally, in the kidney of the rabbit by Savouré (1905). Stellate germination occurred producing clubbed hyphae, at first within capsules of host tissue, and then normal growth proceeded outside the capsules. A habitat, perhaps hitherto unrecorded, for *Saprolegnia* sp. was recently found while examining yearling trout which had died from acute enteritis in an aquarium in the Zoological Department, University of Cambridge. The fungus had attacked the gills and fins to a moderate extent, but in addition there was a felted mass of mycelium growing on a much disorganized mucosa throughout the whole length of the intestine, but particularly luxuriant in the rectum. The mycelium was producing abundant sporangia, but no sexual stages were found; the whole organ was very much injected but there were no localized pus-sacs.

A similar intestinal trouble has been recorded in a marine fish, *Mugil chelo*, at Banyuls, caused by an *Oscillatoria*-like protophyte, *Anacamptothrix intestinalis* Lavier (1938), which was thought to have affinities with the Schizophyta.

however, there is a close parallel, for the conidia are liberated in the body of the subterranean stages of the insect host, as they are in the fluid and semi-fluid tissues of mackerel, and the radial germination of the conidia in the insect is also very similar. Azygospores are produced by buds from hyphal bodies into which the protoplasm flows (Speare, 1921); a tentative analogy to this may be made by comparing the bud-like outgrowth of protoplasm from the emptied parent hypha (sometimes growing from a hyphal body) which precedes the production of chlamydospores (see Fig. 1).

Ichthyosporidium can therefore be regarded, provisionally, as a fungus belonging to the Entomophthorales, having similarities also with other Phycomycetes. The species of this genus are ill-defined and much of the variety of form may be due only to the influences of the different host fishes, both marine and freshwater; but the degree of resistance put up by individual hosts is now known to be a potent influence in controlling the growth-forms of these parasites. It is most likely that some of the forms from European freshwater fishes will prove to be distinct from the more luxuriantly growing *I. Hoferi* (Plehn & Mulsow) from trout in Germany, and from various marine fishes round British coasts; and these again may be distinct from the marine forms from the American Atlantic. Provisionally, however, all are here regarded as *I. Hoferi*; but in view of the poor development of the type species, *I. gasterophilum*, the present author hesitates to include it in the synonymy.

There is anything but unanimity of opinion on the systematic position of *I. Hoferi*, but perhaps the recent findings strengthen that of Gwynne-Vaughan & Barnes (1937, pp. 147–8), that it is included in Entomophthoraceae.

The present findings throw no light on the relationship of *Ichthyosporidium* and such forms as *Chytridiopsis* (which Debaisieux, 1916, p. 265, thinks is prematurely placed among Chytrids by Léger & Duboscq, 1909), and *Coelomomyces* Keilin (1921), though there is some evidence of flagellospores in both these forms. The mass of felted mycelium in *Coelomomyces stegomyiae* Keilin, which develops over the viscera of the larval culicid host, and the detachment from it of clavate hyphal tips to form definite sporangia with thick pitted walls, is quite unlike anything in *Ichthyosporidium*. The early development of the sporangia in Keilin's species (1921, fig. 5 A–D), showing spheroidal masses with vacuoles and scattered vesicular nuclei, later becoming encapsuled, would, by themselves, have suggested close relationship with the similar bodies in the bodies of fishes described as *Ichthyosporidium* by Robertson (1908, 1909).[1]

[1] The spheroidal forms figured by Robertson and others at once recall *Rhinosporidium*, an internal (and in the early stages intracellular) parasite of mammals. *R. seeberi* (Wernicke, 1900), from nasal polyps of man, as figured by Ashworth (1923) is particularly reminiscent; in the fully grown trophic stage it is spheroidal with a vacuolated protoplasm, large numbers of vesicular nuclei and a double wall, the inner thick one being of cellulose. For this and other reasons listed by Ashworth, it was placed near to the Chytridiaceae. The similarity of

Thus, if too much reliance be placed on the character of the nucleus in such spheroidal masses, occurring alone as parasites, it is easy to be led astray as to their relationships. Jepps (1937, pp. 642–5, fig. 26) identified as *Ichthyosporidium* a rare parasite of the haemocoele of *Calanus finmarchicus*; it occurs as a mycelium with clavate tips, having vesicular nuclei scattered through it, and as she points out, it has much in common with the bouillon cultures obtained by Plehn & Mulsow from *Ichthyosporidium Hoferi* cysts. She advances the attractive hypothesis that *Calanus* may thus act as an intermediate host for the fish parasite; but the identification must, for various reasons mentioned above, be viewed with reserve. Yet it is possible that her identification is correct, and that *Calanus* can act as an occasional reservoir host. But the finding of all apparently essential stages in the mackerel rules out the necessity for an intermediate host in the life cycle. Moreover, its occurrence in *Calanus* is very rare, for though very large numbers of this and similar copepods have been examined by Dr Jepps, and by Dr Lebour over a period of many years, no further infections have been found (personal communications). While examining the stomach contents of mackerel during their copepod feeding phases, none of them was found infected in this way, in spite of the widespread occurrence of the fungus in the mackerel.

It is possible that the entrance of the fungus into mackerel may be facilitated by the perforation of the gut wall by migrating cestode larvae. The fact that cestode cysts accompanied fungus infections in every case affords no supporting evidence, because the former were present in every mackerel examined; also the two often occurred in contact among the viscera, just under the peritoneum. Chlamydospores have been found adherent to the outer cyst wall of tetrarhynchid cestodes, though no certain record was made of their occurrence inside the cestode cysts.

From his records of *Ichthyosporidium Hoferi* in herring (*Clupea harengus*) from the Gulf of Maine, Fish (1934) showed that the maximum infection was found among fish in the shallower, landward waters which they frequent at breeding time; but no such correlation of infection rate and migration could be made for the mackerel. The present data have been analysed in various ways but there is no relationship between infection rate and place of capture, season, age or sex of the fish, though it is possible that extended observations may reveal factors which are significant to the spread of the disease. With this in view, complete records are being deposited in the library of the Marine Biological Association at Plymouth.

