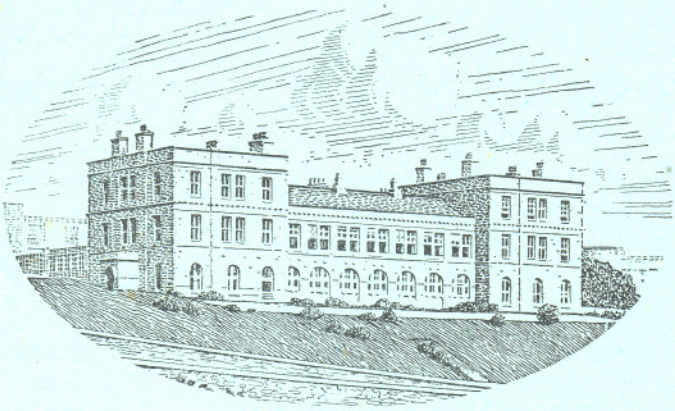
JOURNAL OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM



THE PLYMOUTH LABORATORY

VOLUME XXXI, No. 2

(issued October 1952)

CAMBRIDGE
AT THE UNIVERSITY PRESS
1952

Price Thirty-three Shillings net

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A PHOTOGRAPHIC SURVEY OF CERTAIN AREAS OF SEA FLOOR NEAR PLYMOUTH

By H. G. Vevers, M.A., D.Phil.
Zoologist at the Plymouth Laboratory

(Plate I and Text-figs. 1–2)

Introduction

The present work is a continuation of that carried out in the period July 1949–October 1950 (Vevers, 1951). The underwater photographic apparatus has been modified and improved; the main changes are (*a*) the lamps are now carried on a tubular metal semicircle instead of on a ring of strip metal, (*b*) the bottom of the pole is bent at an angle to the main pole, and (*c*) an improved junction box fixed above the foot switch allows the main electrical cable to be detached completely from the remainder of the apparatus. These modifications can be seen in Text-fig. 1.

The apparatus is still capable of taking a series of photographs, each 1 m.^{2} in area or less, and in the present work the camera has actually been set at a distance of 1 m. from the ground so that each picture covers an area of $\frac{1}{4}$ m.^{2} (50 × 50 cm.). This lower position of the camera is also shown in Text-fig. 1.

There is no doubt that with the camera in this lower position (1 m. from the ground) the definition of the photographs is greatly improved. This may be partly due to a reduction in the absolute amount of suspended particulate matter between the camera lens and the object.

The length of pole above the camera (in its lower position) might appear to be unnecessary, but in practice it has been found that this helps in steadying the whole apparatus when submerged.

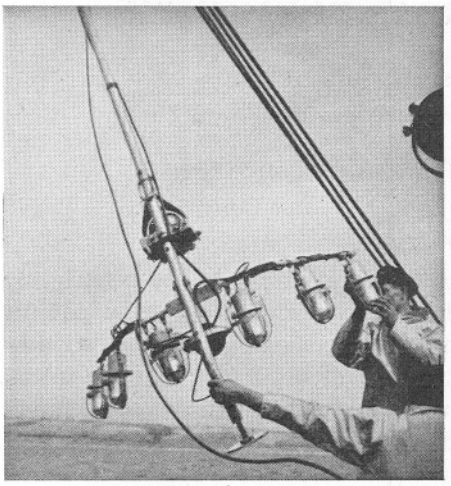
In the previous work, using this apparatus, photographs were taken in four distinct areas near Plymouth, namely:

(*a*) Near Station L4, muddy sand with gravel patches, 55 m.
(*b*) South and south-west of Eddystone, 2–4 miles, clean sand, 70 m.
(*c*) South-east of Looe Island, muddy sand and gravel, 50 m.
(*d*) South-west of Looe Island, muddy sand and gravel, 54 m.

No further work has yet been done in areas (*b*) and (*c*), but additional series of photographs have been taken in areas (*a*) and (*d*). Photographs have also been taken in two new areas:

(i) South-west of Rame Head, 2–3 miles.
(ii) North-west of Eddystone, $\frac{3}{4}$ mile.

The results obtained during the period November 1950 to August 1951 are given below.



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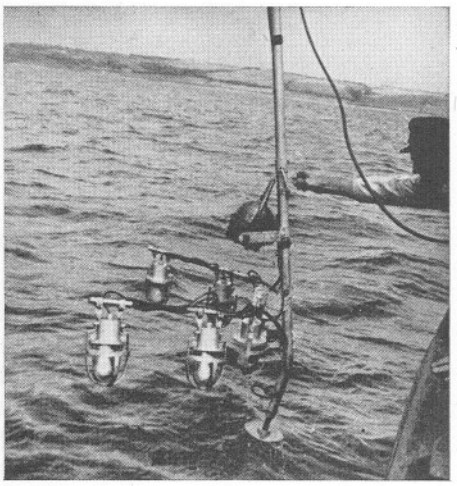

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Text-fig. 1. Underwater photographic apparatus hoisted over side of R.V. *Sabella*, showing new arrangement of photoflood lamps.

Text-fig. 2. Lowering the apparatus into the water. The camera case is in the lower position, to take a series of $\frac{1}{4}$ m.^{2} photographs of the sea bottom.

Area South-west of Rame Head, 2–3 Miles, Depth 50 m.

A total of 167 photographs, each $\frac{1}{4}$ m.^{2} in area, were taken along the transect Rame Head: 058°T., distance 2·2′; 058°T., 2·8′; 050°T., 3·5′. On two photographs there were 17 empty *Turritella* shells (9 on one and 8 on the other), but there were no living epifaunal animals in any of the pictures. The bottom was soft mud, and in many of the photographs the surface showed slight but distinct ripple marks. The area is known locally as the Rame Mud and the characteristic fauna normally dredged there consists almost entirely of burrowing forms (*Cucumaria elongata*, *Psammosolen* (*Azor*) *chamasolen*, *Melinna palmata*). It is therefore not surprising that epifaunal animals should be more or less absent from this area.

Area of Station L4

The new series of photographs in this area were taken along the following transects:

24. xi. 50. Penlee Point: 029°T., 4·9′; 033°T., 4·8′; 037°T., 4·8′; 039°T., 5·0′; 043°T., 4·7′; 044°T., 4·7′.
15. ii. 51. Penlee Point: 030°T., 4·9′; 035°T., 5·2′; 040°T., 5·2′; 050°T., 3·5′.
26. iv. 51. Looe Island; 310°T., 6·3′; 309°T., 6·6′; 309°T., 6·8′.

Transect of 24 *November* 1950. Six films were taken, of which the first four were very close to one of the previous transects in this area (24 August 1949) (Vevers, 1951, p. 105). These four films showed a uniformly poor fauna, similar to that already recorded for this area. A detailed count of the epifauna on 121 interpreted photographs (covering a total area of 30 m.^{2}) gave the following figures: 9 *Ophiura texturata*, 3 *Asterias rubens*, 2 *Marthasterias glacialis*, 2 *Chlamys opercularis*, and a single specimen each of a hydroid, a burrowing anemone and *Trigla* sp. There were also three distinct tracks, probably made by an animal dragging its body along the surface of the bottom.

The first half of the fifth film showed the same type of poor epifauna, but at a point about $\frac{1}{4}$ mile north of the previous transect (24 August 1949) the nature of the fauna changed without any visible corresponding change in the nature of the bottom. In the last half of this film and in the first half of the

TABLE I

Film	Total of $\frac{1}{4}$ m.^{2} frames interpreted	Total of $\frac{1}{4}$ m.^{2} frames with *O. fragilis*	Total number of *O. fragilis*
I	29	—	—
II	23	1	3
III	31	2	16
IV	21	5	35
V	36	27	436
VI	30	—	—

sixth film nearly every frame showed crowded *Ophiothrix fragilis*. In thirty-one interpreted frames (each $\frac{1}{4}$ m.^{2}) there were 547 *O. fragilis* and 2 *Ophiocomina nigra*, giving a mean density of 70 brittle-stars per m.^{2}. In the second half of the sixth film there were only four frames showing *Ophiothrix fragilis*. All six films in this area showed a bottom of muddy sand with gravel, but it is probable that the last few photographs of the sixth were taken near the southern edge of the Rame Mud as they showed patches of bottom with empty shells of *Dentalium* and *Turritella*.

Transect of 15 *February* 1951. Six films were taken, five of them to the south of the transect of 24 August 1949, and the sixth film to the north. Here again, the majority of the 170 $\frac{1}{4}$ m.^{2} frames interpreted showed only a poor fauna. The total numbers of epifaunal animals, excluding *Ophiothrix fragilis*, in this part of the area were: 6 *Ophiura texturata*, 1 *Marthasterias glacialis*, 3 *Asterias rubens*, 4 *Chlamys opercularis*, 1 *Pecten maximus*, 12 *Eupagurus prideauxi*, 1 *Portunus* sp., 1 burrowing anemone and 14 clumps of *Cellaria* sp. This transect has also cut across a dense population of *Ophiothrix fragilis*, whose distribution is given in Table I.

The group of brittle-stars found on this transect is only $\frac{3}{4}$ mile west of the population photographed in the transect of 24 November 1950, and it is probable that both samples belong to the same large aggregation. Both these

groups of *O. fragilis* (transects of 24 November 1950 and 15 February 1951) did, in fact, occur in the neighbourhood of the first transect (24 August 1949) photographed in this area, but which did not show any specimens of *O. fragilis*. It is possible then that the ophiuroid population found in 1950 and 1951 was new to this locality, but it is more likely that the 1949 transect in this area just missed it.

Transect of 26 April 1951. Three films were taken along this transect which lay to the north-west of the previous two transects. The bottom was muddy sand with patches of fine gravel (see Pl. 1, fig. 8). The epifauna, as shown by the photographs, was very poor, and the total of eighty-nine frames, representing 22 m.^{2} of the bottom, showed only 7 hydroids, 3 clumps of *Cellaria* sp., 4 burrowing anemones, 1 small crab, and 1 narrow track.

Area South of Looe Island

Photographs were taken along two transects:

24. iv. 51. Looe Island: 353°T., 4·8′; 000°T., 5·0′; 005°T., 5·0′; 010°T., 5·2′.
25. vii. 51. Looe Island: 000°T., 5·1′; 349°T., 5·1′; 345°T., 5·3′; 341°T., 5·4′; 342°T., 5·0′.

Transect of 24 April 1951. This transect of four films ran from east to west and crossed the previous transect photographed in this area on 2 August 1950. The first film showed a bottom of sand and muddy sand and gravel with a very poor epifauna. On the second and third films the pictures showed a population of *Ophiothrix fragilis* somewhat less dense than that photographed on 2 August 1950. The total numbers of animals counted on this part of the transect (50 $\frac{1}{4}$ m.^{2} frames) was: 706 *O. fragilis*, 1 *Ophiocomina nigra*, 2 *Chlamys opercularis*, and 1 specimen each of *Pecten maximus*, *Marthasterias glacialis*, and a hydroid. The density of *Ophiothrix fragilis* was therefore about 56 individuals per m.^{2}. The fourth film of this transect showed no aggregations of brittle-stars except on two frames, and the only other animals recorded were 3 *Chlamys opercularis* and 1 swimming crab (*Portunus* sp.).

Transect of 25 July 1951. This transect of four films ran to the east of the previous transect, and covered a distance of about 2$\frac{1}{4}$ miles. Nearly every frame contained a large number of *Ophiothrix fragilis*, denser in numbers than in the previous transect (see Pl. I, figs. 1–4):

Total no. of frames	No. of frames with *O. fragilis*	Total no. of *O. fragilis*	Mean no. of *O. fragilis* per $\frac{1}{4}$m.^{2} frame
110	99	3143	32

These photographs therefore show a mean density of over 120 *O. fragilis* per m.^{2} in the area traversed by the present transect.

Apart from this crowded population of *O. fragilis* the epifauna in this area was poor, and the only other animals shown in the 110 interpreted frames

(representing 275 m.^{2}) were 30 *Ophiocomina nigra*, 5 *Ophiura texturata*, 5 *Marthasterias glacialis*, 1 *Asterias rubens*, 1 *Echinus esculentus*, 5 *Eupagurus prideauxi*, 5 *Chlamys opercularis*, 7 burrowing anemones, 3 hydroids and 1 clump of *Cellaria* sp. These figures suggest that very few other epifaunal invertebrates live in an area with a crowded population of brittle-stars. It was, however, noticed that the brittle-stars tend to avoid the area immediately surrounding a burrowing anemone; this is shown in Pl. I, fig. 4.

Area North-west of Eddystone, ¾ Mile, Depth 48 m.

On 18 July 1951, R.V. *Sabella* was allowed to drift from position Eddystone bearing 147° T., 0·73 miles, to Eddystone bearing 136° T., 0·80 miles, while the first film was taken. The ship then steamed back to the first position and the second film was taken along the same transect.

The photographs on these two films show the greatest density of brittle-stars recorded in the present investigation:

Total no. of frames interpreted	No. of frames with *O. fragilis*	Total no. of *O. fragilis*	Mean no. of *O. fragilis* per ¼m.^{2} frame
36	36	3053	85

This gives a mean density of 340 *O. fragilis* per m.^{2}. These 36 ¼ m.^{2} frames also contained 22 *Ophiocomina nigra*, 1 *Marthasterias glacialis* and 1 *Echinus esculentus*.

The photographs from this transect (Pl. I, figs. 5–7) show that the individual brittle-stars, although much more numerous, were also considerably smaller than those photographed in the other two brittle-star areas (south of Looe and area of Station L4). The figure of 340 individuals per m.^{2} may be regarded as a minimum, since in most frames the brittle-stars were living on top of each other, and the counts made could only reckon the top layer and those disks of animals in the lower layer which were not obscured by the tangled arms of the top layer.

Distribution of *Ophiocomina nigra*

The black brittle-star, *O. nigra*, is common in the Plymouth area, but never in such large numbers as *Ophiothrix fragilis*, with which it is nearly always associated in dredge and trawl hauls. The present series of photographs gives an opportunity of determining the proportions in which it occurs in these mixed populations. From the figures in Table II it appears that there is, on the average, less than 1 *Ophiocomina nigra* to 100 *Ophiothrix fragilis*.

TABLE II

Date	Locality	*O. fragilis*	*O. nigra*	Percentage of *O. nigra* in total brittle-star population
24. xi. 50	S.W. of Rame Head	547	2	0·4
15. ii. 51	S.W. of Rame Head	436	0	0
24. iv. 51	S. of Looe Island	763	1	0·1
25. vii. 51	S. of Looe Island	3143	30	0·95
18. vii. 51	N.W. of Eddystone	3053	22	0·72

DISCUSSION

There is now no doubt that the dense population of *Ophiothrix fragilis*, 5 miles south of Looe Island, is not a seasonal phenomenon and that it is of a more permanent nature. Photographs of these brittle-stars have been taken on three different occasions in 1950–1, and from them it appears that this population is at least 2 miles in length and $\frac{1}{2}$ mile in breadth, and it may be considerably larger. The mean density of brittle-stars in this area, calculated from the large number of photographs taken on the three transects, is about 97 per m.^{2}, or 392,000 per acre. The amount of food, in the form of animal and plant detritus, consumed by such a population must be very large, and further work is in progress to determine the food requirements of this type of detritus-eating brittle-star.

In the *Ophiothrix* population living $\frac{3}{4}$ mile north-west of Eddystone the minimum figures are 340 per m.^{2} or about 1·3 million per acre; here the individual brittle-stars were somewhat smaller than those in the population south of Looe Island. These photographs were taken, by chance, in the middle of Allen's (1899) Ground X, coarse gravel and muddy sand, which he speaks of as characterized 'by the very great abundance of *O. fragilis*, which occurs almost to the exclusion of every other species'. His catches were taken with a dredge so that he had no exact measure of abundance, but there is little doubt that his *Ophiothrix* ground sampled at the end of the nineteenth century is essentially the same as that photographed in 1951.

The permanent nature of these brittle-star populations suggests that they rely for their food supply more on a steady flow of suspended material than on a settled bed of living or dead organic matter. It is possible that much of this suspended matter is carried back and forwards over the *Ophiothrix* bed by the tidal streams, and the position of the Looe and Rame beds at 5 and 4 miles respectively from the coast would favour this. The tidal streams in the neighbourhood of Eddystone are well known, and they would also tend to gather suspended material and carry it over the massed brittle-stars with their food-collecting net of tangled arms.

SUMMARY

An improved underwater photographic apparatus has been used to take further series of photographs of the sea bottom near Plymouth. The photographs in the present series are each $\frac{1}{4}$ m.^{2} in area instead of 1 m.^{2}, and at this scale definition is much better.

Photographs of the bottom in the Rame Mud area showed ripple marks but no living epifaunal animals. In an area south of the Rame Mud, on a muddy sand and gravel bottom and in a similar area 6 miles south of Looe, dense populations of the brittle-star, *Ophiothrix fragilis* were photographed. In the area south of Looe this type of population (density more than 100 individuals per m.^{2}) has been photographed on three different occasions in 1950–1. In a similar but still denser *Ophiothrix* population found $\frac{3}{4}$ mile north-west of Eddystone, there were about 340 individuals per m.^{2}, and this aggregation was apparently of long standing, since exceptionally large dredge hauls of *Ophiothrix* were taken there in the last decade of the nineteenth century. It is suggested that the food supply for these populations, in the form of suspended material, is brought to them largely by the tidal streams and that the crowded beds are in localities where this is likely to happen.

From the photographic data it appears that in these dense populations of brittle-stars there is rather less than 1 *Ophiocomina nigra* to 100 *Ophiothrix fragilis*.

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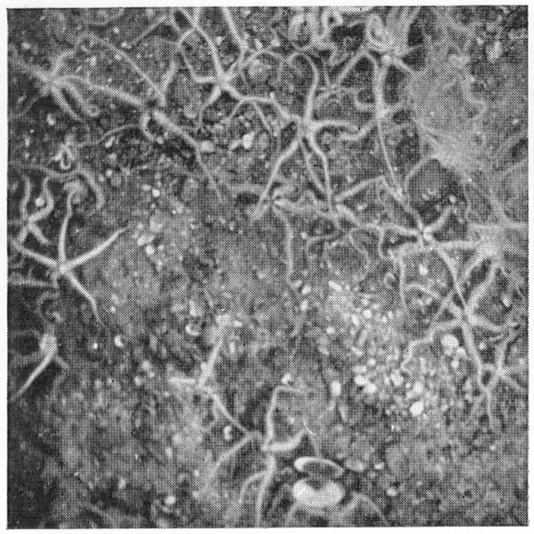
EXPLANATION OF PLATE I

Underwater photographs, each covering $\frac{1}{4}$ m.^{2} of the sea bottom.

Figs. 1–4. Showing samples from a dense population of *Ophiothrix fragilis*, 5 miles south of Looe Island. Density of over 100 brittle-stars per m.^{2}. In fig. 4 a burrowing anemone (where lines *a* and *b* cross) appears in a clearing among the brittle-stars. Depth 55 m.

Fig. 5–7. Showing samples from a dense population of *O. fragilis*, $\frac{3}{4}$ mile north-west of Eddystone. Density of about 340 brittle-stars per m.^{2}; individual brittle-stars smaller sized than in figs. 1–4. In fig. 6 the bottom is rock and a single *Echinus esculentus* is attached to a vertical face. In fig. 7 the bottom is shell gravel. Depth 48 m.

Fig. 8. Barren ground of muddy sand and gravel with shell fragments but no living epifaunal invertebrates. One mile west of Station L4. Depth 54 m.



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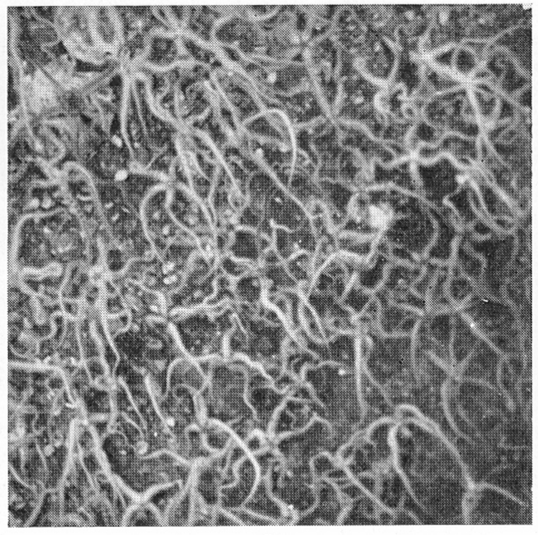

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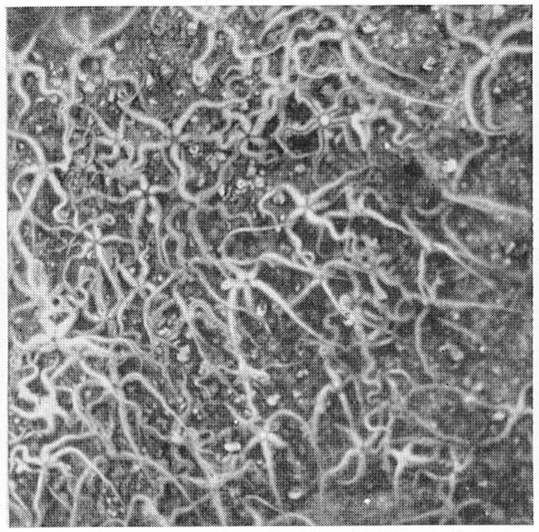

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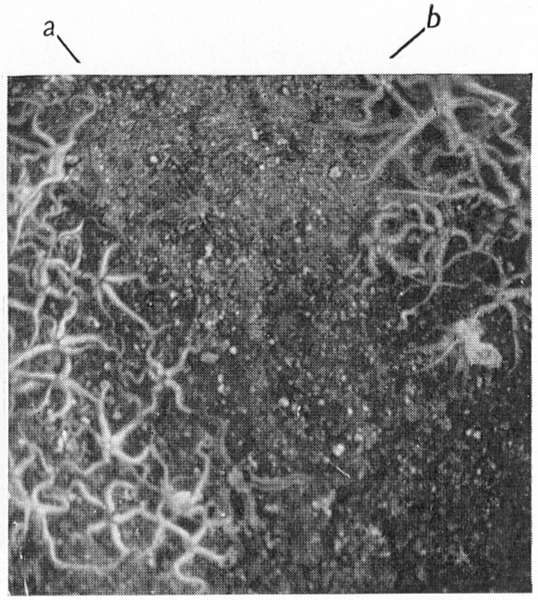

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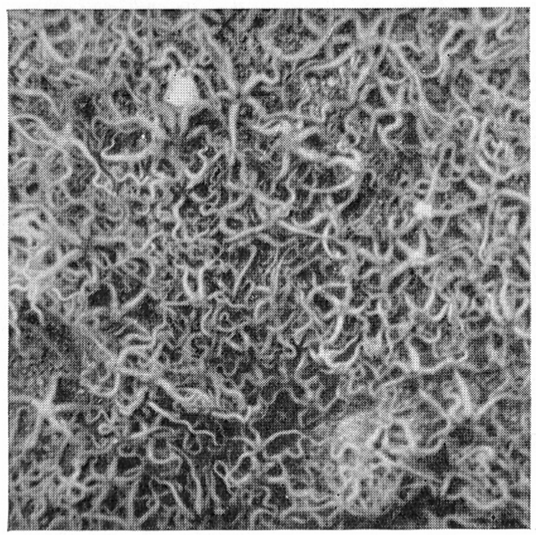

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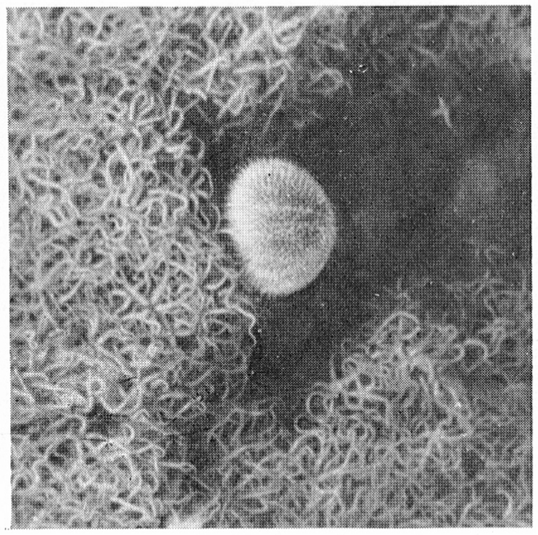

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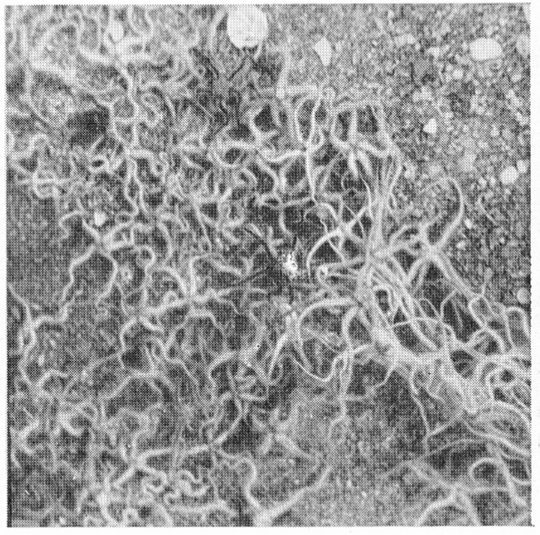

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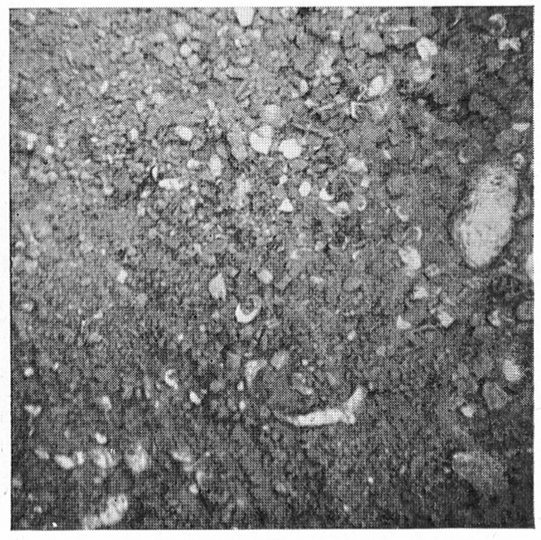

8

OBSERVATIONS IN THE SEA ON THE REACTION TO ULTRA-VIOLET LIGHT OF CERTAIN SOUND SCATTERERS

By R. E. Craig and I. G. Baxter

Scottish Home Department, Marine Laboratory, Aberdeen

(Text-figs. 1 and 2)

The use of lanterns to attract herring is reported for British waters as early as the fifteenth century (Jenkins, 1927). No such methods are in use here to-day, although in Australia positive results have been reported in the case of pilchard, and in Japan and the Far East the use of light lures has become traditional (Maeda, 1951).

The physiological importance of the ultra-violet component of natural light prompts us to consider it equally with visible light as a possible stimulus. The human eye has become adapted to the red-violet range, centred on yellow, which is the strongest component of the sun's spectrum at the surface. In sea water there is differential absorption so that the centre of maximum intensity is displaced somewhat towards shorter wave-lengths, the precise effect depending upon depth and the nature of the sea water. We should not, therefore, be surprised to find marine creatures sensitive to a range including a portion of the ultra-violet spectrum.

An earlier experiment, using visible light, has already been reported (Parrish & Craig, 1951). This showed that some organisms producing echo-traces are affected by light, and that certain deductions are thus possible about the nature of these organisms.

Ultra-violet light has been known to attract trout and pike ('Reflector', 1949). Experiments on herring conducted off the Belgian coast by the Netherlands research vessel, however, did not lead to definite results (de Boer, 1950). A number of experiments have been carried out on the East Coast during the past summer, by Mr Parrish and the present authors. In these an ultra-violet lamp was lowered where echo-traces were found. The traces were of various ill-defined forms, but included a typical shallow scattering layer. No reaction was observed in any case.

We report here two experiments in which positive results have been obtained using the ultra-violet light.

The source was a 125 W. 'black' ultra-violet lamp housed in a vertical glass cylinder with cast-iron ends. The horizontal intensity is therefore much

greater than the vertical, and the upward and downward components are not dissimilar. When this lamp is lowered at night to a few fathoms depth in the summer sea, it produces at first no visible illumination. After about 5 min. a violet glow is visible in the surrounding water, and this intensifies until it can be seen to extend 3 to 4 m. from the lamp, the shadows of the lamp bolts cutting clear lanes through the luminescence. We take this to indicate that numerous fluorescent organisms are attracted by the light, though these have not yet been identified. The gathering of such a mass of small organisms may obviously affect the behaviour of their predators, and in work such as this it is necessary to distinguish between such secondary effects which must take some little time to develop, and immediate reactions to switching *on* of a light, which must presumably imply direct visual stimulus. The switching *off* of the lamp, however, is a visible event even to the human eye since the distinct luminescent glow vanishes abruptly.

Traces in Figs. 1 and 2 were obtained on board the R.V. *Clupea*, using a Kelvin and Hughes recording echo-sounder, type MS 22.

Recording I (see Fig. 1). Position: 7 miles S.E. × S. from Stornoway in 100 m. of water. Recording begins 20.10 hr. and ends 22.00 hr. 25 September 1951. Sky overcast, no moon. The ship is lying to drift nets.

A confused trace with a peculiar 'saw edge' appearance to its upper position extends from 20 to 60 m. depth, and the lamp is lowered into the centre of this to a depth of 35 m., appearing on the recording as a distinct horizontal line. Some avoiding action is evident and then the trace increases in density around the lamp. When this is switched on separation takes place into two distinct traces, the upper lying between 8 and 14 m. above the lamp, and the lower between 6 and 14 m. below it. The upper trace consists of crescents each of which may be attributed either to a single subject or to a small distinct group, the lower is of homogeneous appearance and may represent a more uniform distribution of scatterers (though it must be remembered that greater depth in itself gives a more uniform appearance to any distribution of this kind, owing to the larger cross-section area of the supersonic beam). We consider this lower trace to be similar in cause to the scattering layers described by Burd & Lee (1951) and Parrish & Craig (1951).

Half an hour later, after sampling has been carried out with the Hensen net to 38 m., the lamp is raised to 20 m., whereupon the lower trace rises, maintaining a constant depth below the light, and the upper trace descends to merge with the lower, forming a dense trace in which the components are not readily separable. Ten minutes later the light, still switched on, is lowered rapidly to 50 m., driving before it some fast-moving organisms, and then to 80 m. at which depth it is out of range of the echo-sounder and the trace returns above it. In this connexion it must be remembered that the space close to the light, which is devoid of scatterers, is probably in the form

Fig. 2.

Fig. 1.

(*face* p. 224)

of a sphere, and that to the side we have presumably an undifferentiated layer of scatterers. The reappearance of the shallow trace may therefore be explained as a horizontal concentration of organisms, and does not necessarily imply the return of those forced down by the light. Finally the lamp is raised slowly to the surface and remains there for a while switched on. The trace reappears as a very dense band between 10 and 40 m., and remains thus even after the lamp is switched off. An attempt to affect this trace by directing the beam of an Aldis signal-lamp downwards through the water produced no certain reaction. The rate of apparent vertical movement of the lower (homogeneous) trace may be stated with reasonable accuracy as: descent, 3 m./min.; ascent, 5 m./min. The rate of movement of the upper (heterogeneous) trace cannot be accurately assessed, but it is clearly much greater than this.

The Hensen sample revealed that copepods were abundant, euphausids, decapod larvae and *Sagitta* common, and others present in small numbers included pteropods and hyperiids. This is not significantly different from other plankton hauls in the Minch at this season.

The drift net catch consisted of 39 herring, 24 common mackerel, 1 horse mackerel, 5 young dogfish and 1 whiting, and the trace originally observed was within reach of these nets, so we can feel certain that these are not caused by abundant adult herring. Fishing with 'dandy' lines and with baited hand-lines throughout this experiment produced no result.

Recording II (see Fig. 2). Position: 6 miles S.E. from Stornoway in 120 m. of water. Recording begins 20.50 hr. and ends at 22.30 hr. 1 October 1951. Clear sky, no moon. The ship is again lying to drift nets.

A peculiar jagged trace is observed superimposed on one of spotty appearance, each of these extending roughly from 8 to 30 m. depth. A few ill-defined marks appear below this. The 'jags' are caused by objects rising very uniformly at about 14 m./min. and these are not seen descending. They could be caused either by gas bubbles, or by fish swimming up under the ship and then away horizontally. The former would appear to be a more probable explanation[1] and presumably indicates the presence of physostomatous fish. Catches of horse mackerel (*Caranx trachurus*) and dogfish (*Squalus acanthias*) were obtained at this position using a 'dandy line' which carries a series of bare hooks.

When the lamp is lowered into the centre of the trace some avoiding action is apparent, and when it is switched on, the trace disappears for about 3 min. and then begins to re-form under the light, the spotty component returning first, followed after a lapse of another 10 min. by heavier markings

[1] The literature on the rising velocity of bubbles has been summarized by Worster (1948), and reference to his figures show that for bubbles between 0·04 and 1·4 cm. diameter, the rate of rise is roughly independent of size, and is of the order of 15 m./min. This would appear to confirm our conclusion.

which may be caused by the same fish as the original jagged trace but no longer rising. Some 15 min. later two components can still be distinguished, the lower homogeneous one maintaining a depth of about 20 m. below the lamp, whilst the top of the upper is at exactly the depth of the lamp. This might be explained as a reorganization within the layer, but the appearance is more suggestive of the arrival on the scene of fresh recruits.

By 21.55 hr. the lamp has been at the 20 m. mark for 50 min., and it is then lowered to 40 m. and subsequently to 50 m. *In a period of the order of 1 sec. from the first movement* of the lamp, the topmost of the organisms producing the lower trace either descend 12 m. or remove themselves horizontally from the scene of action. The lower organisms appear to descend more sedately, remaining at a constant depth below the lamp, and then disappear. The upper layer maintains its distance below the lamp, and also fades out.

The lamp is then hauled slowly to surface and remains there switched on for a time. The lower trace reappears at 50 m. depth and remains there, and the spotty trace re-forms. The immediate effect on the lower trace of the sound of starting up the main engine is of interest.

The drift net catch consisted of 31 herring, 44 horse mackerel, 24 common mackerel and 77 dogfish, and we can therefore exclude abundant adult herring as the cause of the upper water trace, although *not* as a possible cause of the lower one which is below the reach of the nets. In fact, the speed of reaction to stimulus of the latter is highly suggestive of herring or other active fish.

These experiments are not by themselves conclusive, and it is particularly unfortunate that the underwater camera was not available on this cruise. When we lay the evidence alongside the work of many other investigators, however, we can suggest associating the traces as follows:

(1) Recording I	Upper trace	Fish, unidentified
(2) Recording I	Lower trace	Plankton organisms, unidentified
(3) Recording II	Spotty trace	Dogfish
(4) Recording II	Jagged trace	Horse mackerel
(5) Recording II	Deep trace	Probably herring, though whiting or other adult fish are a possible cause

It will be seen that results such as these are of intrinsic biological interest in that reactions to light can be measured using the echo-sounder. They also give hope of deriving ultimately a set of tests which would be of commercial value by giving greater certainty in the identification of the causes of echo traces. For both these reasons, experiments of this type will continue during the present year.

SUMMARY

Two experiments on the reaction to ultra-violet light of certain sound scatterers in the area are described.

The source was a 125 W. ultra-violet lamp.

The scatterers were detected using a Kelvin and Hughes recording echo-sounder, type 22.

The traces on both occasions were of the confused type caused by a number of different organisms, apparently lying between 20 and 60 m. and 8 and 30 m. respectively.

The responses of the different organisms to the ultra-violet light as shown by the components of the traces are described and their speeds of reaction calculated.

The types of organisms causing the traces are suggested.

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VITAMIN A AND CAROTENOIDS IN CERTAIN INVERTEBRATES. I. MARINE CRUSTACEA

By L. R. Fisher, S. K. Kon and S. Y. Thompson

National Institute for Research in Dairying, University of Reading

(Text-figs. 1–6)

CONTENTS

INTRODUCTION

It has for long been accepted that carotene is converted in the liver to vitamin A, but recent work has established that, in several mammalian species at any rate, the conversion takes place in the small intestine (see, for example, the recent review by Kon & Thompson, 1951).

During the study of the conversion of β-carotene to vitamin A in the intestine of rats and pigs (Thompson, Ganguly & Kon, 1947, 1949), Prof. B. C. P. Jansen of Amsterdam drew our attention to the work of Wagner (1939), who claimed to have observed the phenomenon in the intestine of blue and fin whales at the Lopra Whaling Station in the Faeroes and stated that they derived the β-carotene from krill ('Gattung der *Euphausia superba* Dana'). *E. superba* Dana is exclusively antarctic, so that the krill which Wagner examined must have been composed of other Crustacea, of which the most likely species in the krill of Faeroese waters is *Meganyctiphanes norvegica* (M. Sars). Wagner claimed that in his krill β-carotene was present to the extent of 14·5 mg./kg. This was suprising, since astaxanthin is the characteristic carotenoid pigment of Crustacea and the presence of such relatively enormous quantities of β-carotene did not seem likely.

Thompson *et al.* (1949) obtained, therefore, through the courtesy of Dr Robinson of the whaling factory ship *Balaena*, samples of food from the stomachs and intestines, and portions of the intestinal wall, of two antarctic

fin whales. The krill from these whales was identified as *Euphausia superba* Dana. It contained large quantities of astaxanthin but only small traces of β-carotene. Preformed vitamin A, identified, after chromatography, by the antimony-trichloride test, absorption at 328 mμ, behaviour on mixed chromatography with pure vitamin A and liver-storage tests with rats depleted of vitamin A, was present, however, in appreciable amounts, in one of the whales to the extent of about 6 i.u./g. stomach contents, with smaller concentrations farther along the intestine. Astaxanthin occurred in the intestinal contents in increasing concentration along the gut; no carotene was detected (Kon & Thompson, 1949*a*).

In northern waters, the main food supply of blue and fin whales is derived from the euphausiids, *Meganyctiphanes norvegica* and *Thysanoessa inermis* Krøyer (Einarsson, 1945). With the kind help of the workers at the Millport Marine Station, Kon & Thompson (1949*b*) got from Loch Fyne specimens of *Meganyctiphanes norvegica* and of *Thysanoessa raschii* (M. Sars), closely related to *T. inermis*, and found much larger quantities of vitamin A than in other Eucarida caught there simultaneously.

The occurrence of vitamin A or its precursors in marine invertebrates has been studied by others since Hjort (1922), by biological tests with rats, detected vitamin A activity in extracts from some marine plants and animals, including *Crangon* sp. and *Pandalus borealis*. The evidence, however, is fragmentary and often conflicting; in several instances the total vitamin A activity was measured biologically, leaving undecided the presence of preformed vitamin A.

Drummond & Hilditch (1930) reported that copepods, *Nephrops norvegicus*, and *Meganyctiphanes norvegica* contained little or no vitamin A.

Drummond & Gunther (1930, 1934), studying fatty constituents of marine plankton, looked for vitamin A but concluded that 'vitamin A as such is apparently absent from both phytoplankton and zooplankton'. The statement was based for phytoplankton on an examination of oils isolated from the diatoms *Chaetoceras* spp. and *Lauderia borealis*, and for zooplankton on a similar study of mixed copepods and *Calanus finmarchicus* (Collin, Drummond, Hilditch & Gunther, 1934). In *Calanus* caught at the end of May off the north coast of Norway, Lederer (1938) found no trace of vitamin A. Drummond & MacWalter (1935) examined oil from antarctic krill (which consisted mainly of *Euphausia* sp.), but did not look specifically for vitamin A. Extracts of the non-saponifiable portion contained a pigment which gave a slightly blue-green colour with antimony trichloride. They pointed out, with reference to earlier work based on biological tests, that certain isomeric forms of carotene, among the naturally occurring lipochromes, are converted into vitamin A by the rat. Gillam, El Ridi & Wimpenny (1939) studied by chemical and physical methods the seasonal variation of vitamin A in gross plankton samples from the North Sea; the highest content of vitamin A

coincided with the first phytoplankton maximum and the zooplankton breeding period, diminishing later in the year.

Pugsley (1941) found vitamin A to the extent of 600 i.u./g. in oil extracted from the viscera of tinned crabs (*Cancer magister*); the oil constituted 6 % of the weight of these tissues.

The retina of the squid, *Loligo pealii*, contains 1–2 μg. of vitamin A_1 (Wald, 1941) and about three times this amount of retinene$_1$, and no trace of these or other carotenoids was found in other squid tissues, but the eyes of the crabs *Uca pugnax* and *Carcinus maenas* and those of the lobster (unspecified) contain high concentrations of vitamin A_1, but no retinene. In the squid vitamin A remains constant in all conditions of light and darkness and does not, therefore, appear to participate directly in the visual processes. Wald (1943) also found vitamin A_1, retinene$_1$ and astaxanthin in the eyes of the fresh-water crayfish, *Cambarus virilis*. Neilands (1947) studied the conversion of carotene to vitamin A in the lobster, *Homarus americanus*, and found 36 i.u./g. in the hepatopancreas and 100 i.u./g. in the eyes on a carotene-free diet, and 53 i.u./g. in the hepatopancreas and 183 i.u./g. in the eyes on a diet supplemented with β-carotene.

Recent developments in the micro-analysis of vitamin A in the presence of a large excess of carotenoids made it possible to undertake a more detailed and systematic study than those hitherto attempted. The present paper is partly concerned with work on krill outlined above and in subsequent studies published only in abstract (Batham, Fisher, Henry, Kon & Thompson, 1951; Fisher, Kon & Thompson, 1951) and partly with work on other species and on geographical, developmental and seasonal variations and anatomical distribution of vitamin A in those animals found to possess it.

Material and Methods of Collection

The material consisted of plankton collected in Loch Fyne, the Faeroe-Shetland area and north-west of the coast of Norway; krill obtained from whales in arctic and antarctic waters, and littoral and benthic animals from Loch Fyne and the Essex coast.