It is highly probable that this disease is in a large measure responsible for the widespread unpopularity of mackerel as a food, unless freshly caught.

the fully grown encysted hyphal bodies of *Ichthyosporidium Hoferi* to the cysts of the recently described *Rhinosporidium pulmonale* Kirschenblatt (1939), from the lungs of voles in the U.S.S.R., is also striking. Further investigation, however, shows that there is no thallus development in these mammalian parasites beyond the large spherules, the whole of the thallus becoming differentiated into uninuclear spores with chitinous envelopes (as in *Amoebidium*).

The high food value of this fish is generally accepted, and its fat content is nearly double that of the herring (25·2 and 13·3% respectively, according to Chipman & Langstroth, 1930). Sawyer (1929) investigated the growth in culture of *Entomophthora* spp., and found that the hyphal tips have strong proteolytic enzymes which break down the animal tissues on which they feed; and in insects they penetrate the cuticle (entrance via the intestine was never observed). He proved (pp. 104–7) that while fats and carbohydrates are not essential to the growth of these fungi, proteins are. It is well known, however, that fatty substances accumulate in insects during the growth of these parasites. Even in moderately advanced infections of the mackerel large globules of free fat are found to flow out immediately the kidney is opened, and there is frequently a milky emulsion of fat covering large blood vessels in organs which are infected with non-encapsuled hyphae. The first gross sign of protein decomposition in mackerel, even before its odour becomes offensive, is furnished by the ribs breaking away from the body wall when the venter is slit. Further development of the infection, or post-mortem growth of an originally moderate one, causes the wall of the intestine to be attacked (probably by proteolytic enzymes in solution in the body fluid) and this is soon ruptured, allowing the putrefactive organisms from the lumen to escape and spread, greatly accelerating the general decomposition of the muscles. The presence of a few fish in this state of rapid decay in a barrel will quickly contaminate all the others, not by the direct products of the fungus infection, but secondarily, by their being centres of dissemination of putrefactive bacteria. The remedy is fortunately very simple: splitting and gutting of the fish as soon as possible after they are caught, and subsequently packing them in dry *crushed* ice (the value of which has recently been emphasized for mackerel marketing in the U.S.A. by Stansby & Lemon, 1941). In the process of gutting the fish, any badly infected ones would be at once apparent by the brown sauce-like contents of the body cavity, and could be discarded. The rough removal of the alimentary canal, etc. usually involves the tearing away of a considerable portion of the kidney, so that in this simple process the chief sites of infection are removed, and the mackerel, while being slightly more costly, would be a reliable product of comparatively high keeping quality. The offal should, on no account, be tipped into the sea, as it would form centres of infection for other fish, as was shown by Fish (1934).

Most of this work has been carried on during the tenure of the Keddey Fletcher-Warr Studentship, granted by the University of London; the examination of fishes was done mainly at the Marine Biological Laboratory, Plymouth, where samples were kindly put at my disposal. Much gratitude is due to the Director, Dr Stanley Kemp, F.R.S., for his kind co-operation and encouragement, and for arranging for samples of fish to be sent to Cambridge for the later work; to Dr Marie V. Lebour for her kind assistance in the search for infected copepods, and to Dr Margaret W. Jepps for the

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Summary

A fungus has been found causing a fatal disease among mackerel in British waters, and a very high rate of infection has been maintained for over three years. It is spread throughout the viscera by the circulation, being particularly common in the kidney and spleen: it is very rare in the muscles and has never been found in the gonads or central nervous system of these fish.

Growth of the aseptate, sparsely branched hyphae is usually radial, from one of three types of central body. The length and thickness of the hyphae varies according to the density of the infected tissue and the degree of resistance which is set up. Connective tissue capsules are laid down round spores and hyphal bodies, occluding the small vessels or capillaries in which they become lodged. Growth of the parasite stretches the capsule, which may become a tubular gallery containing many growth stages. This may effectively seal the parasites which then degenerate; or, more usually, the strong proteolytic enzymes secreted by the advancing hyphae perforate it, and proceed to convert the whole organ into a necrotic mass in which hyphae grow to great lengths. There is always a tendency for hyphal walls to collapse behind the outgrowing hyphae, giving the appearance of hair-like threads with swollen ends.

Any of the following developments may occur, apparently on any hypha, in tissue undergoing necrosis: (1) Bunches of large elongated *chlamydospores*, with a very hard exospore and a thick (?) gelatinous endospore—a germination pore is present; (2) Single *dome-shaped conidia* (like those of Entomophthoraceae); (3) *Hyphal bodies* of various shapes, either growing at once where they become lodged or becoming rounded and encysted—these may subdivide irregularly, each spherule having a separate cyst; (4) *Branched conidiophores* with rounded tips which contain *endo-conidia*—liberated as minute amoeboid bodies into the blood vessels; (5) *Simple clavate sporangia* from the ends of unbranched hyphae, also containing *endo-conidia*; (6) *Hyphal fusions* of numerous kinds, immediately proceeding to further outgrowths of similar hyphae; (7) '*Spores produced by hyphal fusion*': fusion of two hyphae followed by the participation of neighbouring hyphae which also contribute to form the outer, resistant, rugose wall.

Form (7) is comparatively light and may be the means of dispersal (by faeces or dead fish) in the plankton; infection is thought to take place through the gut wall, especially through the pyloric caeca. The role of the abundantly

numerous endo-conidia is uncertain. No nuclear division or fusion has been seen in this material. Since growth from the three types of resting body (1), (3) and (7) occurs in the mackerel, no intermediate host is necessary.

Previous descriptions of similar growth forms from freshwater fishes from Europe and from marine fishes from both Europe and America are reviewed; none show the profusion or variety of growth met with in the present investigations on mackerel. Forms (1), (6), (7), and the further development of (4) are described for the first time, as well as some other details of structure.

The affinities with other forms are discussed, and it is decided to regard similar forms from other hosts as provisionally conspecific, and their differences in development as being due to the nature of the hosts—the correct nomenclature being *Ichthyosporidium Hoferi* (Plehn & Mulsow, 1911) Pettit, 1913. The genus is placed in the Entomophthoraceae, but it has similarities with several other Phycomycetes.