Regular visits were made to the Marine Station, Millport, at monthly, or slightly less frequent, intervals, and the principal species obtained were *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa raschii* (M. Sars), *Euchaeta norvegica* Boeck, *Calanus finmarchicus* (Gunnerus), *Crangon allmani* Kinahan, *Pandalus bonnieri* Caullery and *Nephrops norvegicus* L. The Faeroe-Shetland area was visited in the Scottish Home Department's Fisheries Research Vessel *Scotia* during November 1950, and *Meganyctiphanes norvegica* and *Thysanoessa inermis* Krøyer were the most important animals brought back from these waters. Antarctic krill was kindly supplied from the W.F.S. *Balaena*, and arctic specimens were taken from a fin whale caught 200 miles

north-north-west of Bergen and also free-swimming from the same area, in June 1950, by catcher *Hval* 2 from Blomvåg Hvalstasjon, Norway, and from a blue whale caught 40 miles north-west of St Kilda by a catcher from the whaling station of Scottish Whalers Limited, West Loch, Tarbert, Harris. Littoral and benthic Crustacea were collected at Burnham-on-Crouch and other parts of the Essex coast and included *Carcinus maenas* (Pennant), *Eupagurus bernhardus* (L.) and *Gammarus marinus* Leach.

Initially specimens were placed as soon as possible after catching in a measured volume of absolute alcohol, after drying with filter paper. Aluminium containers were used for lightness, chemical inertness and opacity. Alcohol is an excellent preservative for vitamin A and carotenoids, but, since it leaches them out, distribution in the various organs cannot be studied and only the total content can be measured. Later it was found more convenient and accurate to place specimens, immediately after catching, for a minute or so in boiling sea water. Boiling fixes vitamin A and carotenoids in their original sites and anatomical separation is later possible. As shown below, the method also allows more accurate weighing of the specimens. The specimens thus treated were transported in aluminium containers without preservative and kept as cool as possible. The greatest attention was always paid to protection from strong light, in order to reduce photochemical effects.

Chemical and Physical Tests

Methods

Weighing of Specimens

The weight of the alcohol-preserved specimens was determined by weighing the containers full and again empty. The volume of absolute alcohol being known, the weight of the animals or tissues could be calculated, but indirect weighing was not accurate enough with small animals or parts of animals.

Table I. Recovery of Oil, Vitamin A and Carotenoids from Specimens of *Meganyctiphanes norvegica* preserved by Alcohol (A) or by brief Boiling in Sea-Water (B)

Preserved by	Length (cm.)	No. of specimens	Oil (mg./specimen)	Vitamin A (i.u./specimen)	Astaxanthin (μg./specimen)
A	<3	238	3	1·2	4·5
B	<3	93	3	1·3	4·8
A	3–4	95	18	4·2	16
B	3–4	60	20	5·4	23
A	>4	44	44	27	44
B	>4	20	39	26	44

Comparison of alcohol-preserving with boiling showed equal recovery of vitamin A and carotenoids by both methods (Table I). As a further check the right eye of each of a group of 150 *Meganyctiphanes norvegica*, all of average length greater than 40 mm., was removed and preserved in alcohol. The

animals were then boiled and the left eyes were removed. The two lots of eyes were analysed separately with the following results:

	Vitamin A (i.u./eye)	Carotenoids (μg./eye)
Eyes preserved in alcohol	10·9	4·7
Eyes boiled	11·7	5·0

The water in which the specimens had been boiled was examined and no trace of vitamin A or carotenoids was found in it.

To determine the effect of boiling on the weight of the animals, ten *M. norvegica* were weighed alive after removal of surplus moisture, and ten after boiling; they were then dried at 105° C. for 20 hr. The effect of boiling was negligible, since the live lost 69 % and the boiled 72 % of their weight on drying.

After any necessary dissection had been completed in red light, boiled specimens or parts of them were weighed and preserved in alcohol.

Extraction of Lipids, Vitamin A and Carotenoids and Measurement of Total Carotenoids

This was done as described by Thompson *et al.* (1949). Specimens were macerated in a Waring Blendor jar, proportions taken for each homogenization being about 20 g. of tissue, 60 ml. absolute alcohol and 200 ml. light petroleum (b.p. 40–60° C.). Before maceration, nitrogen was bubbled through the mixture and into the mouth of the jar which was then closed with a lid. The mixture was homogenized for about 2 min., transferred to a separating funnel and the bottom layer was run off and re-extracted with a further 200 ml. of light petroleum. The two extracts were combined, the volume determined and the total carotenoids measured in the photoelectric spectrophotometer of Thompson (1949) at 451 mμ, that is, at the absorption maximum for β-carotene. For animals whose only carotenoid was astaxanthin this reading was used as a measure of the pigment. Values obtained by this means were probably some 10 % lower than those based on the measurement of astaxanthin at its absorption maximum and referred to the extinction for the pure substance.

The solvent was evaporated and the oil weighed and dissolved in *n*-hexane.

Separation of Vitamin A from β-Carotene and other Carotenoids

The chromatographic method of Thompson *et al.* (1949), employing alumina columns, was used. The separation and measurement of vitamin A, total carotenoids and β-carotene is shown schematically in Fig. 1. Two alternatives could be followed: (*a*) direct saponification of the extract in *n*-hexane and subsequent chromatography on aluminium oxide; (*b*) direct chromatography of the extract which separated vitamin A ester and alcohol. In (*b*), the two fractions were saponified and rechromatographed to obtain

a further purification from carotenoids of the vitamin A, now in the alcohol form. Method (*a*) was used for routine work where a separation of the two

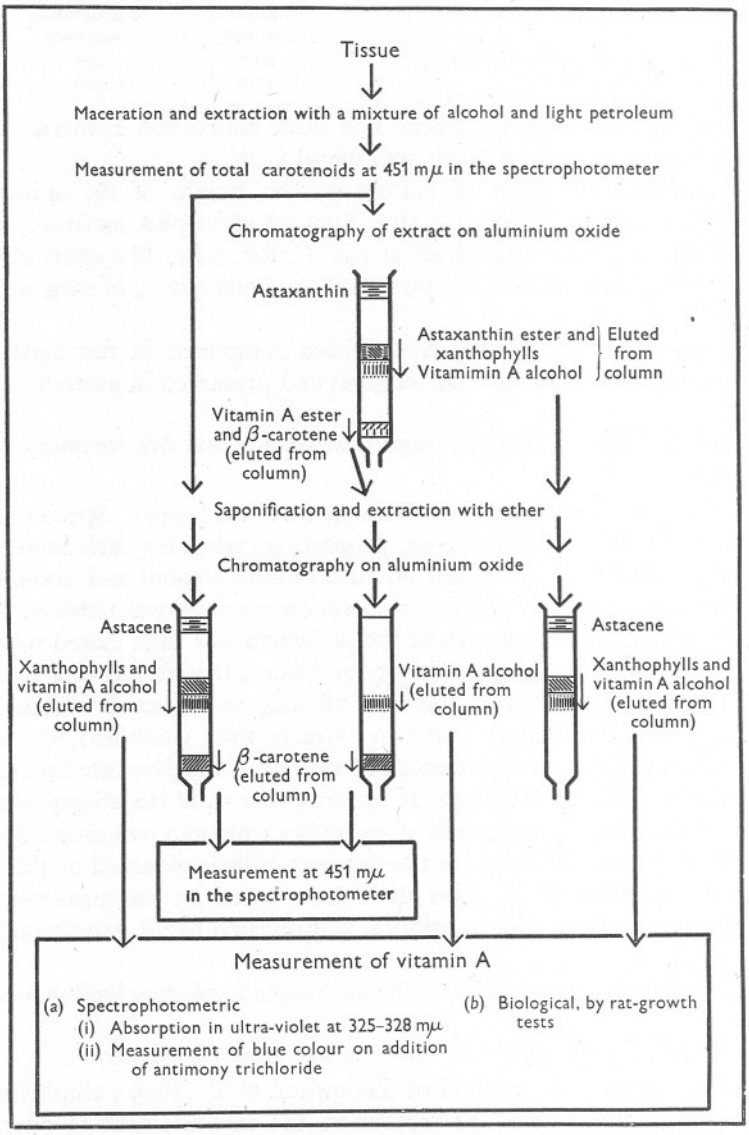

Fig. 1. Outline of methods of separation and measurement of vitamin A, astaxanthin and β-carotene in marine animals.

forms was not required and the pigments were such that they did not contaminate the vitamin A fraction. β-Carotene, if present, was separated by either method and collected at the stages indicated in the figure.

Astaxanthin and xanthophyllic pigments, if present, were not, as a routine procedure, measured after chromatography. It will be noticed from the figure that we were unable to separate xanthophylls from vitamin A alcohol. Where these pigments were present in relatively large quantities they vitiated the determination of vitamin A in this form. The difficulty did not arise with euphausiids and was probably of little consequence with the other Crustacea.

The fractions containing vitamin A were taken up in 1·5 ml. chloroform and that containing β-carotene in 5 ml. *n*-hexane. Vitamin A was measured by the antimony-trichloride reaction, and β-carotene determined on the photoelectric spectrophotometer as described by Thompson (1949) and Thompson *et al.* (1949). Absorption curves for vitamin A in ultra-violet and for β-carotene and astaxanthin in ultra-violet and visible light were obtained on the Beckman quartz photoelectric spectrophotometer.

For euphausiids, the following procedure was adopted for the identification of astaxanthin and its ester. The absorption curve of the total extract in *n*-hexane was determined. The pigment was further identified by its behaviour on chromatography (Goodwin & Srisukh, 1949) and its low solubility in diethyl ether after saponification.

Results

The Form of Vitamin A in the Crustacea

As stated above (p. 234) vitamin A ester and alcohol were not always separated in routine tests, and for a number of species only values for total vitamin A are at present available. Our observations on Euphausiacea and certain Decapoda show that in them vitamin A was present mainly as the ester. Details are given in the sections dealing with the relevant species.

TABLE II. VITAMIN A AND CAROTENOIDS PER GRAM IN GUT CONTENTS OF ANTARCTIC FIN WHALES (NOS. 1 AND 2) AND OF BLUE WHALE (NO. 3)

	No. 1		No. 2		No. 3*	
	Vitamin A (i.u.)	Carotenoids (μg.)	Vitamin A (i.u.)	Carotenoids (μg.)	Vitamin A (i.u.)	Carotenoids (μg.)
Stomach	6·0	41	2·5	38	2·0	22
Small intestine	0·5	2·2	3·8	49	—	—
Caecum	2·1	89	4·3	79	—	—
Rectum	1·1	85	1·6	103	—	—

* No. 3, blue whale, stomach oil 2·1 %, vitamin A 91 i.u./g. oil and carotenoids 1·02 mg./g. oil.

Krill from Antarctic Whales

Contents of the alimentary canals of two fin whales and one blue whale were examined. They had been preserved by deep-freezing, and were identified by Prof. C. H. O'Donoghue as being mainly *Euphausia superba* Dana. Results obtained are shown in Table II.

The lower value obtained for the stomach contents of fin whale 2 was possibly correlated with their greater fluidity. They were either in a more advanced stage of digestion or contained less krill in proportion to the digestive juices. Judging from the appearance of the material the former explanation was more likely. In the light of later work (see p. 239), it is also possible that the difference in concentration of vitamin A was due to differences in the developmental stage and size of the krill eaten by the two fin whales. Vitamin A was present mainly in the ester form.

So far no free swimming *E. superba* has been available to us for an examination of its contents of vitamin A and carotenoids.

Organs of Antarctic Whales

Segments of the alimentary canals of the two fin whales whose stomach contents were analysed were also examined, along with organs from three blue whales, and the results obtained are shown in Table III. The gradient of vitamin A decreased from the small intestine to the rectum, in agreement with our findings on the absorption of vitamin A in other mammals (Thompson *et al.* 1949). It seems possible that the absorption of vitamin A is incomplete as it was still found in the caecal and rectal contents.

TABLE III. VITAMIN A CONTENT (I.U./G.) IN ANTARCTIC FIN AND BLUE WHALES

	Fin no. 1	Fin no. 2
Small intestine: Mucosa	0·34*	0·64†
Wall	0·21	0·29
Caecum	0·12	0·26
Rectum	0·19	0·21

* Washed. † Unwashed.

Blue whale No. 1 (83 ft. lactating), liver 6300; No. 2 (88 ft. lactating), liver 6120; No. 3 (87 ft.), kidney 3·6.

In contradistinction to vitamin A the pigments did not appear to be absorbed, since they became steadily more concentrated in their passage along the alimentary canal (Table II).

Krill from Arctic Whales

The contents of the alimentary canals of two whales were examined. One of these was a fin whale shot 200 miles from the coast of Norway and the other was a blue whale shot 40 miles north-west of St Kilda. The results are shown in Table IV. In both instances the krill was identified as *Meganyctiphanes norvegica* (M. Sars).

The low figures for vitamin A and astaxanthin in the mouth contents of the blue whale were probably due to considerable leaching out by sea water while the whale was being towed 80 miles back to the whaling station at Tarbert. The krill in the mouth was much paler in colour than that collected

from farther along the gut. In the stomach of the blue whale, the euphausiids had undergone little digestion and individual animals were still distinguishable. The presence of krill in the mouth and oesophagus indicates possible regurgitation, which also may have taken place between the four parts of the stomach, as happens when a whale is shot. Unfortunately, no information is available to indicate from which part of the stomach the contents were taken in any of the whales, either arctic or antarctic, examined.

TABLE IV. OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM IN THE GUT CONTENTS OF ARCTIC WHALES

	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)	Astaxanthin (mg./g. oil)	β-Carotene
		Fin whale, 11. vi. 50, off Norway				
Stomach	0·8	1·5	188	22	2·81	Trace
Small intestine	0·1	2·5	2380	5·0	4·80	Trace
		Blue whale, 22. viii. 50, 40 miles north-west of St Kilda				
Mouth	0·7	0·5	87	1·6	0·24	None
Oesophagus	0·1	3·1	325	46	4·79	None
Stomach	0·1	5·0	392	48	3·78	Trace

TABLE V. OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM IN FREE-SWIMMING *MEGANYCTIPHANES NORVEGICA* (M. SARS)

Locality	Date (1950)	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)	β-Carotene
Loch Fyne	18. viii*	2·2	15	680	42	Faint trace
Loch Fyne	4. i	3·1	26	835	70	Trace
North Sea (63° 20′ N., 0° 30′ E.)	30. vi	5·3	15	288	46	None
Loch Fyne	17. viii	6·7	40	596	112	Trace
Sandy Bank, Faeroes (61° 54′ N., 5° 45′ W.)	6. xi	5·6	19	343	57	None

* 1949.

Free-swimming Arctic Krill

Meganyctiphanes norvegica. The most important species of euphausiid in arctic krill, forming the food of baleen whales, is *Meganyctiphanes norvegica*, and, in order to obtain results comparable with those from animals taken from whales, free-swimming animals from different areas of the sea were examined. The work of Macdonald (1927) on this species in Loch Fyne indicated that this sea-loch was a good and convenient source of supply. Other samples of arctic krill were got from the Norwegian whaling area and from the Sandy Bank area, near the Faeroes. Table V shows the results of analyses of these specimens. Of the vitamin A, 94 % was in the ester form and was chromatographically homogeneous before saponification with pure vitamin A acetate and after saponification with vitamin A alcohol prepared from the acetate by saponification. The chromatographic homogeneity was observed by fluorescence under ultra-violet light.

The Loch Fyne specimens were caught at depths of 120–140 m., about 20 m. from the bottom in a 1 m. stramin net. Those from the Norwegian whaling ground were taken from the surface of the sea in daylight. The haul in the Sandy Bank waters was made with a 1 m. coarse silk net at 11 p.m. at a depth of 20 m., where the sounding was 274 m.

The much higher concentration of vitamin A in the free-swimming animals than that in those from the whales is very striking, but we noted that the average overall length of specimens taken from the blue whale at Tarbert was only about 30 mm., whereas those caught in Loch Fyne were over 35 mm. in length. It was necessary, therefore, to investigate any possible relationship between size and vitamin A concentration. Conditions of sorting specimens on the ship where large numbers had to be dealt with as quickly as possible rendered the best means of size-grouping, i.e. weighing, impossible of

TABLE VI. RELATIONSHIP BETWEEN OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM AND LENGTH AND WEIGHT IN *MEGANYCTIPHANES NORVEGICA* (M. SARS)

(β-Carotene absent)

Date	Length overall (cm.)	No. of specimens	Mean wt. (mg.)	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)
4. x. 50	<3	76	68	1·7	9·6	555	78
4. x. 50	3–4	131	320	10·1	13	131	55
4. x. 50	>4	53	500	8·6	34	397	60
21. xi. 50	<3	93	85	3·2	15	466	56
21. xi. 50	3–4	60	380	6·0	16	263	68
21. xi. 50	>4	20	580	6·7	44	660	75
10. i. 51	<3	3424	90	2·9	21	717	66
10. i. 51	3–4	1072	330	4·9	24	475	63
10. i. 51	>4	140	570	6·5	43	666	83

application, and so overall length was taken as a criterion. In the initial experiments, three size-groups of specimens taken in Loch Fyne from hauls by the M.V. *Calanus* were examined, those animals less than 30 mm. long, those between 30 and 40 mm., and those over 40 mm. Each group was weighed in order to determine the average weight of individual members. The results of these experiments are shown in Table VI.

The concentration of vitamin A, even in the smallest of the size-groups, was still much higher than the highest obtained for *Meganyctiphanes* from the whale, even though the average size of these was greater.

The noteworthy feature of the table is the marked increase in the vitamin A content with size. At each examination the concentration was about the same in the two smaller groups but was more than doubled in the largest. The content of astaxanthin also increased, but the increase in concentration in the largest groups was much less marked than for vitamin A. β-Carotene was not present in sufficient quantity to be detected.

To determine more precisely the relationship between vitamin A content and size, grouping of sizes was carried out in greater detail as a result of practice and experience. On 14–15 February 1951, a series was obtained with a size interval of 2 mm. Macdonald's (1927) method of measuring the length from the tip of the rostrum to the base of the telson was also adopted at this stage, in preference to using the overall length as previously. These groups were weighed and analysed as before, and Table VII shows the results obtained. The vitamin A content per specimen increased at first gradually, but the increase became disproportionately great in the larger size-groups, and the concentration, which was fairly constant in the smaller animals, showed an upward trend in the last four groups. Astaxanthin increased steadily in content with the size of the animal without any clear-cut change in the concentration.

TABLE VII. RELATIONSHIP BETWEEN OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM AND LENGTH AND WEIGHT IN *MEGANYCTIPHANES NORVEGICA* (M. SARS), TAKEN ON 14–15 FEBRUARY 1951, IN LOCH FYNE

(β-Carotene absent)

No. of specimens	Length* (mm.)	Mean wt. (mg.)	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)
12	17	45	4·9	22	455	88
43	19	70	2·2	17	759	60
47	21	94	1·8	13	700	57
32	23	115	1·7	20	1171	51
25	25	155	2·4	21	858	54
49	27	209	2·0	21	1035	53
116	29	265	3·1	16	529	51
207	31	312	3·4	18	524	54
123	33	394	3·6	22	603	51
134	35	469	4·6	32	704	72
102	37	513	5·6	50	895	75
37	39	636	5·5	62	1120	76
8	41	738	5·3	58	1089	69

* Length measured from tip of rostrum to base of telson.

Fig. 2 presents graphically the relationship between vitamin A and astaxanthin content and weight of specimen. In Fig. 3 the concentrations of vitamin A and astaxanthin have been plotted against size. The two substances measured show almost identical fluctuations.

Thysanoessa raschii. Next in importance to *Meganyctiphanes norvegica* as a food animal for whales in arctic krill is *Thysanoessa inermis* Krøyer. Because the closely related species *T. raschii*, which Einarsson (1945) regards as a fjord dweller, is available and obtained in large numbers in the same hauls as *Meganyctiphanes norvegica* in Loch Fyne, vitamin A was also studied in this species of euphausiid. Presence of the vitamin in high concentrations is shown in Table VIII. The ester form accounted for 95 % of the total.

The much higher concentrations of both vitamin A and astaxanthin in the January haul compared with the two August samples, which agree well between themselves, indicated a possible seasonal variation, but all these groups were random collections of different-sized animals, and experience

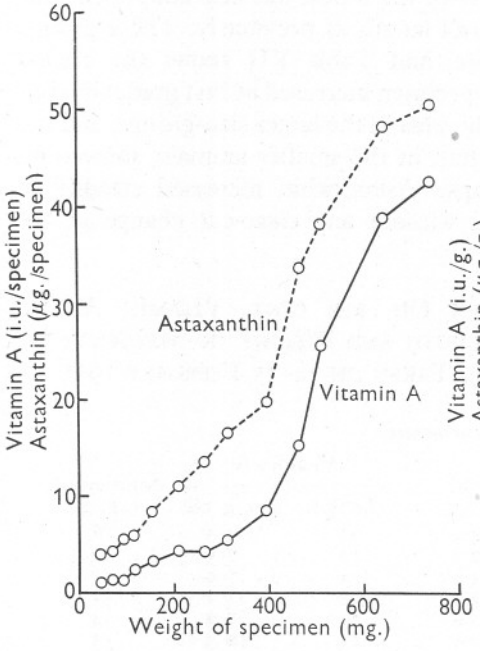

Fig. 2.