The detrimental effect of the disease on mackerel as a commodity is discussed and remedial measures suggested to ensure a higher quality product.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

On the Ciliary Mechanisms and Interrelationships of Lamellibranchs. Part VIII: Notes on Gill Musculature in the Microciliobranchia

By D. Atkins

Quart. Journ. Micr. Sci., Vol. 84, 1943, *pp.* 187–256

In the gill axes of the Microciliobranchia (Arcacea—less the Trigoniidae—Anomiacea, Pteriacea, Pectinacea, and Ostreacea) the most important muscles are longitudinal and transverse. The longitudinal muscles are: (*a*) those extending from one extremity of the gill axis to the other, inserted on the shell anteriorly, and (*b*) those in the free posterior portion of the axis, inserted on the shell where the axis becomes attached. Together these muscles act as branchial retractors. Withdrawal of the gills prevents (*a*) their being caught and crushed by the edges of the shell when the valves are suddenly closed, and (*b*) excessive fouling with sudden intake of muddy or noxious water. The transverse muscles below the chitinous structure arching the axial food groove serve to draw the demibranchs of a gill together, while those above the arch serve to separate them. Such swaying movements of the demibranchs rid them of unwanted material.

In the demibranchs are: (1) muscles of the free edges. These include (*a*) muscles responsible for movements of the walls of the food grooves, and (*b*) longitudinal muscles, which effect antero-posterior contraction and assist the longitudinal muscles of the axis in retraction of the gills; (2) vertical muscles of the demibranchs, found chiefly in the Pteriacea, and responsible for dorso-ventral contraction of the demibranchs; (3) muscles of the interlamellar junctions serving to draw the two lamellae of a demibranch together, expelling the contained water; (4) horizontal muscles of the lamellae, present in forms with plicate and heterorhabdic gills and effecting by their action changes in the shape of the frontal surface of the principal filaments and movements of the plicae important in connexion with the ciliary sorting mechanism; their contraction increases the folding of the lamellae and decreases the length of the gill: and (5) fine muscle fibres forming the intrafilamentar 'septum'. D.A.

The Vitamin C Saturation Test

By W. R. G. Atkins

Brit. Med. Journ., 27 *Feb.*, 1942

Slight changes in the conditions of the Harris and Abbasy test as performed in the Army effected a saving of several weeks in calculations on the examination of 600 soldiers, as compared with an equal number on the earlier

procedure. The period of retention of urine was limited to the fourth and fifth hours after dosing with $\frac{3}{4}$ g. of vitamin. The volume passed was not measured, but was made up to $\frac{1}{2}$ or 1 l., of which 10 ml. was mixed with 1 ml. of acetic acid and 2·2 ml. used for titration. The reagent, 2:6 dichlorophenol indophenol, is best adjusted so that 1·0 ml. corresponds to 0·1 mg. of vitamin C. W.R.G.A.

The Vitamin C Saturation Test of Harrid and Abbasy

By W. R. G. Atkins

Nature, Vol. 151, 1943, *p.* 21

The examination of 1200 men showed the method to be reliable and capable of distinguishing between groups of 100 living under slightly different conditions. The results cannot be disclosed, but the form of the curves obtained is instructive. These were drawn with the number of daily doses required to approach saturation on the vertical axis and the percentage of men who reacted on the horizontal. The distribution obtained shows why some of a ship's company get scurvy and others escape. Saturation is obtained sooner when the vitamin is given after food. Vitamin C is not stored in quantity for long; very little residual effect could be detected four months after saturation. W.R.G.A.

A Note on an Abnormal Specimen of *Elphidium crispum* (L.)

By Arthur Earland and Margaret W. Jepps

Journ. Roy. Micr. Soc. Vol. LXIII, 1943, *pp.* 43–47

An abnormal shell of *Elphidium* (*Polystomella*) *crispum* from Plymouth is figured and designated var.nov. *detorquens*.

The genus *Ozawaia* Cushman, 1931, is superfluous, and should be regarded as a synonym of *Elphidium* Montfort, 1808, in part. Nautiloid specimens have all the typical features of that genus, and the few specimens with final linear chambers should be regarded as variations. So the genotype of *Ozawaia* becomes *Elphidium tongaense* (Cushman), and its var. *ozawaia*.

An account is given of the Millett specimens of *Elphidium* remaining in the Heron-Allen and Earland collection at the British Museum of Natural History, London. M.W.J.

The Giant Myelinated Nerve Fibres of the Prawn

By William Holmes

Phil. Trans. Roy. Soc., B, *Vol.* 231, 1942, *pp.* 293–311

The structure of the giant fibre system in the central nervous system of the prawn *Leander serratus* was examined, using cytological and neurological techniques. Evidence was obtained that the median and lateral giant fibres are syncitial structures, each formed by the fusion of the processes of many segmental nerve cells. The motor giant fibres, on the other hand, are the processes of single cells.

The prawn giant fibres are almost as heavily myelinated as vertebrate nerve fibres of the same diameter and the structure of the prawn axon sheaths shows many significant similarities to that of the sheaths of myelinated fibres in the higher animals.

The contention of Johnson (1924) that the structure of the synapses in the crustacean nervous system is incompatible with current views on the nature of the synaptic transmission mechanism is shown to be unfounded. W.H.

Relative Growth of the European Edible Crab, *Cancer pagurus*: I. Growth of the Carapace

By Donald C. G. MacKay

Growth, Vol. 6, 1942, *pp.* 251–8

This is the first of several papers dealing with form changes in the European edible crab, *Cancer pagurus*. In this paper the relative growth of the carapace is analysed by Huxley's method. An analysis of eight carapace widths from anterior to posterior in relation to carapace length indicates an orderly change in values for the constant k from 0·70 to 1·12. This is found to be in the form of an anterior-posterior gradient in which the low point is at the extreme anterior of the animal. Values for immature individuals are in general slightly higher for the same dimension than are those of mature individuals.

D.C.G.McK.