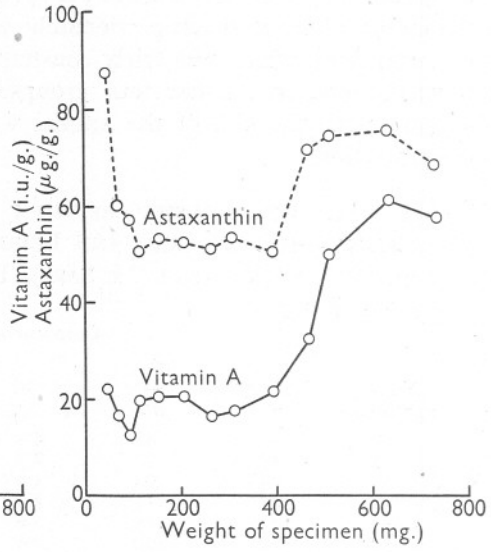

Fig. 3.

Fig. 2. Relationship between content of vitamin A and astaxanthin and size in *Meganyctiphanes norvegica* (M. Sars).

Fig. 3. Relationship between concentration of vitamin A and astaxanthin and size in *Meganyctiphanes norvegica* (M. Sars).

TABLE VIII. OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM IN *THYSANOESSA RASCHII* (M. SARS) FROM LOCH FYNE

(β-Carotene absent)

Date	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)	β-Carotene
18. viii. 49	6·6	32	495	33	Faint trace
4. i. 50	5·6	76	1366	58	Trace
17. viii. 50	6·1	32	520	31	Trace

with *Meganyctiphanes* suggested that a similar relationship between vitamin A content and size might occur in *Thysanoessa*. *T. raschii* was, therefore, separated into two size-groups of less and more than 20 mm. long, and a marked difference in vitamin A content was found, as is shown in Table IX.

A more detailed grouping of sizes was again done as with *Meganyctiphanes*, with results illustrated in Table X. With both vitamin A and astaxanthin the content increased with size, but the concentrations fluctuated considerably. These points are emphasized by the graphs in Figs. 4 and 5.

TABLE IX. RELATIONSHIP BETWEEN OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM AND LENGTH AND WEIGHT IN *THYSANOESSA RASCHII* (M. SARS)

(β-Carotene absent)

Date	Length overall (cm.)	Mean wt. (mg.)	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)
3. x. 50	<2	27	7·2	60	833	43
3. x. 50	>2	52	10·7	83	781	40
21. xi. 50	<2	24	6·9	51	734	38
21. xi. 50	>2	45	12·0	86	714	62
10. i. 51	<2	33	3·0	50	1680	44
10. i. 51	>2	81	3·0	69	2293	46

TABLE X. RELATIONSHIP BETWEEN OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM AND LENGTH AND WEIGHT IN *THYSANOESSA RASCHII* (M. SARS), TAKEN ON 14–15 FEBRUARY 1951, IN LOCH FYNE

(β-Carotene absent)

No. of specimens	Length* (mm.)	Mean wt. (mg.)	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)
32	11	10	6·6	77	1170	105
309	13	18	3·0	84	2790	58
479	15	23	2·9	75	2580	41
109	17	23	4·0	91	2270	54
30	19	38	4·9	113	2300	83
29	21	55	5·9	100	1690	37

* Length measured from tip of rostrum to base of telson.

Thysanoessa inermis. In hauls taken with 1 m. coarse silk nets at depths of 0, 20 and 100 m. in the Sandy Bank area (61° 54′ N., 5° 45′ W.) at 11 p.m., 6 November 1950, specimens of *T. inermis* were present in the tow-nets along with those of *Meganyctiphanes norvegica* already mentioned. The specimens were small, with a maximum length of 15 mm. in a species which, according to Einarsson (1945), reaches up to 32 mm. The analytical results are shown in Table XI.

Vitamin A was present in one group in concentrations comparable with those in *Thysanoessa raschii*. The most significant feature of these results, however, was that the oil content increased markedly with the depth from which the specimens were taken, irrespective of their size as shown by weight and, more interesting still, the vitamin A content and concentration also increased in a similar fashion. The content of astaxanthin, on the other hand, did not appear to be related to the depth. In *Meganyctiphanes norvegica*,

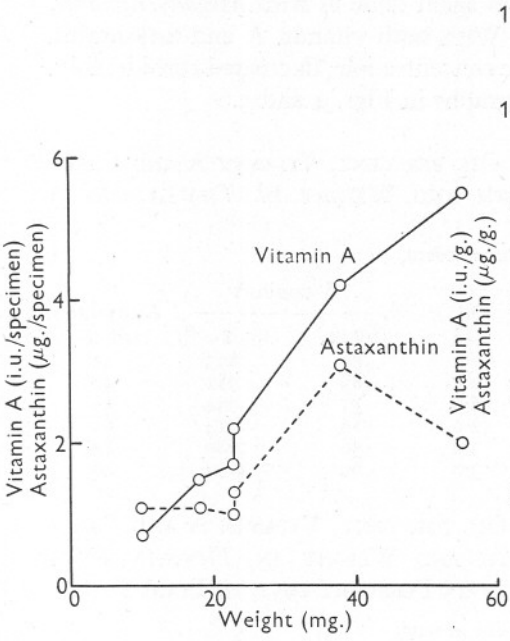

Fig. 4.

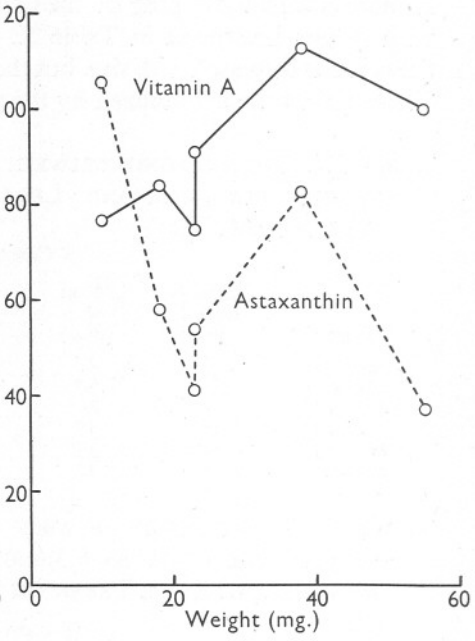

Fig. 5.

Fig. 4. Relationship between content of vitamin A and astaxanthin and size in *Thysanoessa raschii* (M. Sars).

Fig. 5. Relationship between concentration of vitamin A and astaxanthin and size in *Thysanoessa raschii* (M. Sars).

TABLE XI. OIL PER CENT, VITAMIN A AND CAROTENOIDS PER GRAM IN *THYSANOESSA INERMIS* KRØYER AND *MEGANYCTIPHANES NORVEGICA* (M. SARS) IN RELATION TO DEPTH OF HAUL

(β-Carotene absent)

Depth (m.)	No. of specimens	Mean wt. (mg.)	Oil (%)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./g.)
			Thyanoessa inermis			
0	374	8	5·2	5·7	110	73
20	253	11	8·3	12	148	66
100	124	7	12	55	474	86
			Meganyctiphanes norvegica			
0	91	80	3·9	16	410	65
20	200	100	5·6	19	343	57
100	225	100	4·1	16	381	55

taken in the same hauls with *Thysanoessa inermis*, no relationship was evident between content of vitamin A or oil and the depth. The results with *T. inermis* are, so far, only for an isolated set, but indicate that further investigation of a possible relationship between depth of haul and vitamin A content in this species may prove extremely interesting.

Benthic and Littoral Eucarida

So that comparisons with the Euphausiacea might be made, members of the other order of the subclass Eucarida, the Decapoda, were studied. Some of these animals were taken from the sea-bottom in the areas of Loch Fyne from which the euphausiids were obtained, and others were from shallower waters of this and other coasts. Details of the species studied and the results of analyses are given in Table XII.

The concentration of vitamin A was considerably less than anything found in the Euphausiacea, although in some of the larger animals, such as *Portunus*, *Pandalus*, and *Nephrops*, the vitamin content of individuals was on a scale comparable with that found in single specimens of *Meganyctiphanes* and *Thysanoessa*. *Crangon allmani*, *Pandalus bonnieri* and *Spirontocaris spinus* were all taken from depths of 140 m. with an Agassiz trawl in waters from which large numbers of *Meganyctiphanes* and *Thysanoessa* were caught in a 1 m. stramin net attached to the warp of the trawl about 10 m. above it. The figures for total carotenoids are given as such rather than for astaxanthin, since in some instances other pigments were present but were not isolated and identified. The concentration of carotenoids was lower than that of astaxanthin in the euphausiids, although larger species again showed high individual contents. β-Carotene was present in measurable quantities in oil extracted from *Eupagurus* and *Portunus*.

Other Crustacea

Pelagic Crustacea taken in the same hauls with *Meganyctiphanes* and *Thysanoessa* in Loch Fyne were the copepods, *Calanus finmarchicus* (Gunnerus) and *Euchaeta norvegica* Boeck. These were obtained on several occasions in sufficient quantities for vitamin A analysis. Other Crustacea also examined were the copepod, *Euchaeta barbata* Brady, which was taken during a deep oblique haul with a 1 m. silk net at midday on 7 November 1950, in the Faeroe-Shetland channel (61° 28′ N., 3° 42′ W.) with 1600 m. of warp out at a sounding of 1200 m.; the cladoceran, *Evadne nordmanni* Lovén, taken off the Norwegian coast, near Bergen; the littoral amphipod, *Gammarus marinus* Leach; and the isopod, *Orchomenella nana* (Krøyer), of which many were found feeding in the carapace of a dead crab. Table XIII shows the results obtained from examinations of these species.

Lederer (1938) examined *Calanus* caught at the end of May off the north coast of Norway and found no vitamin A in it. The results given in the table

Table XII. Oil per cent, Vitamin A and Carotenoids per gram in some Decapods

Species	Date	Locality	Oil (%)	Vitamin A (i.u./specimen)	Vitamin A (i.u./g.)	Vitamin A (i.u./g oil)	Total carotenoids (μg./specimen)	Total carotenoids (μg./g.)	Total carotenoids (μg./g. oil)	β-Carotene (μg./g.)	β-Carotene (μg./g. oil)
Crangon allmani Kinahan	31. viii. 49	Loch Fyne	1·3	0·5	0·4	30	7·0	5·0	390	—	Trace
	21. xi. 50	Loch Fyne	1·6	0·3	0·4	23	2·7	3·8	238	—	None
	15. ii. 51	Loch Fyne	1·7	0·7	0·7	41	5·3	5·5	324	—	None
Crangon vulgaris L.	28. vii. 49	Bay of Holland, Stronsay, Orkneys	0·8	—	0·2	21	—	5·0	550	—	Trace
Eupagurus bernhardus (L.)	11. xii. 50	Burnham-on-Crouch	1·3	1·2	0·2	15	240	41	3170	4·8	369
Nephrops norvegicus L.	13. ii. 51	Loch Fyne	0·6	7·7	0·04	7·3	1850	11	1800	0·02	3·8
Pandalus bonnieri Caullery	30. viii. 49	Loch Fyne	2·3	8·9	2·1	89	101	24	1000	—	Faint trace
	15. ii. 51	Loch Fyne	1·6	7·2	1·5	94	225	46	2850	—	None
Portunus puber (L.)	4. i. 50	Loch Fyne	0·8	28	0·3	39	2150	24	3100	2·8	350
Spirontocaris spinus (Sowerby)	31. viii. 49	Loch Fyne	2·9	0·8	0·6	22	34	27	950	—	Trace
	15. ii. 51	Loch Fyne	1·4	1·0	1·1	79	24	28	1970	—	None

Table XIII. Oil per cent, Vitamin A and Carotenoids per gram in some Entomostraca and Peracarida

Vitamin A absent, save in *Euchaeta norvegica*, 4 January and 17 August, 0·3 i.u., with 2 and 12 i.u./g. oil.

Species	Date (1950)	Locality	Oil (%)	Total carotenoids (μg./g.)	Total carotenoids (μg./g. oil)	β-Carotene (μg./g.)	β-Carotene (μg./g. oil)
Calanus finmarchicus (Gunnerus)	4. i	Loch Fyne	1·6	7	420	—	Trace
	17. iv	Loch Fyne	2·0	18	970	0·1	7
	26. vi	Near Norwegian coast	6·2	57	918	—	None
	4. x	Loch Fyne	7·9	24	331	—	None
	7. xi	Faeroe-Shetland channel	9·5	12	122	—	None
Euchaeta norvegica Boeck	4. i	Loch Fyne	11	107	1000	1·3	12
	17. viii	Loch Fyne	2·7	21	770	—	None
	3. x	Loch Fyne	11	73	642	—	None
	5. iv*	Loch Fyne	5·1	19	367	—	None
Euchaeta barbata Brady	7. xi	Faeroe-Shetland channel	10	72	693	—	None
Evadne nordmanni Lovén	5. vi	Near Norwegian coast	0	0	0	—	None
Gammarus marinus Leach	18. ix	Essex coast	2·1	35	1660	—	Trace
Orchomenella nana (Krøyer)	10. x	Burnham-on-Crouch	1·4	13	922	—	Faint trace

* 1951.

provide a confirmation and extension of this observation, since the samples were taken at other seasons and from different places, and show that vitamin A is permanently absent from this species.

The first two extracts of *Euchaeta norvegica*, taken in January and August, from hauls weighing 56 and 26 g. respectively, contained measurable quantities of vitamin A, since they gave, after chromatography, a good blue colour with antimony trichloride, but subsequent samples, taken in October and April and weighing 59 and 26 g., did not. In those specimens in which vitamin A was present, the concentration was, however, small (Table XIII). The oil content and total carotenoid concentration also fluctuated to a considerable extent, and more seasonal data are necessary to obtain a clear picture. The large deep-sea species, *E. barbata*, gave similar results to those obtained with the seasonally nearest sample of *E. norvegica*, namely, that taken on 3 October 1950.

Evadne nordmanni contained no detectable vitamin A in the quantity examined, but information is lacking as to weight or numbers of this sample. 556 specimens of *Gammarus marinus*, weighing 14 g., produced no reaction for the vitamin, nor did 4 g. of the carrion feeder, *Orchomenella nana*.

Anatomical Distribution of Vitamin A and Carotenoids

Concurrently with studies of the quantitative aspects of vitamin A and carotenoids in marine Crustacea, attempts were also made to determine whether these substances were locally concentrated or diffusely distributed throughout the tissues of the animals. The first dissection was crude. Cooked prawns (*Leander serratus* (Pennant)) from the fishmonger were divided into exoskeleton, cephalothorax and abdomen. Results of analyses showed a vitamin A concentration in the exoskeleton of 4·8 i.u./g.; in the cephalothorax, 0·4 i.u./g.; and in the abdomen, 0·1 i.u./g.

The observations of Wald (1941, 1943, 1945), Neilands (1947) and other workers on the presence of vitamin A in the eyes of various Crustacea, and general knowledge of its importance as a factor in the visual cycle, drew attention to the eyes as possible sites of accumulation of vitamin A. In addition, the eyes of euphausiids, which are rich in vitamin A, are bigger in relation to the rest of the animal than those of other Eucarida in which the vitamin is present in much smaller amounts. Lönnberg (1934) tested extracts from the eyes of several species of Eucarida and these gave, in every instance, a blue colour with antimony trichloride, especially intense with *Meganyctiphanes norvegica*. His technique, however, did not separate vitamin A and carotenoids.

Euphausiacea. At our request, Messrs Ash and Brachi, of the scientific staff of W.F.S. *Balaena*, divided some boiled specimens, weighing 20 g., of *Euphausia superba* from the stomach of a whale into three anatomical groups,

soft parts, exoskeleton and eyes, subsequently preserving them in alcohol. The oil was extracted from each group and tested for vitamin A. That from the soft parts contained 6 i.u./g., or 5·6 % of the total vitamin A of the 20 g. sample, that from the exoskeleton 38 i.u./g., or 27·7 %, and that from the eyes 1000 i.u./g., or 66·7 %.

Separation of the eyes from the rest of the animals was then carried out in the northern euphausiids, *Meganyctiphanes norvegica* and *Thysanoessa raschii*, and the eyes contained 92–98 % of the total vitamin A present in the former and 82–98 % in the latter. Typical results of these experiments are

TABLE XIV. DISTRIBUTION OF OIL PER CENT, VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN WHOLE ANIMAL (A) AND EYES (E) OF NORTHERN EUPHAUSIIDS OF DIFFERENT WEIGHTS

Tissue	Wt. (mg.)	Oil	Vitamin A (i.u./specimen)	Vitamin A (i.u.)	Vitamin A (i.u./g. oil)	Astaxanthin (μg./specimen)	Astaxanthin (μg.)	Astaxanthin (mg./g. oil)	Vitamin A (*V*) and Astaxanthin (*A*) in eyes as percentage of that in whole animal: *V*	*A*
					Meganyctiphanes norvegica (M. Sars)					
A	70	2·2	1·2	17	760	4·2	60	2·7	—	—
E	2	6·2	1·1	717	11,600	2·2	1,440	23	·92	52
A	312	3·4	5·5	18	520	17	54	1·6	—	—
E	5	4·7	5·4	1,150	24,400	5·6	1,200	26	98	33
A	738	5·3	43	58	1,090	51	69	1·3	—	—
E	11	1·0	40	3,610	361,000	14	1,220	122	94	27
					Thysanoessa raschii (M. Sars)					
A	18	3·0	1·52	84	2,790	1·1	58	1·9	—	—
E	0·5	8·3	1·48	2,740	33,000	0·8	1,490	18	97	73
A	38	4·9	4·2	113	2,300	3·1	83	1·7	—	—
E	0·5	15	4·1	7,750	51,300	2·5	4,680	31	98	81
A	55	5·9	5·5	100	1,690	2·0	37	0·6	—	—
E	0·8	9·0	5·4	7,000	77,700	1·5	1,980	22	98	75

shown in Table XIV. There was no marked variation in the percentage of vitamin A in the eyes throughout the series of size-groups. The high concentration of vitamin A in the oil from the eyes of the larger *Meganyctiphanes* is particularly striking, since it may represent a content of up to 5 % pure vitamin A. It is noteworthy that a high proportion also of the total astaxanthin content of the animal is present in the eyes, the amounts being 20–50 % in *Meganyctiphanes* and 60–80 % in *Thysanoessa*.

Further dissection of larger specimens of *Meganyctiphanes* was done in order to ascertain the location of the small portion of vitamin A not present in the eyes. The anatomical groups examined and the results derived from them are shown in Table XV. The body vitamin A appears to be about equally divided between the exoskeleton and the contents of the cephalothorax.

Decapoda. The anatomical distribution of vitamin A in the Decapoda was studied, and results obtained were similar to those given by the Euphausiacea

although certain differences correlated with the smaller concentrations of the vitamin present were noticeable. Cooked specimens of the common lobster (*Homarus vulgaris* M.-E.) were examined at an early stage in this connexion, but results for the whole animals are not available, since parts suitable for human consumption had been retained by the catering firm who kindly supplied the lobsters. In particular, the hepatopancreas was absent and so results for comparison with those of Neilands (1947), who found that this organ contained about one-third of the vitamin A present in the eyes in the

TABLE XV. DISTRIBUTION OF OIL PER CENT, VITAMIN A AND ASTAXANTHIN PER SPECIMEN AND PER GRAM IN *MEGANYCTIPHANES NORVEGICA* (M. SARS)

		Vitamin A			Astaxanthin		
	Oil (%)	(i.u./specimen)	(i.u./g.)	(i.u./g. oil)	(μg./specimen)	(μg./g.)	(μg./g. oil)
		Mean wt. of specimen, 386 mg.					
Exoskeleton	9·8	0·21	1·3	13	19	116	1,180
Cephalothorax contents	34	0·16	2·7	7·9	11	187	545
Abdomen contents	3·3	0	0	0	1·7	11	330
Eyes (pair)	11	14·3	2,460	22,400	11	1,950	17,700
Whole animal	10	14·7	38	376	43	111	1,100
		Mean wt. of specimen, 513 mg.					
Cephalothorax exoskeleton	6·6	0·7	5·3	80	14	100	1,520
Abdomen exoskeleton	3·1	0·3	3·4	110	0·8	11	362
Cephalothorax contents	9·2	0·8	7·8	85	6·6	63	680
Abdomen contents	2·1	0·2	1·2	57	0·9	5·6	267
Eyes (pair)	3·4	24	2,880	84,700	12	1,400	41,100
Whole animal	5·1	26	55	1,080	34	73	1,430

American lobster (*Homarus americanus*), are not yet available. Results for the lobster and other decapods are given in Table XVI. Though most of these animals have vitamin A present exclusively in the eyes, *Crangon allmani* and *Pandalus bonnieri* are interesting in that the vitamin is present also in the body, in amounts comparable with those found in bodies of *Meganyctiphanes* of similar sizes. The great difference is in the eyes, which are relatively much smaller in the Decapoda and contain less vitamin A, the concentration in *Pandalus* eyes, for instance, being only about one-tenth of that in those of *Meganyctiphanes*. The eyes of lobsters contain about 90 % of their vitamin A in the ester form, and a similar figure was obtained for the eyes of *Nephrops norvegicus*.