Relative Growth of the European Edible Crab, *Cancer pagurus*: II. Growth of the Abdomen

By Donald C. G. MacKay

Growth, Vol. 7, 1943, *pp.* 217–26

This is a continuation of the study of form changes in the European edible crab, *Cancer pagurus*. In this paper the widths of six abdominal segments and the telson in relation to carapace length are analysed by the method of

Huxley. The results are based on 4643 measurements and indicate a considerable range of values for the constant k. The widths of all abdominal measurements show positive heterogony, k, varying between 1·07 and 1·50. This is in the form of a gradient lowest at the anterior end of the abdomen and highest in the middle segments. Considered in conjunction with the carapace gradients for the same species it is apparent that the differential growth ratios are higher in the abdomen than in the cephalothorax and that the growth centre is in the middle abdominal segments.

Immature and mature crabs differ in the values of the relative growth constant, mature crabs having a higher k. Changes in form are correlated with the onset of sexual maturity and probably are causally related thereto. In general females are found to have a higher k for the abdominal segments than males. This is accentuated after sexual maturity by an increase in the differential growth ratio in females and a decrease in males.

Very few crabs of this species were found to be parasitized by *Sacculina*.

D.C.G.McK.

A Quantitative Study of the Productivity of the Foraminifera in the Sea

By Earl H. Myers

Proc. Amer. Phil. Soc., Vol. 85, 1942, *pp.* 325–42

Samples of populations of the foraminifer *Elphidium crispum* Linnaeus numbering from 500 to 1000 individuals were taken both in the littoral and sublittoral zones of Plymouth Sound at intervals of one month for 12 consecutive months. Percentage frequency distribution curves based on the number of chambers in the tests as determined from protoplasmic casts revealed that the life span in tide pools is usually 1 year, and the life cycle including a sexual and an asexual phase 2 years, while below low-tide level 2, 3 or even 4 years are required. Growth is limited to the spring and summer months and the rate of growth is 40% greater and the diameter of the test 60% larger in the sublittoral zone. Sexual and asexual reproduction as determined from the presence of juvenile individuals in the samples and cytological evidence of gametogenesis are limited to March and April, although some asexual reproduction takes place in the sublittoral zone in September. From the number of megalospheric juveniles produced in cultures and the ratio of microspheric to megalospheric individuals in the sea it was determined that the annual rate of increase is about thirtyfold and fortyfold in the littoral and sublittoral zones respectively. Populations well in excess of 1000 individuals per sq. ft. were observed at a number of stations. In a

later paper an attempt will be made to correlate these observations on the sequence of events in the life activities of this species with measurable ecological conditions in the sea. E.H.M.

The Effect of Wave-length on the Relation Between the Intensity of Illumination and the Current in Selenium Rectifier Photo-cells

By H. H. Poole and W. R. G. Atkins

Sci. Proc. Roy. Dublin Soc., Vol. 22, 1941, *pp.* 395–400

Fall in sensitivity with increasing illumination is greater for wave-lengths exceeding 6600 A. than for those shorter. With increase in resistance the resultant relative fall in current for a given illumination is a function of the zero-resistance current only and is independent of the wave-length. The decreased sensitivity found in deep red light is therefore not due to increased leakage of current in the cell, as this would be greater with large external resistance. The effect may be due to the occurrence of a threshold for the selenium cell in the neighbourhood of 6600 A. W.R.G.A.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1942–43

Dr E. J. Allen.

By the death of Dr E. J. Allen, which occurred suddenly on December 7, the Association has been deprived not only of one of its oldest and most distinguished members, but of a man to whom more than to any other it owes the growth and prosperity of the Plymouth Laboratory. Throughout the greater part of his life Dr Allen's interests were concentrated on the Laboratory and the encouragement of marine research, and it was his devotion and enthusiasm during his 42 years' service as Director which carried the Association through its many early difficulties to the success of later years. So long as the Plymouth Laboratory stands his name will be remembered with affection and gratitude.

The Council and Officers.

During the year Mr H. G. Maurice has been appointed a Governor of the Association, representing the Zoological Society of London, in succession to the late Prof. E. W. MacBride.

Four ordinary meetings of Council were held during the year. Three of these were held in the rooms of the Royal Society and the thanks of the Association are due to the Society for the continuance of this privilege. One meeting, on May 2, was held at the Plymouth Laboratory. The average attendance at the four meetings was 15.

The Plymouth Laboratory.

Plans for the restoration of the Laboratory premises have been carried further during the year, and at the January meeting of Council a Building Committee, consisting of the Chairman of Council, Mr A. T. A. Dobson, Dr C. F. A. Pantin, Prof. C. M. Yonge, Mr A. Thorpe (Architect to the Ministry of Agriculture and Fisheries) and the Secretary, was appointed.

When the war ends the Association will be faced with two urgent necessities: the restoration of the Tank Room to avoid the loss of further income from this source and the reconstruction of the Easter Class Room. Very few improvements have been made in the Tank Room since it was originally built; the lighting is most defective and in many other ways the installation is out-of-date. Heavy damage was done during the air-raids of 1941, and the Council considers that when the war ends the room should be refitted on modern lines. Detailed plans, which include better lighting arrangements, service passages behind the

tanks, an improved entrance hall and the provision of public lavatories, have been prepared by Mr D. P. Wilson.

Although accommodation for the Easter Class will be needed immediately at the end of the war it has been necessary to plan the reconstruction of the whole of the eastern end of the laboratory premises, for the Director's house with the out-buildings behind it has been completely destroyed and part of the North Building has been badly shaken and must be rebuilt. The Council discussed at three of its meetings whether the house for the Director should be reconstructed, or whether it would be preferable for the Director to live away, and to use the whole of the site for laboratories. At their meeting in October Council decided to adopt the latter course. The preliminary plans which have been prepared provide for a block of buildings linking the main Laboratory with the North Building at the eastern end; on the ground floor there are fishery laboratories and a new and enlarged Easter Class Room, with cloak-rooms and lavatories, and on the first floor the Director's office and other laboratories.

War Damage Compensation.

During the year the Association has received payments from the War Damage Commission to cover the cost of the emergency repairs carried out at the Laboratory. Agreement has also been reached with the Board of Trade on the sum payable as compensation for movable property which was damaged or destroyed: the amount will be paid later, with interest at $2\frac{1}{2}$ % from March 1941. It has not yet been possible to ascertain what compensation will ultimately be paid by the War Damage Commission in respect of damaged or destroyed buildings.