BIOLOGICAL TESTS

Methods

Preparation of Material for Tests with Rats and Standards used

The method of extraction was as described earlier in this paper. The oil obtained was diluted suitably with arachis oil and given directly to rats, or

TABLE XVI. DISTRIBUTION OF OIL PER CENT, VITAMIN A AND CAROTENOIDS PER SPECIMEN AND PER GRAM IN SOME DECAPODS

Part of animal	Date	Locality	Oil (%)	Vitamin A (i.u./ specimen)	Vitamin A (i.u./g.)	Vitamin A (i.u./g. oil)	Carotenoids (μg./ specimen)	Carotenoids (μg./g.)	Carotenoids (μg./g. oil)	β-Carotene (μg./g. oil)
Homarus vulgaris M.-E.										
Exoskeleton (anterior)	2. v. 50	—	1·0	0	0	0	10,500	48	4,800	60
Exoskeleton (posterior)	2. v. 50	—	2·0	0	0	0	1,550	72	3,600	44
Mixed internal organs*	2. v. 50	—	6·9	0	0	0	3,200	19	274	36
Ovaries	2. v. 50	—	16	0	0	0	—	151	911	100
Laid eggs	2. v. 50	—	14	0	0	0	—	139	1,010	154
Eyes (pair)	2. v. 50	—	1·6	11	23	1,410	35	75	4,700	59
Carcinus maenas (Pennant)										
Hepatopancreas	10. x. 50	Burnham-on-Crouch	2·0	0	0	0	57	33	1,640	368
Testes	10. x. 50	Burnham-on-Crouch	—	0	0	0	—	—	—	—
Eyes (pair)	10. x. 50	Burnham-on-Crouch	—	1·5	—	—	5	—	—	—
Crangon allmani Kinahan										
Body less eyes	21. xi. 50	Loch Fyne	1·5	0·3	0·5	31	2·9	4·4	293	None
Eyes (pair)	21. xi. 50	Loch Fyne	5·5	0·2	43	778	—	—	—	—
Cephalothorax exoskeleton	15. ii. 51	Loch Fyne	1·1	0·2	0·9	82	2·1	7·7	700	None
Abdomen exoskeleton	15. ii. 51	Loch Fyne	1·0	0·2	0·8	80	1·9	7·9	790	None
Cephalothorax contents	15. ii. 51	Loch Fyne	3·9	0·3	2·3	59	1·0	8·3	213	None
Abdomen contents	15. ii. 51	Loch Fyne	1·1	0	0	0	0·7	2·0	182	None
Eggs from 'berried' females	15. ii. 51	Loch Fyne	7·2	—	0	0	—	12	171	None
Eyes (pair)	15. ii. 51	Loch Fyne	12	0·1	28	231	0·4	75	631	None
Eupagurus bernhardus L.										
Body, less eyes	10. x. 50	Burnham-on-Crouch	3·6	0	0	0	178	43	1,200	38
Eyes (pair)	10. x. 50	Burnham-on-Crouch	0·6	0·5	23	103	0·5	46	8,250	None
Nephrops norvegicus L.										
Body, less eyes	13. ii. 51	Loch Fyne	0·6	0	0	0	1,840	11	1,790	4
Eyes (pair)	13. ii. 51	Loch Fyne	0·3	7·7	14	4,590	6·8	12	4,060	None
Eggs from 'berried' females	20. xi. 50	Loch Fyne	6·5	—	0	0	—	27	421	34
Pandalus bonnieri Caullery										
Average weight of specimens 4·9 g.										
Body, less eyes	15. ii. 51	Loch Fyne	1·6	2·4	0·5	31	224	46	2,870	None
Eyes (pair)	15. ii. 51	Loch Fyne	0·8	4·8	92	11,500	1·1	21	2,600	None
Average weight of specimens 1·7 g.										
Body, less eyes	15. ii. 51	Loch Fyne	1·5	1·0	0·6	40	35	20	1,350	None
Eyes (pair)	15. ii. 51	Loch Fyne	1·0	2·0	91	9,100	0·8	37	3,720	None
Spirontocaris spinus (Sowerby)										
Body, less eyes	15. ii. 51	Loch Fyne	1·4	0	0	0	24	27	1,940	None
Eyes (pair)	15. ii. 51	Loch Fyne	4·2	1·0	203	4,800	0·3	72	1,700	None

* Hepatopancreas and other edible parts absent.

subjected to chromatography to remove the bulk of the pigments, or saponified and chromatographed as for the chemical test, and the non-saponifiable residue containing vitamin A in the alcohol form was diluted with arachis oil for feeding to rats. For the rat-growth tests, the oils were kept under nitrogen in the refrigerator and tested periodically for vitamin A by the Carr-Price test.

For the liver-storage test, the standard was a fish-liver oil at 106,000 i.u./g., and for the rat-growth experiments the International Standard for vitamin A at 10,000 i.u./g. in cottonseed oil was used. Both were diluted suitably for feeding with arachis oil stabilized with hydroquinine.

Preparation of the Rats

Hooded Norwegian rats of our own breeding were used. Rats partly deficient in vitamin A were prepared exactly as described by Thompson *et al.* (1949). It will be recalled that such rats have vitamin A neither in the liver nor in the intestine, but have not stopped growing.

To obtain rats wholly deficient in vitamin A the mothers were deprived of milk, liver and carrots, their dietary sources of vitamin A, as soon as the young were born; from the 16th day of lactation they were given our vitamin A-deficient diet (Henry, Kon, Mawson, Stanier & Thompson, 1949). The young were weaned on to this diet at 21 days of age and continued on it during the 'running-out' and dosing periods.

Partly deficient rats were dosed by the method described by Thompson *et al.* (1949), except that actual or presumptive quantities of the order of 100, 50 and 25 i.u. of vitamin A from the standard or the oils under test were added to 400 mg. of arachis oil.

Experiment 1. In a preliminary experiment, rats were given the vitamin A alcohol chromatographically separated from the non-saponifiable residue of oil obtained from krill forming the stomach contents of fin whale 1 (see Table II), consisting mainly of *Euphausia superba*. They were anaesthetized after 3 hr., and the intestinal contents were washed out *in vivo*; the intestinal wall and contents and the liver were then analysed as described by Thompson, Braude, Coates, Cowie, Ganguly & Kon (1950).

Experiment 2. The non-saponifiable residue from oil of the same source as in Exp. 1 was diluted with arachis oil to a concentration of approximately 200 i.u./g. Three rats were used for each of three levels of standard or krill oil and were killed after 3 hr., the livers being removed for analysis.

Using wholly deficient rats the following rat-growth tests (Booth, Kon & Gillam, 1934) were performed.

Experiment 3. Groups of eight (four of each sex) deficient rats were dosed at the rate of 2 or 4 i.u. International Standard Vitamin A daily or with the non-saponifiable residue of the body oil of *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *Euphausia superba*; these were suitably diluted with

arachis oil and given to the rats to supply 2 and 4 i.u. vitamin A as determined chemically. The rats were dosed twice a week.

Experiment 4. Groups of fourteen (seven of each sex) deficient rats were dosed twice weekly, at the rate of 1, 2 and 4 i.u. daily with vitamin A standard or the non-saponifiable residue, dissolved in arachis oil, of the oil of *Meganyctiphanes norvegica* caught in Loch Fyne in January 1950.

Experiment 5. Groups of ten (five of each sex) deficient rats were used. Oil from *Thysanoessa raschii*, caught in Loch Fyne in January and August 1950, was tested intact or after chromatographic removal of the pigment; these oils were fed undiluted at levels supplying about 1, 2 and 4 i.u. vitamin A daily. The standard was also fed at these levels. Animals were dosed twice a week as in the other experiments.

Results

Experiment 1. The vitamin A in the intestinal wall of the rats was largely in the ester form, while in the liver both forms of vitamin A were present in roughly equal amounts. There was no vitamin A in the gut contents. The behaviour of the vitamin A from krill was, therefore, exactly the same as of that formed from β-carotene or of pure vitamin A, when given under similar conditions (cf. Thompson *et al.* 1950).

Experiment 2. The results of this experiment are given in Table XVII. In Fig. 6 the net vitamin A* stored in the liver is plotted against the dose of vitamin A for the standard. It will be noticed that the points lie on a straight line which does not pass through the origin. This curve can be used to estimate the potency of the krill oil by reading off, against the net liver stores of vitamin A, the corresponding amount of vitamin A in each dose.

These results show a strong similarity in the behaviour of vitamin A from krill and from fish-liver oils, though naturally storage in the liver cannot be taken as a decisive biological proof of the identity of the stored substance with vitamin A.

Experiment 3. Table XVIII shows the results of this experiment and indicates that the chemical potency was two to three times higher than the biological, despite the findings that the euphausiid vitamin A was chemically and physically indistinguishable from pure vitamin A.

Experiment 4. Table XIX shows that, even with the larger number of rats used and a more satisfactory test, the chemical result was almost twice the biological.

Experiment 5. The discrepancy between the chemical and the biological potencies is again apparent in Table XX, which also indicates that the pigments (astaxanthin) did not affect the biological activity, since there was no difference between results obtained with whole oil and those with whole oil less pigments. This also confirms biologically the absence of β-carotene or other precursors of vitamin A from the pigments.

* Net vitamin A = vitamin A stored in liver less vitamin A found in control livers.

TABLE XVII. EXP. 2. VITAMIN A, ALCOHOL AND ESTER, AS I.U. PER ORGAN, IN LIVER OF PARTLY VITAMIN A-DEFICIENT RATS DOSED WITH 0·4 G. ARACHIS OIL CONTAINING VITAMIN A FROM FISH-LIVER OIL (B) OR KRILL OIL (C)

Dose (i.u.)	Rat no.		Alcohol	Ester
100 B	1		14·2	9·1
	2		12·1	13·8
	3		10·8	7·7
		Mean:	12·4	10·2
50 B	4		7·3	5·2
	5		8·1	6·0
	6		5·2	5·2
		Mean:	6·9	5·5
25 B	7		3·6	3·4
	8		3·3	3·4
	9		3·3	3·6
		Mean:	3·4	3·5
79 C	10		4·3	8·6
	11		7·2	8·6
	12		8·2	9·9
		Mean:	6·6	9·0
39·5 C	13		3·7	3·0
	14		4·5	4·3
	15		3·5	3·2
		Mean:	3·9	3·5
19·8 C	16		3·0	2·6
	17		3·2	2·8
	18		2·8	2·8
		Mean:	3·0	2·7

Mean for two control rats: 1·0 alcohol, 2·7 ester.

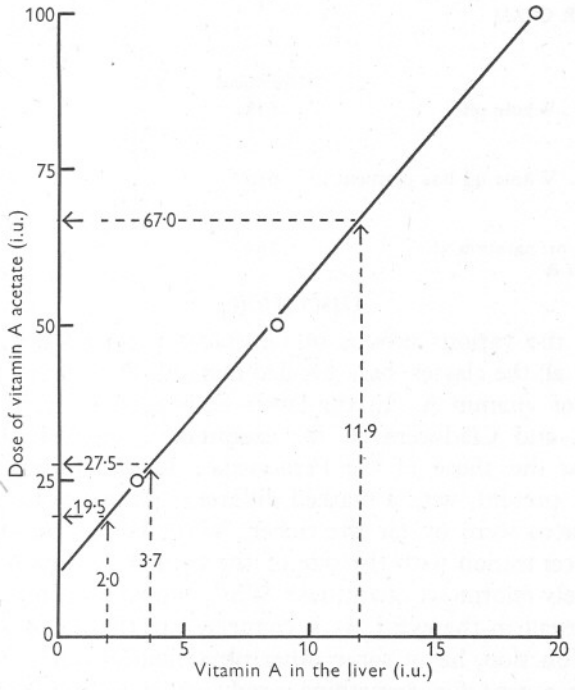

Fig. 6. Exp. 2. Liver storage tests with rats given the non-saponifiable residue of euphausiid oils. Graph showing relationship between dose of pure vitamin A acetate and vitamin A stored in the liver, and the calculation of doses of vitamin A corresponding to storage of vitamin A found in test rats.

TABLE XVIII. EXP. 3. CHEMICAL (ANTIMONY-TRICHLORIDE) AND BIOLOGICAL TESTS ON EXTRACTS FROM EUPHAUSIID OILS FED TO WHOLLY VITAMIN A-DEFICIENT MALE RATS, IN I.U. PER GRAM

	Chemical	Biological Value	Biological True fiducial limits ($P=0.95$)
M. norvegica	147	55·7	5·4 to 113·6
T. raschii	148	64·3	4·5 to 227·3
E. superba	158	71·3	9·9 to 138·5
Standard preparation of vitamin A	228	—	—

TABLE XIX. EXP. 4. CHEMICAL (ANTIMONY-TRICHLORIDE) AND BIOLOGICAL TESTS ON EXTRACTS FROM EUPHAUSIID OILS FED TO WHOLLY VITAMIN A-DEFICIENT RATS, IN I.U. PER GRAM

	Chemical	Biological Value	Biological True fiducial limits ($P=0.95$)
M. norvegica	378	—	—
♀ Rats	—	234	153 to 390
♂ Rats	—	307	192 to 612
Standard preparation of vitamin A	174	—	—

TABLE XX. EXP. 5. CHEMICAL (ANTIMONY-TRICHLORIDE) AND BIOLOGICAL TESTS ON EUPHAUSIID OILS FED TO WHOLLY VITAMIN A-DEFICIENT RATS, IN I.U. PER GRAM

	Chemical	Biological Value	Biological True fiducial limits ($P=0.95$)
T. raschii: Whole oil	678	—	—
♀ Rats	—	333	204 to 632
♂ Rats	—	391	249 to 730
T. raschii: Whole oil less pigment	610	—	—
♀ Rats	—	332	200 to 645
♂ Rats	—	443	279 to 869
Standard preparation of vitamin A	169	—	—

DISCUSSION

The study of the various groups of Crustacea reported here, though not covering so far all the classes, has revealed marked differences in content and concentration of vitamin A. In the lower Crustacea, the representatives of the Copepoda and Cladocera so far examined contained no measurable vitamin A, nor did those of the Peracarida. In the Eucarida in general vitamin A was present, with a marked difference between the two orders in that Euphausiacea were by far the richer. Why should the vitamin, rising sharply in concentration with the size of the animal, be found in this order in such relatively enormous quantities? Why, moreover, should it be almost exclusively present in the eyes? Is it connected in these animals with some special visual function, has it some other physiological duty, or are the eyes merely storage organs for something produced or accumulated in excess?

Decapods are predominantly benthic in their habits, and perhaps in their constant contact with the sea floor they have less need for acute vision than the free-swimming euphausiids. Admittedly other free-swimming Crustacea such as copepods contain no vitamin A, but their reaction to light may be of a different character from that of euphausiids, and in any case the structure of their eyes is much simpler. In fact, the exceptionally large and prominent eyes are a characteristic feature of euphausiids which may be specially well adapted for adequate vision in the low intensity of light at the depth they frequent. It will be recalled that a large specimen of *Meganyctiphanes norvegica* may contain in its eyes some 40 i.u. of vitamin A, and even allowing for the special demands of this order it seems hard to believe that vitamin A is needed there in such quantities solely for the functions of vision. In *Meganyctiphanes* the concentration of vitamin A in the eyes is in the range 2400–12000 i.u./g. dry weight (taking the water content as 70 %). With these figures may be compared the findings of Wald (1935) that mammalian retinas have vitamin A concentrations of about 70 i.u./g. dry weight and frog retinas have 1200 i.u./g., whereas the pigmented layers of the frog eye contain 6000 i.u./g. Morton & Rosen (1949) give results for seasonal variations of vitamin A in frog eyes. The highest value they obtained was about 3·5 μg./eye; in a frog of 20 g. weight of which the eyes account for about 1 % this gives a vitamin A concentration of 105 i.u./g. wet weight, or approximately 300 i.u./g. on the dry basis.

We intend to investigate the distribution and anatomical location of vitamin A in euphausiid eyes in the hope of finding thereby something more about its purpose there. In the meantime the possibility of its being to some extent an excretory substance cannot be dismissed.

Be it as it may, it is evident that baleen whales can derive from krill immense quantities of vitamin A, quite sufficient to account for the great stores of the vitamin in whale liver. According to Einarsson (1945) a large whale may have up to 1200 l. of krill in its stomach. This would be roughly a ton, and with a vitamin A potency of, say, 20 i.u./g. would yield about 2,000,000 i.u.

The richness in vitamin A of the food of baleen whales associated with the high concentration of vitamin A in their livers may be contrasted with its lack in another crustacean, *Calanus finmarchicus*, and the corresponding paucity in vitamin A of animals whose principal food it forms, the herring and the basking shark.

In the euphausiids studied by us vitamin A was accompanied in the eyes by astaxanthin in high concentrations and in fact a large proportion (20–50 % in *Meganyctiphanes norvegica* and 60–80 % in *Thysanoessa raschii*) of the total pigment of these animals was present there. The function of this characteristic pigment of Crustacea is not yet understood. Its value, if any, for the higher animals, preying on Crustacea, presents an interesting problem deserving

further study. Thus Wald (1945) found astaxanthin in the eyes of birds; Grangaud & Massonet (1950) report that it prevents and cures xerophthalmia in vitamin A-deficient rats, though it does not alleviate other signs of the deficiency or promote growth, and it is well possible that the pigment has some vitamin-like function. Its chemical constitution is such that it can hardly act as precursor of vitamin A itself. Furthermore, in our biological tests it proved entirely inactive in this respect. As corroborative evidence may be cited the fact that *Calanus finmarchicus* is at times quite rich in the pigment without apparently affecting the low vitamin A content of herring.

Again, we found no β-carotene in euphausiids, observations sharply at variance with those of Wagner (1939), who reported large quantities of β-carotene in northern krill, and we are entirely at a loss to understand how he came to detect this pigment. The finding of vitamin A in large quantities in certain euphausiids accounts, we hope adequately, for the immediate source of the vitamin A of the whale. It makes it also clear that baleen whales obtain most of their vitamin A as such and have no need and, indeed, no opportunity, to form it from precursors, though in common with other mammals they no doubt are able to do so. One link of a food chain is thus accounted for, but the fundamental problem of the site of origin of the vitamin A of marine organisms remains unexplained. The focus of attention has been moved from the whale to its food, and the question arises whether euphausiids in turn obtain their vitamin A preformed or whether they manufacture it themselves from precursors in their food.

Though our work on vitamin A in marine animals began more than two years ago, the more systematic study has been going on for little more than a year. In so short a period variations due to seasonal and other causes could be observed only in a very broad outline.

The relationship between size and vitamin A concentration in *Meganyctiphanes* stands out so clearly as to indicate close correlation. At first, size and content increase *pari passu*; with large animals the concentration also rises steeply. This may well indicate a change in food or metabolism around the weight stage of about 0·4 g.

Our data are, so far, insufficient to indicate seasonal variations in vitamin A content of *Meganyctiphanes*, especially as the size of the animal exerts such marked influence, but with *Thysanoessa raschii* the indications are clearer that the concentration of vitamin A may be higher during the winter months. Our evidence so far is that *Thysanoessa* differs from *Meganyctiphanes* in that concentration of vitamin A does not increase with size.

The isolated observation of the relation between vitamin A content and depth of haul in *Thysanoessa inermis* is striking, especially since the animals were of uniform size and *Meganyctiphanes* taken in the same hauls, also of uniform size, did not exhibit this variation.

In the decapods studied vitamin A was also largely concentrated in the eyes,

though in some species, of which *Crangon allmani* is the notable example, at least half of the vitamin was present in other parts of the body. We do not know yet whether in these animals it was adventitious in the alimentary canal or as a true constituent. We are also in a similar doubt about the small quantity of vitamin A found in euphausiids not in the eyes.

The values quoted for vitamin A throughout this paper are those derived from chemical and physical measurements. We are satisfied that these were done with the necessary care and after adequate purification and separation, but we are aware that so far all our biological tests have indicated a potency lower than that of corresponding laboratory measurements. This difference exists for all species studied regardless of the purity of the preparations fed, and suggests either the presence of growth-inhibiting substances closely associated with the vitamin A fraction or the presence in these purified fractions of chemically related substances giving rise to an artefact.

The work described in this paper has been supported by a grant from the Development Commission. Its success so far has largely depended on the ready assistance given by many people engaged in marine biological work and in the whaling industry, whom we have from time to time visited either for discussion or for the use of facilities they control. The unique facilities for collecting euphausiids in Loch Fyne have meant that the Marine Station at Millport has had much more than a fair share of our visits, and we are extremely grateful to Mr E. Ford and his staff, especially Drs S. M. Marshall, A. P. Orr and D. T. Gauld, for all their help and forbearance. We must also mention Dr C. E. Lucas and his staff at the Fisheries Laboratory, Aberdeen; Dr J. A. Lovern of the Torry Research Station, Aberdeen; Dr J. G. Sharp of the Low Temperature Research Station, Cambridge; Messrs Blomvåg Hval, their manager, Mr A. Hojem and Capt. H. Harneshaug of their catcher, *Hval* 2, in Norway; Messrs Scottish Whalers Ltd., and their manager, Capt. H. Jespersen, at West Loch, Tarbert, Harris; Messrs United Whalers Ltd. and their chemists, Mr C. E. Ash and Mr R. M. Brachi, of W.F.S. *Balaena*; Messrs M. Graham and R. S. Wimpenny of the Fisheries Laboratory, Lowestoft; Mr F. S. Russell and his staff at the Marine Laboratory, Plymouth; Mr R. D. Waugh and his staff at the Oyster Research Station, Burnham-on-Crouch; Drs N. A. Mackintosh and H. Bargmann and Mr R. Clarke and other members of the staff of the Discovery Investigations; Prof. C. H. O'Donoghue, Dr N. B. Eales and Mr M. I. Crichton of Reading University; and Dr E. B. Hughes and Mr D. H. F. Clayson of Messrs Lyons' Laboratories, Hammersmith.

We are deeply grateful to our colleague, Dr K. M. Henry, for the biological tests on rats, and we gladly acknowledge the collaboration of Miss I. E. Batham, M.H.Sc. (N.Z.), who took part in certain aspects of the study while on leave of absence from Otago University. We have had much analytical assistance from Miss W. M. Vardy.

SUMMARY

Planktonic, benthic and littoral Crustacea were collected from localities around the British coast, from Norwegian and Faeroese waters and from the Antarctic, and their content of preformed vitamin A and carotenoid pigments was measured.

Methods are described for the preservation of specimens, the extraction and separation of vitamin A and carotenoids and the measurement of vitamin A by chemical, physical and biological tests, and of carotenoids by physical tests.

Free-swimming euphausiids were found to contain, in addition to large quantities of astaxanthin, high concentrations of preformed vitamin A, but no β-carotene.

Krill, taken from the stomachs of whales, consisting of *Meganyctiphanes norvegica* in arctic waters and *Euphausia superba* in antarctic waters, also contained no β-carotene, but preformed vitamin A was present, although in lower concentrations than in free-swimming animals.

In *Meganyctiphanes norvegica*, the vitamin A concentration increased with the size of the animal, but in *Thysanoessa raschii* it was unchanged. In both species, the astaxanthin content, but not concentration, was higher in the larger animals.

The eyes of the euphausiids contained over 90 % of their total vitamin A, the rest being in the exoskeleton and contents of the cephalothorax. A high proportion of the total astaxanthin was also in the eyes.

The vitamin A concentration was much lower in the decapods, the difference being in the eyes, since their bodies contained the vitamin in quantities comparable to those found in the bodies of euphausiids.

Vitamin A was absent from the amphipods, isopods and Cladocera examined. In the Copepoda, *Calanus finmarchicus* was devoid of the vitamin, but it was present in small quantities in some samples of *Euchaeta norvegica*.

Biological tests with rats on oils or concentrates from euphausiids indicated potencies about one-half those expected from results of chemical and physical tests. The pigments showed no biological activity.

It is suggested that the high vitamin A content of euphausiids forming the food of whales is adequate to account for the rich liver stores of the vitamin in those mammals.

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NOTES ON THE GROWTH AND BIOLOGY OF THE PRAWN *PANDALUS BONNIERI* CAULLERY

By R. B. Pike

The Marine Station, Millport

(Text-figs. 1 and 2)

Pandalus bonnieri Caullery has for a long time been known to occur in considerable numbers in the deeper waters of the Clyde Sea Area. Its life history and growth have been investigated, with special reference to sexual development, since the genus *Pandalus* contains not only species that are dioecious, but also those that are protandrous.

The author expresses indebtedness to the skipper and crew of M.V. *Calanus* for their unfailing help in collecting the material, and to Miss E. R. Wallace for assistance in measuring specimens. Thanks are also due to Dr A. Ritchie at the Fisheries Laboratory, Aberdeen, for supplying records of the occurrence of *P. bonnieri* on the west coast of Scotland and in the North Sea, and to colleagues at the Marine Station for assistance in preparing this paper.

Collection of Material and Data

All adult prawns were caught in the Firth of Clyde on trawling grounds off the Island of Bute (National Grid Reference 26/1159–1162) at a depth of 70–90 m. The gear used was an 8 ft. Agassiz trawl having a net mesh of $\frac{1}{2}$ in. bar, which was found to retain prawns above 7 mm. carapace length (3·7 cm. total length). The duration of a haul was 15 min., and such hauls were repeated until a sufficient number of specimens had been obtained for the day's sample.

For catching prawns smaller than 7 mm. carapace length, a 2 m. stramin net was fixed to a small beam trawl, so modified that the net worked about 6 in. above the muddy bottom. Early post-larval stages were seldom obtained in any numbers.

All specimens above 5 mm. carapace length were measured with fine calipers in the fresh condition and then fixed in 10% formalin for subsequent preservation in 70% alcohol.

The standard measurement made was the 'length of the carapace', being the distance from the posterior margin of the eye socket to the dorsal posterior

margin of the carapace. Measurement was made to the nearest 1 mm. below, and the data were recorded in 1 mm. groups.

An approximation to the *total* length, including the rostrum, can be obtained by multiplying the *carapace* length in the male by 5·2, and in the female and juvenile by 5·4. In both males and females of carapace length exceeding 17 mm., however, the total length calculated in this manner works out on the high side.

Geographical Distribution

P. bonnieri Caullery is essentially a deep-water prawn and, like *P. borealis* Krøyer, is usually found at a depth of about 100 m. Its distribution extends from Iceland (Stephensen, 1939, p. 22) to the Bay of Biscay (Caullery, 1896). It does not appear to be very plentiful round Iceland or to enter Greenland waters. From Norway it is recorded by Wollebaek (1908) from several localities in both the south and west. Dr Ritchie has kindly supplied me with sixty records of its occurrence in the North Sea and from the west coast of Scotland. These records show that it is taken frequently in the North Sea from the Shetland Isles to Peterhead, and on one occasion was taken as far south as 56° 03′ N., 1° 45′ W. The majority of specimens were obtained beyond the 100 m. line along the western edge of the deep central basin of the North Sea, but they were not abundant at any locality. On the west coast of Scotland it is also taken beyond the 100 m. line and appears to be generally distributed, the greatest numbers being obtained off the Butt of Lewis and south of South Uist. In general, records are absent for the north of Scotland and west of the Outer Hebrides, but the prawn has been obtained on two occasions west of the Orkneys. Dr Ritchie suggests that their absence from these areas may be due to the texture of the sea-floor in those localities. Calman (1899) was the first to record it from the Firth of Clyde. He also records it from the west coast of Ireland and off Rockall. Kemp (1910) states that it is abundant in the Irish Sea and off the west coast of Ireland, but it has not so far been taken off the south of Ireland. It is not recorded in the *Marine Fauna of the Isle of Man* (Moore, 1937), but Mr N. S. Jones of the Marine Biological Station, Port Erin, informs me that he has taken it frequently since 1946 on muddy bottom in 90–130 m., 7–11 miles north-west of Bradda Head. It does not appear in the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931). Lebour (1940), however, records the larvae as occurring in plankton off Seven Stones Lightship, Scilly Isles (50° 03½′ N., 6° 04½′ W.).

Occurrence in the Clyde

In the Clyde *P. bonnieri* is taken frequently in water as shallow as 40 m., although it is most abundant at depths of 90–130 m., on grounds composed of soft grey mud, inhabited by an animal community similar to that associated with *P. borealis* as described by Hjort & Ruud (1938).

The commonest bivalve molluscs are *Abra alba* (Wood) and various species of *Nucula*, of which *N. nucleus* (L.) and *N. sulcata* Bronn are the commonest. *Thyasira flexuosa* (Montagu) is, however, rare and *Chlamys septemradiata* (Müller) is not very abundant on this ground. Among the annelids, *Pectinaria belgica* (Pallas), *Lipobranchius jeffreysii* (McIntosh) and *Glycera rouxi* Audouin & M.-Edwards are all very plentiful. Of the Crustacea, *Spirontocaris spinus* var. *lilljeborgi* (Danielssen), *Crangon allmani* Kinahan and *Nephrops norvegicus* L. are the commonest species.

Migration

Berkeley (1931) drew attention to evidence that larvae of pandalids metamorphose in shallow water, and Poulsen (1946) also found young *Pandalus borealis* in shallow water round Denmark. In the Clyde the normal prawn grounds, and the shallow water areas in the neighbourhood, were trawled with a bottom stramin net (see collection of material and data) during June and July 1951 for early metamorphosed prawns. These were not obtained in any numbers until 31 July at a depth of 130 m. No information was therefore obtained on the movements of young *P. bonnieri*.

Adult prawns could not be found during August and September 1951 in the Clyde. According to Hjort & Ruud (1938) *P. borealis* rises off the bottom during dull weather and during the hours of darkness. A similar habit in *P. bonnieri* might account for the difference in numbers on successive days, but not for the scarcity of specimens during two months. It is possible that both the young and adults moved into the nearby inshore boulder-strewn grounds where trawling was impossible.

Breeding

In the Clyde the ovaries of adult prawns begin to mature in July, when they show through the carapace as a greenish mass. In September the fully ripe ovaries darken to a deep sage green. Egg-laying begins at the end of October with the larger size-groups laying first (Fig. 1A), and continues for about 6–8 weeks. By the end of December the whole adult female population is in berry (Fig. 1B).

The eggs when first laid are a beautiful deep green colour and oval in shape (*c.* 2 × 1·5 mm.). The sage-green colour of the newly laid egg in *P. bonnieri* is in contrast with the blue-green egg of *P. borealis*, the light emerald green of *P. montagui* Leach and the fawn colour in *P. propinquus* G. O. Sars.

The green colour gradually disappears as the larvae develop, and just before hatching takes place the green is almost replaced by pale violet and yellow pigmentation with the prominent red chromatophores of the thoracic region clearly showing. The eye pigmentation develops gradually and is first seen after about 3 months' incubation.

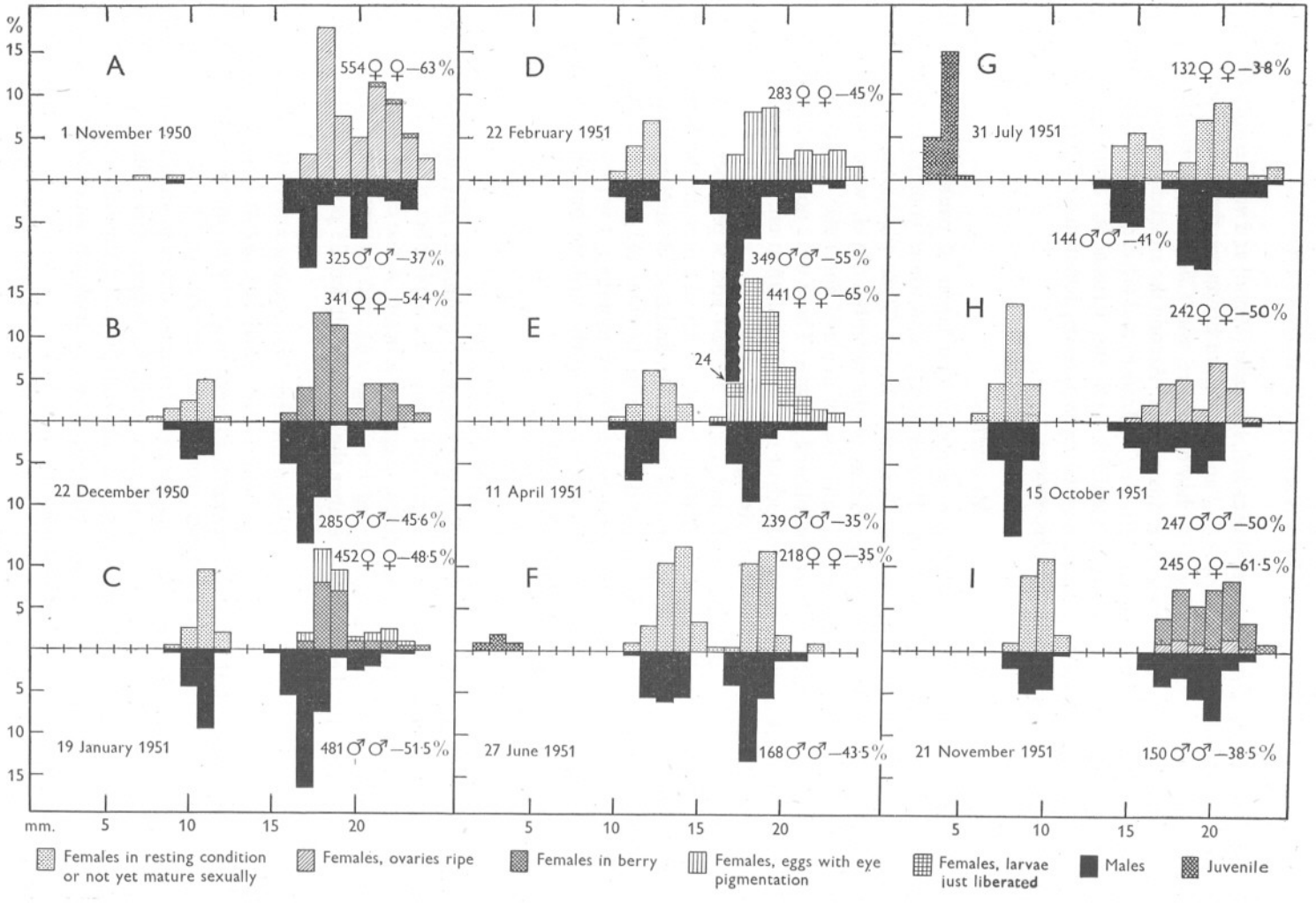
%
15
10
5
A
1 November 1950
554♀♀—63%
325♂♂—37%
B
22 December 1950
341♀♀—54·4%
285♂♂—45·6%
C
19 January 1951
452♀♀—48·5%
481♂♂—51·5%
D
22 February 1951
283♀♀—45%
349♂♂—55%
E
11 April 1951
441♀♀—65%
24
239♂♂—35%
F
27 June 1951
218♀♀—35%
168♂♂—43·5%
G
31 July 1951
132♀♀—38%
144♂♂—41%
H
15 October 1951
242♀♀—50%
247♂♂—50%
I
21 November 1951
245♀♀—61·5%
150♂♂—38·5%
mm.
5
10
15
20
Females in resting condition or not yet mature sexually
Females, ovaries ripe
Females in berry
Females, eggs with eye pigmentation
Females, larvae just liberated
Males
Juvenile

Fig. 1.

The number of eggs laid by *P. bonnieri* increases from approximately 1000 at 16 mm. carapace length to 4000 at 24 mm. carapace length. Within any given millimetre size-group the variation appears to be *c.* ±10%.

In 1951 the first larvae were liberated in the third week in February, although the number of prawns that had completed incubation was too small to be recorded on the graph for 22 February (Fig. 1D). The total hatching period extended over 2 months and all the larvae were liberated by the end of April (Table I).

It is probable that moulting and the loss of the ovigerous setae take place within 10 days of the liberation of the larvae from the eggs, but the period is not known. Höglund (1943) has described and illustrated the ovigerous setae for *P. borealis* and shown the arrangement to be similar for *P. bonnieri*.

TABLE I. BREEDING CONDITION IN SECOND- AND THIRD-YEAR *PANDALUS BONNIERI*

Date (1950–1)	Ovary ripe (%)	Eggs (%)	Eggs with eye pigmentation (%)	Larvae liberated (%)
15 Oct.	100	—	—	—
26 Nov.	22	78	—	—
6 Dec.	3	97	—	—
19 Jan.	—	60	40	—
22 Feb.	—	—	98	2
19 Mar.	—	—	90	10
11 Apr.	—	—	54	46
5 May	—	—	—	100

SEXUAL DIFFERENTIATION IN *PANDALUS BONNIERI*

Over one whole year, the percentage of males in the catches has varied between 35 and 55%, about a mean of 45%, and that of the females between 38 and 65%, about a mean of 55%. The sex was determined by the examination of the pleopods under the binocular microscope. The sex characters of *P. bonnieri* agree very closely with those given by Wollebaek (1908) for *P. borealis*. Among the males no transitional form of pleopod corresponding to that illustrated by Jägersten (1936) for *P. borealis* was found.

Many male prawns were dissected, but not one was found to possess oviducts as well as vasa deferentia. Sections of the male gonad in prawns aged 18–30 months have been prepared, from which it could be seen that the gonad

Legend to Fig. 1.

Fig. 1. The percentage size distribution of *Pandalus bonnieri* in the Clyde Sea Area during 1950–51. Females above and males below the zero line. To the left the date of collection. To the right the number of females and males measured in each sample in total and in percentage of the whole sample. The juvenile population in Fig. 1 is included in the total percentage although captured with a different gear (see p. 259). In the females the state of sexual maturity is also shown.

was composed entirely of testicular tissue with no trace of ovarian tissue such as was found by Jägersten in *P. borealis*.

I therefore think *P. bonnieri* is completely dioecious. This finding is confirmed by Dr Ritchie in a personal communication.

Rate of Growth in *Pandalus bonnieri*

The data obtained on growth are shown in graphic form in Figs. 1 and 2 and summarized in Table II.

In preparing Fig. 2 the graph relates to modal lengths and not to arithmetic means as were used by Hjort & Ruud (1938) for *P. borealis*, by Höglund (1943) for *Leander squilla* (L.) and by Forster (1951, *a*, *b*) for both *L. squilla* and *L. serratus* Pennant.

Table II. Growth of *Pandalus bonnieri*

	O-Group		I-Group		II-Group	
Month of year	Age in months	Carapace length (mm.)	Age in months	Carapace length (mm.)	Age in months	Carapace length (mm.)
Apr.	0–2	0·9–1·2	12–14	♂ 11–12 ♀ 12	24–26	♂ 18 ♀ 18–19
June	2–4	2·5–3·0	14–16	♂ 12–14 ♀ 13–14	26–28	♂ 18 ♀ 18–19
July	3–5	3–5	15–17	♂ 14–15 ♀ 15	27–29	♂ 18–19 ♀ 19–20
Oct.	6–8	♂♀ 7–9	18–20	♂ 16 ♀ 17–18	30–32	♂ 19 ♀ 20
Nov.	7–9	♂♀ 9–10	19–21	♂ 17 ♀ 18	31–33	♂ 20 ♀ 21–22
Dec.	8–10	♂♀ 10–11	20–22	♂ 17 ♀ 18–19	32–34	♂ 20 ♀ 21–22
Jan.	9–11	♂♀ 10–11	21–23	♂ 17 ♀ 18–19	33–35	♂ 20 ♀ 22
Feb.	10–12	♂ 11 ♀ 12	22–24	♂ 17 ♀ 18–19	34–36	♂ 20 ♀ 21

On hatching in March and April the larvae have a carapace length of 0·9 mm. (total length 4·2 mm.), and by the end of June, now from 2 to 4 months old, they have metamorphosed and have a carapace length of 2·5–3 mm. Metamorphosis takes place at about 2·2 mm. carapace length. By the end of July they have increased their carapace length from 3 to 5 mm., and are still juvenile, with the sexes undifferentiated. At 5 mm. carapace length it becomes possible to distinguish the sexes by the shape of the pleopods, but the developing males at this early stage are less readily

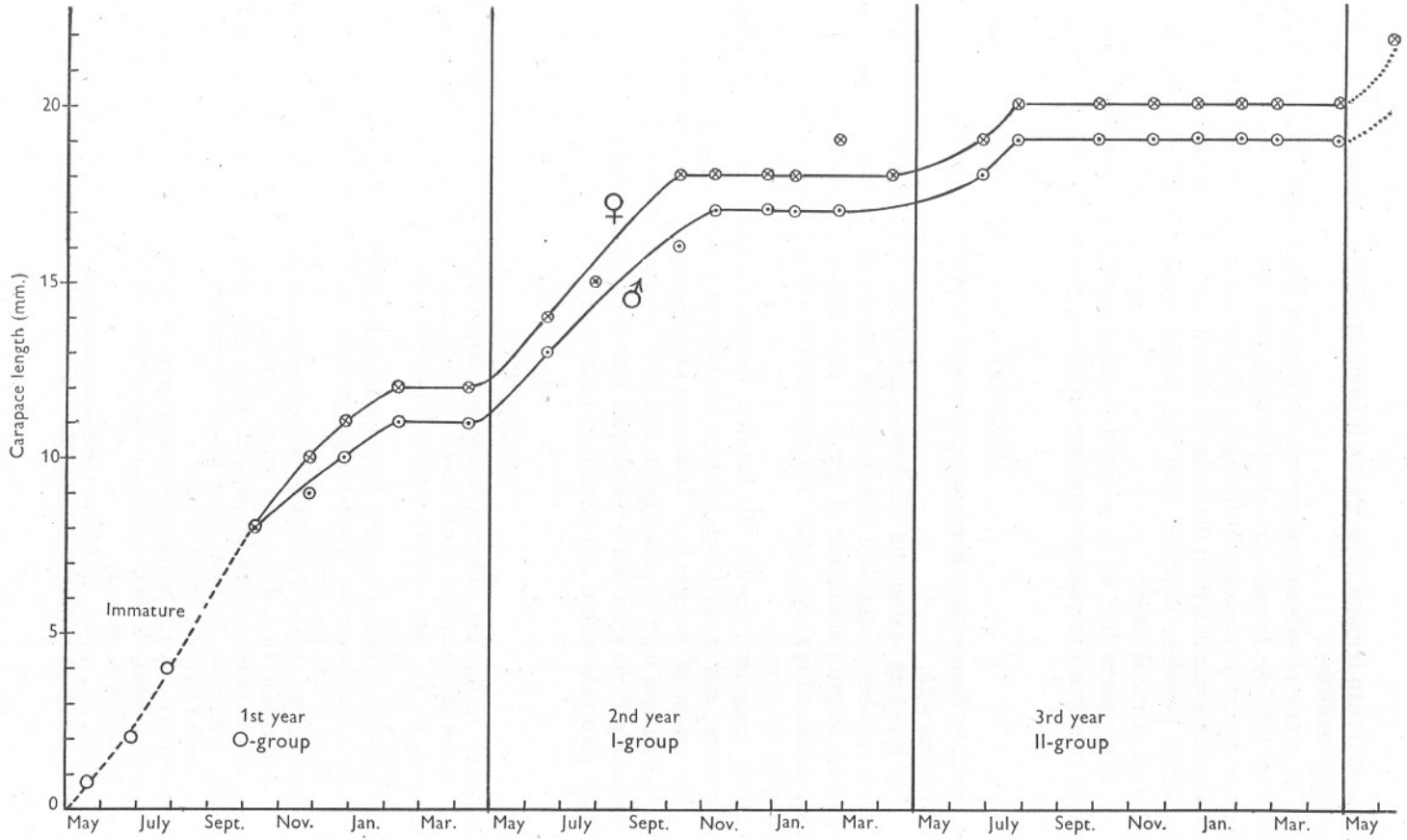

Fig. 2. *Pandalus bonnieri*. Modal lengths of various samples of three year-groups, forming an approximate growth curve.

separated than females from the undifferentiated juveniles because of a more gradual transition.