The Ship and Motor Boat.

The *Salpa* remains under requisition by the Admiralty. The motor-boat *Gammarus* has continued her work over restricted areas.

The Staff.

When Dr W. R. G. Atkins joined the R.A.M.C. in 1941 it was understood that he would be placed in charge of a mobile hygiene laboratory. This was, however, later found to be impossible, and after a time spent on other work, during which he was promoted to Captain, Dr Atkins resigned his commission in August 1942, and returned to Plymouth. He has since accepted a special research appointment in the Meteorological Office.

Mr G. A. Steven has been released from service in the R.N.V.R. to take up a temporary appointment as Fishery Development Officer, Sierra Leone. Mr F. S. Russell has now been promoted to Wing Commander in the R.A.F.V.R. and Mr E. Ford to Flying Officer.

Dr H. W. Harvey has accepted an invitation to join the Marine Corrosion Sub-Committee of the Iron and Steel Institute of which Dr Atkins is already a member.

Mr B. G. Wilson, accountant, resigned from the service of the Association on 14 March 1942. His place has been filled by the appointment of Mrs M. V. Cocker.

Occupation of Tables.

The following have occupied tables at the Plymouth Laboratory during the year:

Miss M. E. BENNETT, London (Algae).
Dr S. P. CHU, Ray Lankester Investigator (Nutritional requirements of Phytoplankton).
L. R. CRAWSHAY, Plymouth (Sponges).
G. H. DAGLISH, Plymouth (General Physiology).
Dr V. FRETTER, London (Opisthobranchia).
Dr M. W. JEPPS, Glasgow (Foraminifera).
Dr M. KNIGHT, Liverpool (Algae).
A. G. LOWNDES, Plymouth (Density of aquatic organisms).
Dr M. PARKE and Miss E. CLAY (Algae).
Miss N. G. SPROSTON (Parasites of fishes).
Prof. T. A. STEPHENSON (Littoral fauna).

No vacation courses were held during the year, but Mr A. N. Lewis brought three boys from Wellington College and Mr A. G. Lowndes four boys from Dorchester Grammar School to study marine biology. Visits were also paid to the Laboratory by Mr A. Gillespie with boys from Blundell's School, by Prof. C. Singer with boys from Par and by Mr H. P. Ramage with boys from Gresham's School.

On 26 August Sir John Graham Kerr, Chairman of the Advisory Committee of the Development Commission, paid a visit to Plymouth and inspected the Laboratory.

Special Research.

During the year the Director has again been consulted by the Colonial Office on fishery problems in different parts of the Empire. Measures to counter war-time difficulties in the West Indies and in West Africa (to which Mr G. A. Steven has now been seconded) have been taken, and in October he was invited to discuss fishery questions with the Colonial Research Committee. The Council is glad to learn that plans for post-war research and development in colonial fisheries are now beginning to take shape.

Research on brown algae, undertaken on behalf of Government, has continued throughout the year. The biological work, in which Dr M. Parke is now assisted by Miss E. Clay, had made good progress; the experiments which are being conducted at Wembury and on the west coast of Scotland are yielding substantial additions to our knowledge, both in the life histories of the common species and in their capacity to regenerate after cutting. Among the Laminarias it has been found that *L. saccharina* fruits in the summer,

L. Cloustoni in the winter, while *L. digitata* can be found fruiting from April to November, with pronounced maxima in spring and autumn. Dr Parke is collaborating with Dr M. Knight, who is carrying out similar experiments in the Isle of Man, and during the year they drew up an interim report on the progress of the work.

The surveys of brown algae, mentioned in last year's Report, which were being made for the Association by Dr V. J. Chapman and a party from the School of Botany at Cambridge, were completed during the year. Work in the field was carried out with the greatest energy, and the results sought were obtained in an unexpectedly short time. An interesting feature of the surveys was the use of a shallow-water echo-sounding machine to determine the extent of beds of algae lying beyond low-water mark. The Council wishes to express its thanks to Dr Chapman and his associates for the very useful work they have accomplished.

During the year the Association, at the request of a number of industrial firms and organizations, has undertaken further tests on the durability of materials used for service requirements under exposure to sea water. At no time in the history of the Laboratory has this work approached its present dimensions.

Scientific Work of the Laboratory Staff.

After his return to Plymouth in August, Dr W. R. G. Atkins was occupied with matters arising out of his membership of the Corrosion Sub-Committee of the Iron and Steel Institute, which deals with the fouling of ships, and of the Sandbag Committee of the Research and Experiments Department of the Ministry of Home Security. He has also given further attention to the preservation of ropes and is preparing for publication work upon the biological effects of daylight.

Dr H. W. Harvey has completed the manuscript of a book on the chemistry and biology of sea water which includes a detailed survey of recent investigations concerning the productivity of the sea. He has also carried out experimental work on copper in sea water and on the settlement and growth of marine organisms on surfaces coated with copper soaps; close contact has been maintained with the investigations in progress at Millport by the Iron and Steel Institute on the fouling of ships' bottoms.

Miss Lebour has completed a paper, shortly to be published in the Association's *Journal*, dealing with the larvae of the two species of *Porcellana* common at Plymouth, *P. longicornis* and *P. platycheles*, and comparing them with *Petrolisthes armatus* from Bermuda. All these were hatched from the egg. The work includes a summary of our knowledge of porcellanid larvae up to date. For the first time all the principal larval stages and the post-larva of the two British species have been obtained by moult. This was made possible by the examination of plankton samples from inshore. Under present conditions tow-nettings cannot be taken outside the Breakwater, and a more

detailed study than is usual was therefore made of the inshore plankton, in which the larvae of both species of *Porcellana* occur. It has been found that the late larvae can be separated easily by the number of pleopods, *P. longicornis* having three pairs and *P. platycheles* four.

The general inshore plankton has been closely studied, especially for decapod and mollusc larvae, and the breeding seasons of species of many groups have been ascertained. Some formerly regarded as rare in the district have proved to be abundant. For instance, *Oithona nana* is found to be very common and breeding freely in winter. Interesting finds include the larva of a second species of *Polygordius*, *P. appendiculata*, and a brackish-water cladoceran, probably *Bosmina maritima*, not previously recorded from the Plymouth area. A regular record of the inshore plankton has been kept, with a few unavoidable interruptions, for over two years. In these records it has been found possible to identify specifically all the decapod larvae and a large number of molluscan and annelid larvae.

Experiments on chromatophores of the larvae of the annelid *Poecilochaetus serpens* were undertaken, and a note on the subject has been published in *Nature*. By keeping the larvae in the dark it was proved that the stellate chromatophores possessed by these larvae became contractile and comparable with those of the leech.

The *Nitzschia closterium* cultures kept by Mr D. P. Wilson have continued to yield interesting details on the variability in form of this diatom. A letter to *Nature*, written jointly with Dr C. E. Lucas, recorded a striking similarity in the behaviour of cultures kept respectively at Plymouth and at Hull. Since the period covered by the letter a close watch has been kept on the Plymouth cultures, and these later data, together with the earlier and with some figures obtained by examination of material previously preserved, strongly suggests that there is a maximal tendency for triradiate forms to change over to the normal during the late autumn.

Throughout the oyster-rearing season Mr Wilson again advised Mr Kingcome at Steer Point on maintaining the water in his rearing tanks in a suitable condition. Many batches of larvae were liberated, but only a relatively small spat-fall was obtained, although larger than in 1941. As only one tank can be used for rearing, little work of an experimental nature is possible at Steer Point, and it is only practicable to follow as closely as possible the principles employed at Conway.

Reports on the biological condition of many of the samples of material under test in Plymouth Sound are now regularly made by Mr D. P. Wilson. The identification of the organisms involved in fouling is frequently of importance, especially perhaps with textiles where disintegration may be greatly accelerated by burrowing or nest-building animals.

Mrs Sexton has been working on the results of breeding experiments with the amphipod *Jassa falcata* (Montagu). This is a species which undergoes many changes of form during growth, particularly in the hand of the second

gnathopod, culminating in striking differences in the full-grown males. This has caused much confusion, various authors having given specific status to practically each developmental stage. But already, from the matings in the laboratory, proof has been obtained that at least several, and probably all of these so-called 'species', are only the growth periods of the young males, from sexual maturity to the 'definitive adult' stage.

The Library.

The library has remained in store outside Plymouth during the year under review. Before the war two important serial publications, the *Annals and Magazine of Natural History* and the *Annales des Sciences Naturelles*, frequently needed in the work of the Laboratory, were borrowed from the library of the Athenaeum in Plymouth, where complete sets of both were available. This library was, however, destroyed in the air-raids of 1941. During the year a set of the *Annals and Magazine of Natural History*, complete up to 1932, has been purchased, and a set of the *Irish Naturalist* has also been obtained, together with a small number of recent books.

The thanks of the Association are due to those institutions and authors who have given books or papers to the library. Sir Sidney Harmer has generously presented forty-five volumes of the *Geographical Journal*, and the Museum of Comparative Zoology at Harvard has very kindly replaced an early volume of the *Bulletin*, which happened to be out of the library and was destroyed in the air-raids. Four books on Tunicata, a monograph and three volumes of reprints, have been presented by Dr John Gurney.

Published Memoirs.

Vol. XXV, No. 3, of the *Journal* of the Association was published in October 1942.

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., 1943. Vitamin C saturation test of Harris and Abbasy. *Nature*, Vol. 151, p. 21.

ATKINS, W. R. G., 1943. The vitamin C saturation test. *Brit. Med. Journ.*, 27 Feb. 1943.

HOLMES, W., 1942. The giant myelinated nerve fibres of the Prawn. *Phil. Trans. Roy. Soc.*, B, Vol. 231, pp. 293–311.

HOWELLS, H. H., 1942. The structure and function of the alimentary canal of *Aplysia punctata*. *Quart. Journ. Micr. Sci.*, Vol. LXXXIII, pp. 357–97.

LEBOUR, M. V., 1942. Stellate chromatophores in the Polychaeta. *Nature*, Vol. 150, pp. 209–10.

LOWNDES, A. G., 1942. Percentage of water in jelly-fish. *Nature*, Vol. 150, pp. 234–5.

LOWNDES, A. G., 1942. Rapid determination of fat in animals and plants. *Nature*, Vol. 150, p. 291.

LOWNDES, A. G., 1942. Ciliary movement and the density of *Pleurobrachia*. *Nature*, Vol. 150, pp. 579–80.

LOWNDES, A. G., 1943. Water content of Medusae. *Nature*, Vol. 151, p. 226.

LOWNDES, A. G., 1943. Density of crabs and lobsters. *Nature*, Vol. 151, p. 336.

MACKAY, DONALD C. G., 1942. Relative growth of the European edible crab, *Cancer pagurus*. I. Growth of the carapace. *Growth*, Vol. VI, pp. 251–8.

MYERS, EARL H., 1942. A quantitative study of the productivity of the Foraminifera in the sea. *Proc. Amer. Micr. Soc.*, Vol. LXXXV, pp. 325–42.

PANTIN, C. F. A., 1942. The excitation of nematocysts. *Journ. Exp. Biol.*, Vol. XIX, pp. 294–310.

POOLE, H. H. & ATKINS, W. R. G., 1941. The effect of wave-length on the relation between the intensity of illumination and the current in selenium rectifier photocells. *Sci. Proc. Roy. Dublin Soc.*, Vol. 22, pp. 395–400.

ROTHSCHILD, MIRIAM, 1941. Observations on the growth and trematode infections of *Peringia ulvae* (Pennant), 1777, in a pool in the Tamar Saltings, Plymouth. *Parasitology*, Vol. XXXIII, pp. 406–15.

ROTHSCHILD, MIRIAM, 1941. The metacercaria of a Pleurolophocerca cercaria parasitizing *Peringia ulvae* (Pennant), 1777. *Parasitology*, Vol. XXXIII, pp. 439–44.