The course of subsequent growth is shown in Fig. 2 and Table II. It will be seen that the females are always larger than the males of a similar age. Sexual maturity is reached at the age of 18–20 months (i.e. October) when the average carapace length in the males is 16 mm. and in the females 17–18 mm. It seems possible, however, that the males reach maturity somewhat in advance of the females.

A few prawns live on to a fourth year, reaching a carapace length of 23–24 mm. but the numbers are very small and insufficient for inclusion.

Summary

Pandalus bonnieri is a dioecious species and no protandrous hermaphrodites have been seen.

The breeding season and incubation period for *P. bonnieri* are described.

The number of eggs laid increases with the size of the female. At 16 mm. carapace length the number of eggs is *c.* 1000 and at 24 mm. carapace length the number of eggs is *c.* 4000. The number for a single mm. size group varies roughly by $\pm 10\%$.

Both male and female *P. bonnieri* become sexually mature at about 18 months, and in the Clyde seldom live beyond 3 years of age.

The colour of the eggs in *P. bonnieri* is sage green, in *P. borealis* blue green, in *P. montagui* light emerald green and in *P. propinquus* fawn.

Juvenile *P. bonnieri* can be separated into males and females by the shape of the pleopods within 4–6 months of hatching.

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A NOTE ON THE BREEDING SEASON, SEX RATIO AND EMBRYONIC DEVELOPMENT OF THE DOGFISH *SCYLIORHINUS CANICULA* (L.)

By John E. Harris

Department of Zoology, University of Bristol

(With an Appendix by C. A. Hoodless and G. A. Steven)

(Text-figs. 1–3)

For many years past the Department of Zoology at Bristol has obtained all its dogfish from a single supplier, Mr E. G. Williams of Ilfracombe. In addition to those fish purchased for dissection, a large number has been obtained for work on the development of the behaviour pattern in the embryo, and over the last 3 years a certain amount of detailed but incidental information has been accumulated on the topics which form the title of this paper. This information supplements the interesting account given by Ford (1921), and since it is not proposed to carry out a more detailed study on these subjects, the material is offered in its present form as a short additional chapter on the biology of a common laboratory type, and in the hope of stimulating further work on these lines.

In addition to noting the numbers and sex of all dogfish delivered at the Department, all well-developed eggs are removed from the oviducts of the females and are reared in the laboratory aquarium, where a very high proportion of the embryos (70–100 % of those received in the cooler months of the year) develop successfully. There is no reason to believe that the fish received are other than random samples of the population caught, and the necessarily tentative deductions made below are based on this assumption.

The Breeding Season

Ford (1921) presents evidence which suggests that eggs are laid throughout the year. This may well be true, but the Ilfracombe fish show a rather more sharply defined breeding season than the Plymouth material. No consignments have ever been delivered in the month of August, but for the remaining months of the year the number and percentage of females carrying egg-purses is shown in Table I and Fig. 2. The deliveries covered a continuous period from May 1949 to December 1951.

While the figures for some months are smaller than one could wish, they appear to show that breeding starts in November when only 18 % of the

females are carrying egg-purses, and continues at least until July. From December to July any sample examined will show about one-third of the females carrying egg-purses, and this proportion remains remarkably constant.

TABLE I

Month	No. of fish delivered			No. of females carrying egg-purses
	Male	Female	Total	
Sept.	7	50	57	0
Oct.	25	44	69	0
Nov.	83	197	280	35
Dec.	49	145	194	41
Jan.	7	172	179	73
Feb.	31	47	78	16
Mar.	115	186	301	62
Apr.	71	61	132	20
May	228	158	386	47
June	119	61	180	19
July	8	34	42	13
Aug.	—	—	—	—

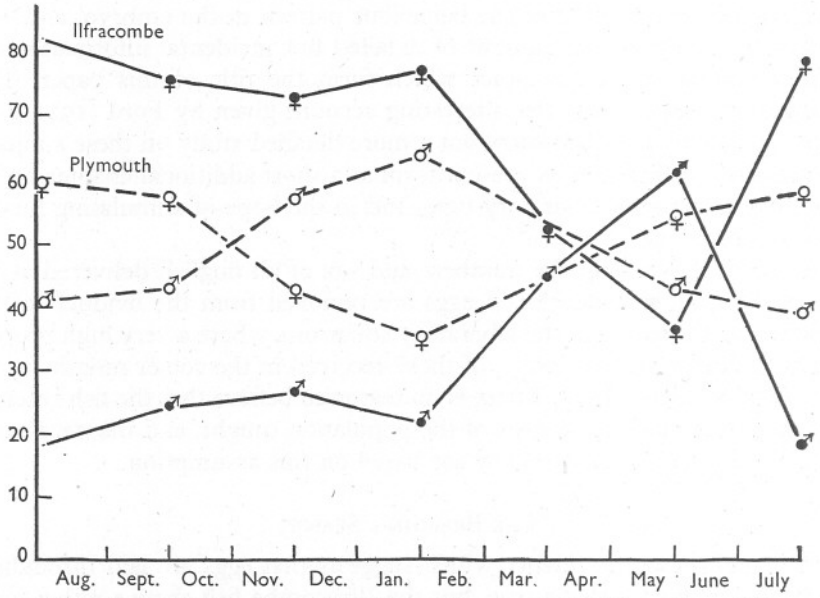

Fig. 1. *S. canicula*. The percentage of males and females in the Ilfracombe and Plymouth samples at different times of year (Plymouth figures from Ford, 1921).

In September and October, however, no egg-purses were found in ninety-four female fish. These are also the 2 months showing the smallest percentage of egg-bearing females in Ford's analysis (his figures for August are based on only five females of which two carried egg-purses). This observation would accord with the statement of Lloyd (1942) that, in the few specimens of

Scyliorhinus canicula taken at Weston in October and November, the gonads were developing.

The constant proportion of females carrying egg-purses over 8 months (perhaps 9) of the year, and the fact that no appreciable size variation has been associated with this condition, tempts one to suggest that within this period *all* the females in our Ilfracombe samples have been mature. Since fish which have just laid and which have not yet formed a hardened egg case around the next egg in the series would, on this assumption, constitute the remaining two-thirds of the female population, the figures suggest that the

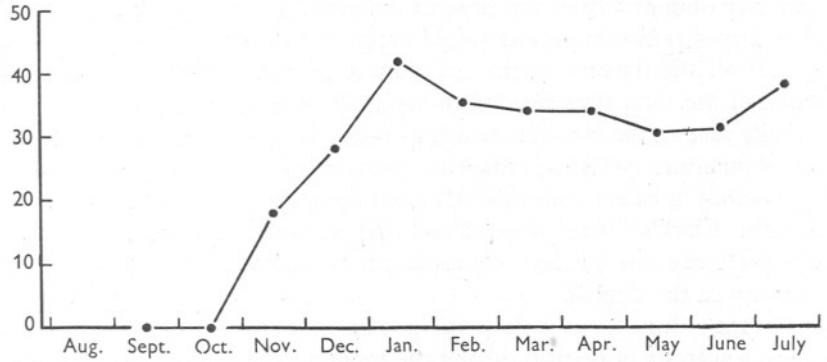

Fig. 2. *S. canicula*. The percentage of females carrying fully formed eggs. The proportion indicated therefore excludes (*a*) all fish which have just laid their eggs and have not yet completed the secretion of the next egg cases in the sequence, as well as (*b*) the immature females in the population.

time occupied by the fully formed egg-purse in the oviduct is one-third of the total time needed from ovulation to laying. If, on the other hand, a substantial number of immature females existed in the population during the winter months, the proportion of egg-bearing fish would be expected to rise as the breeding season progresses—which is apparently not true after November.

The Sex Ratio

The total number of fish examined was 1898, of which 743 or 39·1 % were males. This presents an interesting difference from Ford's figures, in which out of 4368 fish, 2401 or 55·0 % were males. Apart from this predominantly female population in the Ilfracombe fish, the detailed analysis of the seasonal variation shows an almost exactly opposed trend to that at Plymouth; females predominate in the winter and spring months, and only in May and June is there an excess of males (Fig. 1).

The proportion of females in the Ilfracombe population is very high in September, and remains high until the end of January; not until February does the proportion of males begin to increase substantially. Yet we have

supposed that most, if not all, the females caught after November are fully mature and producing fertilized eggs. Metten (1939) has proved that the folds of the shell-secreting portion of the nidamentary gland serve as a sperm reservoir; viable sperm can be stored there for long periods. It is therefore quite possible that the females are inseminated in deeper waters before they come into the Ilfracombe region to lay their eggs. The fact that the Bristol channel region is a natural spawning ground for the females is indicated by records of egg cases taken in Bridgwater Bay, Kilve and Blue Anchor (Lloyd, 1941, 1942).

An approximate estimate of the productivity of the female *S. canicula* can be indirectly obtained from the present material. The maximum variation in age of embryos reared from any single batch of fish received has been about 2 days. If all the females in the population are mature, we have seen that one-third of the total time needed to produce each egg is spent by the fully formed egg case in the oviduct; two eggs must therefore be laid every 6 days. If the population contains immature females, the productivity must be proportionately greater; consequently each female must lay at least ten eggs per month. Clark's (1922) observation that an isolated *Raia brachyura* laid twenty-seven eggs in 49 days is consistent with this high estimate of egg productivity in the dogfish.

Ford's (1921) figures, as well as the present ones from Ilfracombe, appear to suggest a scarcity of dogfish during the months of July and August. This is not in fact true; the low figure for these months merely indicates the holiday season at Ilfracombe, and according to Ford (personal communication) a corresponding absence of records at Plymouth. Neither Ford nor the present writer would claim any quantitative significance in the figures for total catch per month; Hoodless and Steven's table (Appendix, Table II) therefore adds an interesting and useful summary on this point, showing no sign of any fall off in numbers during the summer months.

Growth of the Embryo

In the course of the behaviour studies mentioned it has been necessary to assign accurate growth stages to the embryos, particularly in the period up to the development of the pelvic fins and external gill filaments, by which time the adult physiological pattern has been largely established. It is fortunate that over the whole of this range the correspondence with the stages of development of *Squalus acanthias*, so fully described and figured by Scammon (1911), is almost exact. Scammon's tables have therefore been used throughout the work, and have made possible a fairly accurate picture of the rate of development. The marine aquarium at Bristol is refrigerated and thermostatically controlled, but the refrigeration plant was out of action for a long period. During the whole time, morning and evening records of the

water temperature were kept, and the curves in Fig. 3 show the time taken to attain the various stages described by Scammon at several different temperatures. Where the temperature varied during development, the value given is the mean throughout the whole of the development up to the time the embryo was removed for examination.

The curves are useful for those who wish to obtain specimens of known morphology for embryological work, but they also offer one additional piece of information. The curve for 15·5° C. is reasonably complete, and the few

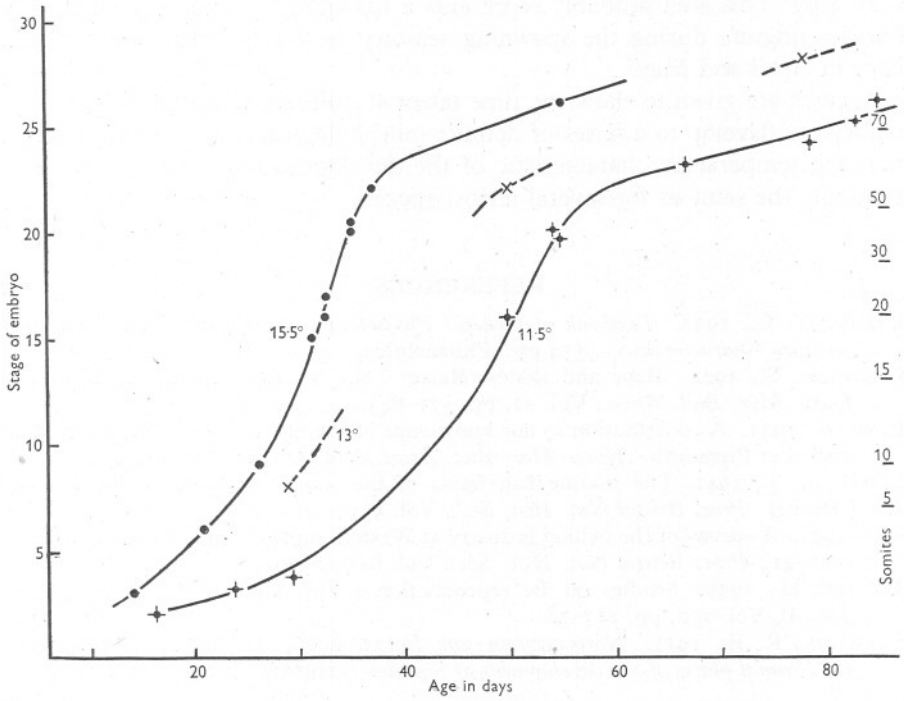

Fig. 3. *S. canicula.* Growth curves of the embryo dogfish. The stages correspond with those given in Scammon (1911).

points available on the 11·5° C. curve correspond exactly to a development time which, stage for stage, is 1·64 times as long as at the higher temperature. For what it is worth, this ratio corresponds to a temperature coefficient of rate of development with a value of $\mu = 20{,}000$. This figure is not very accurate, since the temperatures are not known to a sufficient degree of exactness, but it is probably within $\pm 10\,\%$. It appears, therefore, that the temperature characteristic of the development of this elasmobranch is close to the values obtained for several teleost fishes—trout, cod, plaice, etc. For a summary of these values the reader is referred to Barnes (1937).

As well as to Mr E. G. Williams of Ilfracombe, who supplied the dogfish in such excellent condition, the writer is particularly indebted to Mr C. Bees, without whose accurate records and constant care of the aquarium this short paper could not have been written.

Summary

Records of nearly 2000 dogfish collected from the Ilfracombe region suggest that the spawning season of this fish starts in November and continues at least until July. This area probably represents a spawning ground into which the females migrate during the spawning season; the males follow them much later in April and May.

Figures are given to show the time taken at different temperatures for the embryo to develop to a series of definite morphological stages; these suggest that the temperature characteristic of the development ($\mu = 20{,}000$) is substantially the same as for several teleost species.

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Appendix

Occurrence of Scyliorhinus canicula (*L.*) *off Plymouth*

By C. A. Hoodless and G. A. Steven

From the beginning of 1949 careful records have been kept of the number of adult dogfishes caught by R.V. *Sabella* while trawling off Plymouth. The results, shown in Table II, reveal that *Scyliorhinus canicula* is present in Plymouth waters all the year round, and that there is certainly no significant falling off in numbers during the summer months. Poorest catches are, in fact, generally noticeable in the winter months.

It is believed that the data here presented are a more accurate reflexion of population trends than are those of Ford (1921) and Harris; but even they are not as useful for that purpose as they might be because they are affected to

TABLE II. TRAWLED ROUGH DOGFISH. *SABELLA*. STOCK SIZE

	1949				1950			
	No. of hauls	Hours trawling	No. of dogs	Average catch per hour	No. of hauls	Hours trawling	No. of dogs	Average catch per hour
Jan.	5	10·6	1	0·1	19	29·4	5	0·2
Feb.	11	21·1	8	0·4	3	5·8	51	8·8
Mar.	9	14·0	3	0·2	17	23·5	28	1·2
Apr.	15	25·2	44	1·7	1	2·0	3	1·5
May	9	15·0	195	13·0	7	12·0	86	7·2
June	11	17·7	188	10·6	7	11·2	70	6·2
July	4	5·4	52	9·6	15	27·1	49	1·8
Aug.	9	13·7	95	7·0	13	21·9	78	3·5
Sept.	15	23·3	162	7·0	20	34·2	114	3·3
Oct.	9	12·4	104	8·4	15	23·3	168	7·2
Nov.	17	29·8	83	2·8	16	26·6	127	4·8
Dec.	20	35·2	102	2·9	9	16·6	32	1·9

	1951			
	No. of hauls	Hours trawling	No. of dogs	Average catch per hour
Jan.	13	22·9	70	3·0
Feb.	13	27·7	22	0·8
Mar.	3	5·9	6	1·0
Apr.	16	26·5	73	2·8
May	20	32·8	428	13·0
June	10	17·7	301	17·0
July	19	27·0	677	25·1
Aug.	9	12·4	161	13·0
Sept.	13	18·5	227	12·3
Oct.	16	21·6	418	19·3
Nov.	16	24·6	251	10·2
Dec.	10	15·1	214	14·2

some extent by the requirements of the laboratory supply department. When demands for dogfish are heavy *Sabella* spends extra time on those grounds from which the best catches are to be expected. This influence on *Sabella*'s catches must not be overlooked, even though it cannot be evaluated.

MUSCLE RECEPTOR ORGANS IN THE PAGURIDAE

By J. S. Alexandrowicz

From the Plymouth Laboratory

(Plate I and Text-figs. 1–2)

Material and Methods

The occurrence of muscle receptor organs in stomatopods and decapods being established, it seemed worth while to extend investigation to the hermit crabs (Paguridae), the more so as the thinness of the dorsal wall of the abdomen in these animals offered favourable conditions for examination of the nerve elements in this region. The first observations made in 1939 at Naples on *Pagurus striatus* revealed in its abdominal segments the presence of nerve cells connected with muscles which undoubtedly represented similar receptor organs to those found in other crustaceans. When, however, I tried later to investigate these organs in *Eupagurus bernhardus*, the commonest hermit-crab in Plymouth waters, I was unsuccessful in obtaining suitable preparations. *Eupagurus prideauxi* gave better results, but these, too, were inferior to those given previously by *Pagurus*. With a fresh opportunity to work at Naples in autumn 1950, I resumed the investigations with *P. striatus* and also with *P. calidus* which proved to be very suitable for this purpose. The present account is based chiefly on these two species of the subfamily Pagurinae. Observations on *Eupagurus prideauxi* have shown that their muscle receptor organs, apart from some unimportant differences in their topography, are made on the same pattern and therefore the description given holds good for the two subfamilies of the Paguridae.

The nervous elements were stained by the same methylene-blue technique described previously (Alexandrowicz, 1951[1]). Either the dye was injected into the body of the animal or the tissue was submerged in a solution of the dye, or both. The abdomen was cut along the middle line of the ventral wall and pinned to a paraffin plate with the inside turned upwards. The small 6th segment was not dissected and left out of consideration. All the organs situated in the abdominal sac were removed, and the surface of the muscles cleaned from the attached strands of tissue. The preparations were then put into the methylene-blue solution. The methods of fixation and further procedure were the same as set down in the paper quoted.

[1] Muscle receptor organs in the abdomen of *Homarus vulgaris* and *Palinurus vulgaris*, *Quart. Journ. Micr. Sci.*, Vol. 92, p. 163.

Observations

Topography of the Dorsal Muscles in the Abdomen

Text-fig. 1A shows the dorsal wall and parts of the lateral walls of the abdomen of *Pagurus* seen from the inside. Of the 1st segment only the dorsal muscles are seen: they are composed of three portions each having a slightly different obliquity of its fibres. Of the following four segments (2nd to 5th) the dorsal body-wall and parts of the lateral walls are represented.

The dorsal portion has a segmental arrangement of the muscles and is distinctly delimited from both sides by a gap in the muscle layer. The dorsal (extensor) muscles consist of parallel longitudinal fibres, the length of which corresponds with the length of the respective segments. The fibres of the successive segments meet end to end and become attached along the lines marking the limits between the segments.