ROTHSCHILD, MIRIAM, 1941. Note on life-histories of the Genus *Paramonostomum* Lühe 1909 (Trematoda Notocotylidae) with special reference to the excretory vesicle. *Journ. of Parasitol.*, Vol. XXVII, pp. 363–5.

ROTHSCHILD, MIRIAM, 1942. A further note on life-history experiments with *Cryptocotyle lingua* (Creplin, 1825). *Journ. of Parasitol.*, Vol. XXVIII, pp. 91–2.

ROTHSCHILD, MIRIAM, 1942. A seven-year-old infection of *Cryptocotyle lingua* Creplin in the winkle *Littorina littorea* L. *Journ. of Parasitol.*, Vol. XXVIII, p. 350.

ROTHSCHILD, MIRIAM, 1942. A note on immunity reaction in the black-headed gull (*Larus ridibundus*) infected with *Maritrema oocysta* Lebour 1907. *Journ. of Parasitol.*, Vol. XXVIII, pp. 423–4.

ROTHSCHILD, MIRIAM & SPROSTON, NORA G., 1941. The metacercaria of *Cercaria doricha* Roths. 1934, or a closely related species. *Parasitology*, Vol. XXXIII, pp. 359–62.

THOMAS, H. W. & HARVEY, H. W., 1943. Absorption of iron. *Brit. Med. Journ.*, p. 83.

Membership of the Association.

There have been no changes in the list of Vice-Presidents. The number of Associate members is now 8, Mr H. E. Hurrell of Yarmouth having died during the year. The total number of annual members on 31 March 1943 was 309, compared with 312 at the corresponding date in 1942. During the year one life member was elected and two members compounded for their annual subscriptions. The number of life members at the end of the year was 53.

Finance.

Grant from the Development Fund. The Council has again to express its thanks to the Development Commissioners for their continued support of the Plymouth Laboratory.

Private Income. The Council gratefully acknowledges the following generous grants for the year:

From the Fishmongers' Company (£600), the Royal Society (£50), Magdalen College, Oxford (£25), and the Cornwall Sea Fisheries Committee (£10). The following sums have also been received as rentals of tables in the Laboratory: The Universities of Cambridge (£105), London (£105), Bristol (£25), Birmingham (£15. 15*s.*), Manchester (£10. 10*s.*), Leeds (£10. 10*s.*), Sheffield (£5); the British Association (£50), the Physiological Society (£30), and the Ray Lankester Fund (£20).

President, Vice-Presidents, Officers and Council.

The following is the list of those proposed by the Council for election for the year 1943–44.

President

G. P. BIDDER, Sc.D.

Vice-Presidents

The Earl of STRADBROKE, K.C.M.G., C.B., C.V.O.
The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS WATERHOUSE, K.B.E.
The Lord MOYNE, P.C., D.S.O.
Sir SIDNEY HARMER, K.B.E., Sc.D., F.R.S.
Sir P. CHALMERS MITCHELL, Kt., C.B.E., D.Sc., F.R.S.
Col. E. T. PEEL, D.S.O., M.C.
Lord MILDMAY OF FLETE, P.C.
Col. Right Hon. Sir REGINALD DORMAN-SMITH, M.P.
Sir JOSEPH BARCROFT, Kt., C.B.E., F.R.S.
Prof. J. STANLEY GARDINER, F.R.S.
Prof. WALTER GARSTANG, D.Sc.

COUNCIL

To retire in 1944

C. F. A. PANTIN, Sc.D., F.R.S.
Prof. T. A. STEPHENSON, D.Sc.
Prof. W. M. TATTERSALL, D.Sc.
Prof. C. M. YONGE, D.Sc.
J. Z. YOUNG

To retire in 1945

Prof. A. V. Hill, O.B.E., Sc.D., Sec.R.S., M.P.
Prof. H. GRAHAM CANNON, Sc.D. F.R.S.
The Hon. MIRIAM ROTHSCHILD
C. FORSTER-COOPER, M.A., Sc.D., F.R.S.
Prof. A. C. HARDY, D.Sc., F.R.S.

To retire in 1946

Prof. F. E. FRITSCH, D.Sc., F.R.S.
MORLEY H. NEALE
Miss MARGERY KNIGHT, D.Sc.
MICHAEL GRAHAM
J. E. SMITH, PH.D.

Chairman of Council

Prof. JAMES GRAY, M.C., Sc.D., F.R.S.

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 71 Park Street, London, W. 1

Secretary

STANLEY KEMP, Sc.D., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
The Lord MOYNE, P.C., D.S.O.
A. T. A. DOBSON, C.B., C.V.O., C.B.E. (Ministry of Agriculture & Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.
Major E. G. CHRISTIE-MILLER
Prof. E. S. GOODRICH, D.Sc., F.R.S. (Oxford University)
Prof. J. GRAY, M.C., Sc.D., F.R.S. (Cambridge University)
Sir P. CHALMERS MITCHELL, Kt., C.B.E., D.Sc., F.R.S. (British Association)
H. G. MAURICE, C.B. (Zoological Society)
Sir SIDNEY HARMER, K.B.E., Sc.D., F.R.S. (Royal Society)

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1943

	£	s.	d.	£	s.	d.
SUNDRY CREDITORS:						
Accrued Expenses	97	9	2			
Subscriptions received in advance	25	3	0			
Grant received in advance	150	0	0			
				272	12	2
AQUARIUM GUIDE PRINTING FUND:						
As at 31st March 1942				22	1	6
SPECIAL APPARATUS FUND:						
As at 31st March 1942				10	4	11
MACKEREL RESEARCH FUND:						
As at 31st March 1942	40	8	5			
Less: Expenditure	1	0	7			
				39	7	10
ALGAL RESOURCES SURVEY FUND:						
As at 31st March 1942	188	4	0			
Add: Transfer from Biological Investigations in Algae	22	10	5			
Grant Received	1677	0	4			
	1887	14	9			
Less: Expenditure £1798 17 6						
Remuneration credited to Income and Expenditure Account 88 17 3						
	1887	14	9			
				0	0	0
E. T. BROWNE BEQUESTS FUNDS:						
Building Fund, as at 31st March 1942 ... ... £1082 9 7						
Interest on Investment 33 0 6						
Income Tax Recovered ... 6 14 11						
	1122	5	0			
Library Fund, as at 31st March 1942 ... ... £1062 8 11						
Interest on Investment 32 8 4						
Income Tax Recovered ... 6 12 5						
£1101 9 8						
Less: Expenditure 110 0 0						
	991	9	8			
Special Apparatus Fund, as at 31st March 1942 ... ... £2174 12 5						
Interest on Investment 66 5 8						
Income Tax Recovered ... 13 4 9						
	2254	2	10			
Scientific Publications Fund, as at 31st March 1942 ... ... £1630 19 3						
Interest on Investment 49 14 0						
Income Tax Recovered ... 9 18 7						
	1690	11	10			
				6058	9	4

	£	s.	d.	£	s.	d.
BOATS AND EQUIPMENT, at valuation as estimated by the Director as at 31st March 1941:						
S/S "Salpa"	2000	0	0			
Motor Boat "Gammarus"	100	0	0			
Nets, Gear and General Equipment	30	0	0			
				2130	0	0
LABORATORY APPARATUS, ENGINES AND PUMPS, at valuation as estimated by the Director as at 31st March 1941	4000	0	0			
Addition during the year	50	0	0			
				4050	0	0
LIBRARY, at valuation of Mr Ridgill Trout in January 1941	15750	0	0			
Additions during the year	250	0	0			
				16000	0	0
STOCKS ON HAND, as valued by the Director:						
Specimens	950	0	0			
Chemicals	150	0	0			
Journals	400	0	0			
				1500	0	0
SUNDRY DEBTORS:						
Sales of Specimens and Journals	199	3	7			
Ministry of War Transport—Hire of S/S "Salpa"	67	0	0			
				266	3	7
PREPAYMENT				16	14	10
GENERAL FUND INVESTMENT, at market value as at 31st March 1931:						
£352. 2*s.* 3*d.* Local Loans 3% ... ... (Market value at date £339. 15*s.* 9*d.*)				232	7	10
E. T. BROWNE BEQUEST FUNDS INVESTMENT, at cost:						
£6152. 5*s.* 8*d.* Conversion Loan 3% ... ... (Market value at date £6321. 9*s.* 5*d.*)				6058	9	4
"SALPA" DEPRECIATION FUND INVESTMENTS, at cost:						
£590. 6*s.* 0*d.* Local Loans 3%	506	10	9			
£3637. 16*s.* 11*d.* Conversion Loan 3%	3697	16	9			
(Market value at date £4307. 10*s.* 6*d.*)				4204	7	6
REPAIRS AND RENOVATIONS FUND INVESTMENT, at cost:						
£362. 9*s.* 10*d.* Conversion Loan 3% ... ... (Market value at date £372. 9*s.* 3*d.*)				369	12	10
COMPOSITION FEES FUND INVESTMENTS, at cost:						
£18. 8*s.* 6*d.* Local Loans 3%	15	15	0			
£231. 10*s.* 6*d.* Conversion Loan 3%	236	5	0			
(Market value at date £255. 13*s.* 5*d.*)				252	0	0
CASH AT BANK AND IN HAND:						
Coutts & Company	1197	2	5			
Lloyds Bank Limited	192	13	10			
Cash in Hand	27	3	2			
				1416	19	5

"SALPA" DEPRECIATION FUND:									
As at 31st March 1942			3742	10	3				
Add: Amount receivable from Ministry of War Transport on account of Hire			402	0	0				
Interest on Investments			111	8	10				
Income Tax Recovered			15	8	5				
						4271	7	6	
REPAIRS AND RENOVATIONS FUND:									
As at 31st March 1942			312	16	3				
Add: Transfer from Income and Expenditure Account			50	0	0				
Interest on Investment			7	13	11				
Income Tax Recovered				12	11				
			371	3	1				
Less: Transfer to Income and Expenditure Account			54	3	2				
						316	19	11	
COMPOSITION FEES FUND:									
As at 31st March 1942			220	10	0				
Add: Fees Received			31	10	0				
						252	0	0	
CAPITAL RESERVE ACCOUNT:									
As at 31st March 1942, arising out of revaluation of Library and other assets as at 31st March 1941			17311	8	2				
Add: Transfer from Surplus Account in respect of valuation of fixed assets as at 31st March 1931			4377	0	0				
						21688	8	2	
SURPLUS:									
As at 31st March 1942			7120	14	4				
Less: Transfer to Capital Reserve Account ...			4377	0	0				
			2743	14	4				
Add: Surplus for the year as per Income and Expenditure Account			849	2	1				
						3592	16	5	
						£36,524	7	9	

	£	s.	d.			
M. Parke Fund:						
As at 31st March 1942	4	8	10			
Expenditure	300	12	10			
	305	1	8			
Less: Amounts Recovered ...	293	1	0			
				12	0	8
Biological Investigations in Algae:						
As at 31st March 1942	67	14	0			
Add: Transfer from Algal Resources Survey Fund ...	22	10	5			
Expenditure	994	6	8			
	1084	11	1			
Less: Amounts Recovered ...	1068	19	4			
				15	11	9
						27 12 5
						£36,524 7 9

L. A. HARVEY
STANLEY KEMP } *Members of Council.*

TO THE MEMBERS OF THE 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 1943 according to the best of our information and the explanations given to us and as shown by the books of the Association.

Shinners Bridge, Totnes, S. Devon.
18th May, 1943.

PRICE, WATERHOUSE & CO.

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 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. Marine animals and plants are supplied to educational institutions and at the close of the war arrangements will be made for the resumption of the courses for advanced students formerly held at Easter and in September.

Research work at sea is undertaken by a motor boat, and, in normal times, by a steam drifter, 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.; and have access to the books in the Library at Plymouth.

All correspondence should be addressed to the Director, The Laboratory, Citadel Hill, Plymouth.

CONTENTS

The Council of the Marine Biological Association wish it to be understood that they do not accept responsibility for statements published in this *Journal* excepting when those statements are contained in an official report of the Council.

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