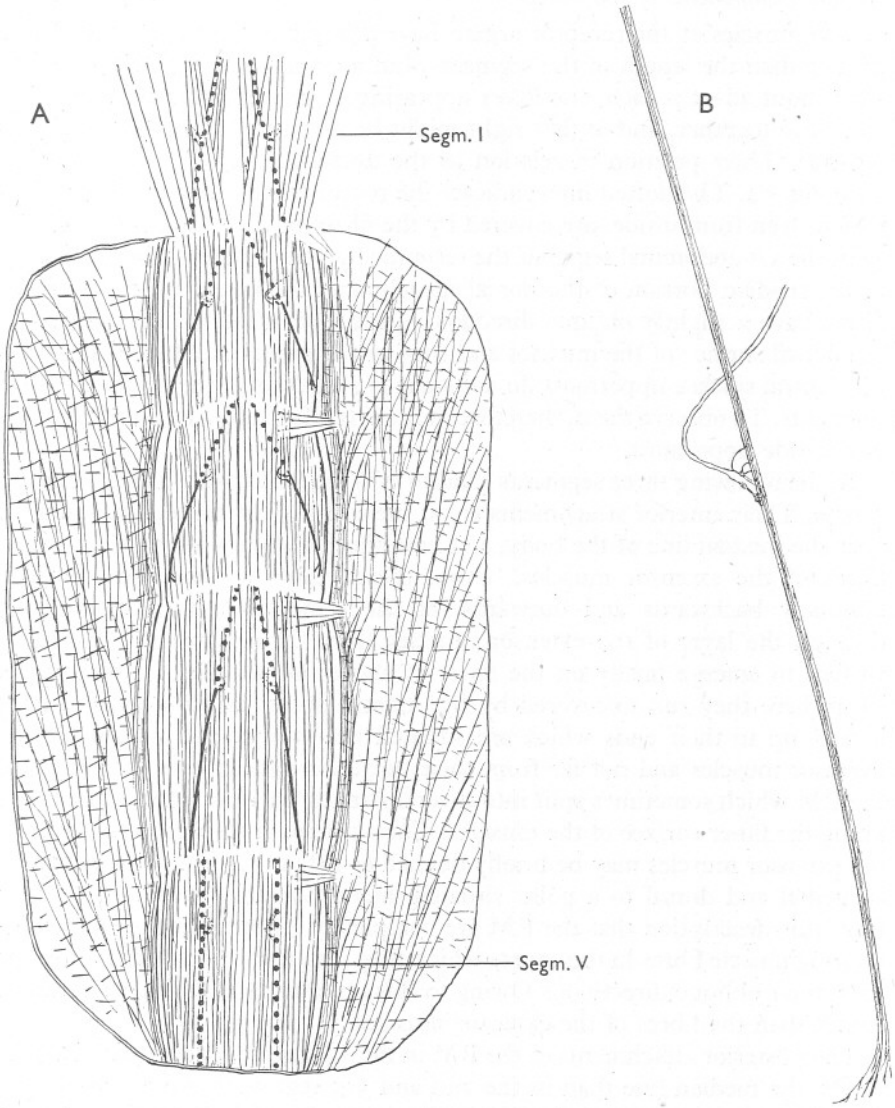
Near the anterior edges of the segments there are small transverse muscles situated asymmetrically on the left side. Their fibres converge towards the basis of each pleopod.

In the lateral walls the muscles are set in three layers. Those of the outer layer are oblique, those in the middle transverse, while the fibres of the inner layer have a more complicated disposition. They are chiefly longitudinal, forming stronger bundles along the gap separating them from the dorsal muscles; more laterally, both longitudinal and oblique fibres are present, anastomosing with each other. Since the oblique fibres of this inner layer intercross the direction of those of the outer layer, there are places where fibres running in four different directions can be seen.

The median longitudinal bundles of the inner layer, being interrupted on the left side by the transverse muscles of the pleopods, show a segmental arrangement: all other muscles of the lateral wall do not exhibit any segmentation.

Muscle Receptor Organs

As in *Homarus* and *Palinurus*, the two species of Macrura investigated (*loc. cit.*), there are in the Paguridae two pairs of muscle receptor organs in each of the 1st to 5th abdominal segments. They are each composed of a very thin but long muscle and a nerve cell which connects with the muscle by means of dendritic processes and sends its axon towards the central nervous system (Text-fig. 1B; Pl. I, fig. 1). The two muscle receptors situated on the same side, which must be regarded as individual units, each have particular features of their own. Their cells are of two different types, one having very long and the other very short distal processes. In the further description the cell of the first type will be referred to as cell 1 and that of the second type as cell 2, and the muscles connected with these cells as RM 1 and RM 2 respectively. For designation of the muscle receptor organ as a whole the abbreviation MRO will be used.



Text-fig. 1. A, view of the dorsal wall and parts of the lateral walls of the 1st to 5th abdominal segments in *Pagurus* showing the position of the muscle receptor organs in relation to the dorsal muscles. The two MRO on each side are represented by a single line; the dotted line shows the MRO or their parts which, seen from inside, are covered by the fibres of the dorsal muscles. B, two muscle receptor organs of the 2nd segment showing their relative length and thickness, drawn to scale. The axons of the receptor cells viewed from inside appear as passing under the muscles; actually they cross these muscles on their dorsal side.

Muscle Components of the MRO

The muscles of the receptor organs have a length equal to or even slightly greater than the length of the segments, but are very thin having a diameter only about 30–40 μ each, the RM 1 appearing to be somewhat thicker. They run close together, and at first sight might be taken for a single fibre (Text-fig. 1 B). Their position in relation to the dorsal muscles is represented in Text-fig. 1 A. The dotted lines indicate the receptor muscles or their portions which, seen from inside, are covered by the fibres of the dorsal muscles.

In the 1st abdominal segment the receptor muscles run near the outer edge of the median portion of the dorsal muscle, and following the course of its fibres have a slightly oblique direction. In this segment the RM lie nearer the dorsal surface of the muscles and thus in the preparations stretched with the ventral surface uppermost do not stain as readily as in the following three segments. To observe them, therefore, it is advisable to attach the preparations dorsal side uppermost.

In the following three segments (2nd to 4th) the RM have a nearly identical course. Their anterior attachments are at the edges of the respective segments near the median line of the body, and here the RM lie dorsally, i.e. upon the fibres of the extensor muscles. From these points of insertion they run obliquely backwards and outwards, at the same time passing gradually through the layer of the extensor muscles from their dorsal to the ventral surface to emerge finally on the latter at about the middle of their course. From here they run uncovered by the muscle fibres (as observed from the inside) up to their ends which are situated near the lateral margins of the extensor muscles and not far from their posterior attachments. The ends of the RM which sometimes split into several strands are inserted into the fascia lining the inner surface of the muscles. Their course in respect to the layer of the extensor muscles may be briefly defined as extending from a point which is medial and dorsal to a point situated laterally and ventrally. It is clear from this description that the RM are completely independent of the neighbouring muscle fibres in the course which they run, as is at first sight apparent from their oblique directions. Owing to this obliquity the RM have a greater length than the fibres of the extensor muscles.

The posterior attachments of the RM in the 4th segment are situated a little nearer the median line than in the 2nd and 3rd segments and as, moreover, the 4th segment is much longer than the others, its RM have a less oblique course.

In the 5th segment the RM anteriorly have superficial attachments similar to those in the foregoing. Running backwards they pass deeper into the layer of the dorsal muscles but do not emerge on their ventral surface, ending between the dorsal muscles at the edge of the segment. In all their course they remain nearly parallel to the median line. Owing to their deeper setting they usually stain less distinctly or even remain invisible.

The arrangement of the RM in *Pagurus calidus* is the same as in *P. striatus*. In *Eupagurus prideauxi* the RM have a less oblique direction and run a little farther from the ventral surface. Their still deeper setting in the muscle layer is presumably responsible for the failure in getting satisfactory staining in *E. bernhardus*. In the 1st abdominal segment of that species, where the dye can have access from the dorsal side to the superficially situated MRO they stain quite well.

It is easy to recognize the two RM as individual muscle units owing to their remarkable property of staining differentially in methylene blue. As a rule one of them, and this is nearly always RM 1, remains almost colourless, while the other stains blue or even dark blue (Pl. I, figs. 1, 5). Rarely the reverse reaction is observed and also rarely both RM appear stained in the same or nearly the same hue. Thanks to this difference in colour it may be stated that RM 1 is situated laterally and somewhat dorsally to RM 2. The differences in the appearance of the two muscles might not, of course, be noticeable when the action of the methylene blue was not long enough or was impeded—as for instance in the anterior portion of the RM situated within the muscle layer—and not easily reached by the dye. For that reason it has been difficult to determine whether both muscles have their anterior insertions at exactly the same point or, as was found in *Homarus*, at different points. It may, however, be assumed that if there is separation between these points of attachment it cannot be great.

The receptor muscles have a similar structure as in the Macrura, i.e. are composed of bundles of myofibrils and of connective tissue fibres running longitudinally between them. The connective fibres are more abundant in RM 1 than in RM 2.[1]

Nerve Cells

The nerve cells are situated at about the middle of the length of the receptor muscles, rather a little anterior to the mid-point, and consequently they lie near the place at which the MRO appear on the ventral surface of the muscle layer; hence in the preparations with this surface uppermost the nerve cells can be well exposed for observation. It happens however, not uncommonly, that they are covered by some muscle fibres, to remove which an attempt should be made cautiously.

In the first segment the nerve cells are situated on the lateral side of their muscles, whereas in the 2nd to 5th segments they lie on the median side. Cell 2 lies behind, and usually close to, cell 1, but the two cells may sometimes

[1] As in previous papers, I prefer to avoid the term 'muscle fibres' when describing the components of the MRO. Being thread-like, they are fibres in the general meaning of this word, but they are not 'muscle fibres' in a strict histological sense, i.e. elements of striated muscular tissue consisting of myofibrils embedded in sarcoplasm with many nuclei and enclosed in a sarcolemma-tube.

be well separated. They differ greatly in their appearance, in the distribution of their processes, and even in their staining properties.

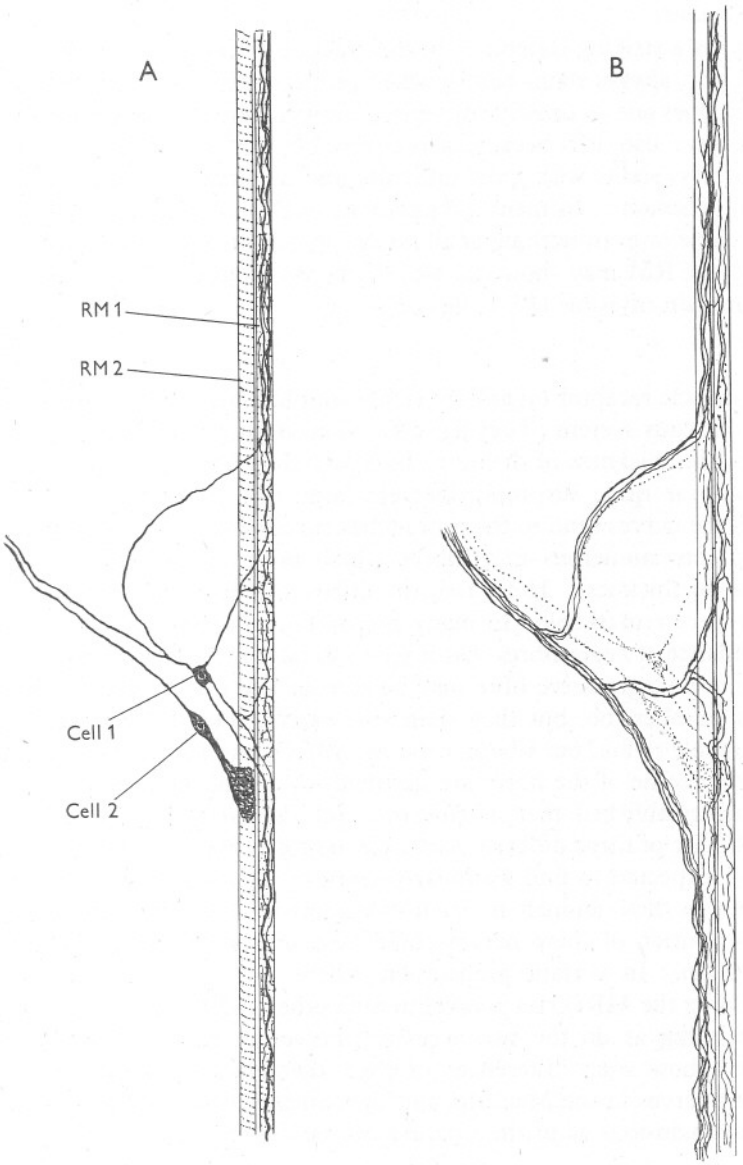
Cell 1 is multipolar, and with its processes arising from various points of the body can have a manifold shape (Pl. I, figs. 1–5). The processes, one or two of which may arise from the axon, pass on to the muscle RM 1 and run in opposite directions giving off numerous ramifications (Text-fig. 2 A). They look quite like the fibres of nerves coming to the receptors from the central nervous system (Pl. I, figs. 3, 4). When associated with the latter in a common bundle the cell processes can be identified only if it is possible to trace them up to the cell and thus detect their origin. This makes it difficult to determine their whole course, but they are seen running far in both directions. As in no instance can the limit of their expansion be noticed, it seems not improbable that they might extend along the whole length of the muscle. The terminations of the longer branches from among those of other fibres are indistinguishable. Those of the branches ending nearer the cell and whose origin is unquestionable are seen to give fine filaments spreading in the RM 1. Since in all the MRO examined in the Macrura the ramifications of the cell processes end not on the muscle itself but on the connective tissue, it is probable that in the Paguridae too the terminations of the cell processes are situated on the connective tissue fibres, which, as mentioned before, are abundant in RM 1. Unfortunately, it is practically impossible to discern the relations of particular nerve filaments, as in the thin receptor muscle all the elements, viz. myofibril bundles, connective tissue fibres and nerve fibres of various origins, run closely intermingled.

Cell 2 is as a rule bipolar with a thick distal process which gives off very short branches. These ramify abundantly and penetrate into RM forming a sort of tuft which occupies the whole thickness of the muscle, but only a small portion of its length, about three times as large as the diameter of the muscle (Text-fig. 2 A, Pl. I, figs. 1, 3). The tuft of nerve branches is so dense that when it is well stained the muscle appears as if it were completely interrupted at this place by the nerve fibres. There is there, of course, connective tissue too.

On the periphery of the cell 2 small blue staining granules can often be observed. Possibly they are disintegrated fine nerve fibres surrounding the cell body.

The axons of the cells join branches of motor nerves running near by. In the first segment the axons are directed laterally. In the 2nd to 5th segments they run at first medially then curve dorsally and laterally, thus crossing the receptor muscles (Text-fig. 1 B). The nerve branch into which they pass near their origin is one of the motor branches supplying the median portion of the extensor muscles.

Both nerve cells are protected by connective tissue arranged in concentric layers. When the cells shrink a little it may be seen that there is a sort of



Text-fig. 2. Semi-diagrammatic view of muscle receptor organs showing in A the nerve cells with their processes and in B the nerve-fibres of central origin supplying the MRO. In both drawings the parts lying anteriorly in the animal body are shown at the top of the figures.

capsule around them but it does not leave such a wide space around the cells as in *Homarus*.

There is a striking difference in the reaction of the two cells to methylene blue. Cell 1 always stains readily when properly exposed to the action of this dye. If it does not, as usually happens in the 5th segment and not uncommonly in the others also, it is because it is covered by the muscle fibres. Cell 2, on the contrary, stains with great difficulty and no similar reason can be found for this behaviour. In many preparations only faint outlines of this cell are recognizable or even nothing at all reveals its presence—only a slight enlargement of the RM may show the area of the distribution of the cell dendrites which remain invisible (Pl. I, fig. 2*c*).

Nerves

The muscle receptor organs are richly supplied by nerves coming from the central nervous system (Text-fig. 2B). Considering the small calibre of the muscles, the thickness of the nerve bundle and its fibres running towards the MRO appear quite disproportionately large (Pl. I, fig. 5). Reaching the muscles the nerves send to them branches running in opposite directions and dividing into numerous finer fibres which penetrate the muscles through their whole thickness. Here, too, the differences in the staining of the two RM are very remarkable. In many preparations in which RM 1 shows such an abundance of nerve fibres that it seems to have more nerves than any other tissue, not a single nerve fibre may be seen in RM 2. In fact, they are there in great number too, but they stain very rarely. For this reason it has not been possible to find out whether the two MRO have an identical innervation or whether some of the fibres are destined for one of them only.

Having established that in *Homarus* and *Palinurus* the nerves supplying the MRO are of three different sorts, viz. motor nerves and the two accessory nerves, I expected to find a similar pattern of innervation in the Paguridae. However, in these animals no such characteristic features in the appearance and distribution of these nerves could be found which would permit their classification. In certain preparations there can be seen that the fibres approaching the MRO run parallel to each other and divide at the same spot, thus behaving as do the two accessory nerves in *Homarus*. They do not, however, show such differences of their diameters as the thick and thin accessory nerves in the Macrura, and their further course being uncertain no definite conclusions as to their nature can be drawn.

Comparison of the Paguridae with the Macrura

As has been pointed out before, the MRO in the abdomen of the Paguridae are made up on the same lines as in the Macrura but there are some differences. For instance, the muscles of the same pair in the Macrura have as a rule their attachments at a certain distance from one another, can have

a more or less different course, and can differ greatly in their length. In the Paguridae they run close together and appear to be of equal or nearly equal lengths. The dissimilarities in their histological structure are much less distinct than in the Macrura, and only the staining properties indicate that they are not of the same kind. On the other hand, in the nerve cells of the Paguridae the characteristic features distinguishing the two types of receptors, viz. the length of the distal cell processes, are accentuated to the highest degree. In fact, the processes of cell 1 extending along the muscle attain unusual dimensions. In the Macrura these processes expand on a limited area which is merely a little larger than that of cell 2.

It should be noted that in certain thoracic muscles in *Homarus* and *Palinurus* there are nerve cells which resemble somewhat cell 1 in *Pagurus* in that they give off long processes ending between the muscle fibres. However, these cells (termed 'cells N') do not belong to the same category of receptors as those situated in the dorsal muscles, for they have not their own receptor muscle and otherwise differ in appearance from the former.[1]

Comparing the nerve supply of MRO in both groups it may be briefly stated that in the Paguridae there are even more than enough fibres for carrying to the MRO the same elements of various sorts as found in the Macrura, but that the disposition of these elements has not been discerned.

In the above account, the MRO in the thoracic segments, as described in the Macrura, has not been taken into consideration although they are certainly present in the Paguridae too. I have seen them in all the four species investigated. One of these MRO, situated superficially on the dorsal side of the thoracico-abdominal muscle, is quite easily noticeable. Since in the thorax of the Macrura four MRO have been found on each side it seemed very probable that the Paguridae should have the same number. However, owing to technical difficulties, I have thus far been unable to find their position or to convince myself that some of these elements are missing in these animals.

Function

When describing the MRO in the Macrura I ventured some suggestions about their function, assuming that they are connected with the action of the system of giant fibres and may perhaps be inhibitory to the latter during the flipping movements of the abdomen. As the MRO in the Paguridae look so like those of the Macrura, it is hardly probable that they would have a different function, but since the abdomen of hermit-crabs does not perform flipping movements the question arises, if the above hypothesis should hold good, what indeed may be the reason for existence of the MRO in these animals. The problem is even more complicated, since an explanation has to be found why the two MRO are so different from each other.

[1] The paper on the receptor elements in the thoracic muscles of *Homarus* and *Palinurus* is being published in *Quart. Journ. Micr. Sci.*

I wish to express my thanks to Prof. Dr R. Dohrn, Director of the Zoological Station, Naples, for his kindness and hospitality and to the British Association for the Advancement of Science for the use of its Table.

I am indebted to Mr G. M. Spooner for his kind help in preparing the manuscript.

Summary

In the dorsal wall of the abdomen in the Paguridae muscle receptor organs have been found similar to those in the Macrura. In each of the first to fifth abdominal segments there are two receptor units on each side. A receptor unit consists of a long thread-like muscle, and a nerve cell connected with this muscle and sending its axon towards the central nervous system. The muscles of each pair run close together in the layer of the dorsal (extensor) muscles, but are independent from the latter following a more or less different course.

The nerve cells in each pair of muscle receptor organs are of two types. One of them has several very long distal processes expanding over one of the muscles. The other cell has one stout distal process giving off numerous but very short branches forming with their subdivisions a dense tuft of fibres terminating in the second muscle. The axons of the cells associate with one of the branches of motor nerves supplying the dorsal muscles and pass along these branches into the main nerve trunks of the respective segments.

Each receptor organ is supplied by several nerve fibres coming from the central nervous system.

EXPLANATION OF PLATE I

All photomicrographs were made from preparations stained with methylene blue, fixed in ammonium molybdate and mounted in xylol-dammar.

Figs. 2–5 have been made with the same magnification. The differences in dimensions of cells represented depend on the various sizes of specimens.

The uneven outlines and irregular courses of the receptor muscles seen at some places are due to deformations caused when isolating the muscle receptor organs from the abdominal wall.

The parts lying anteriorly in the animal body are shown at the top of the figures.

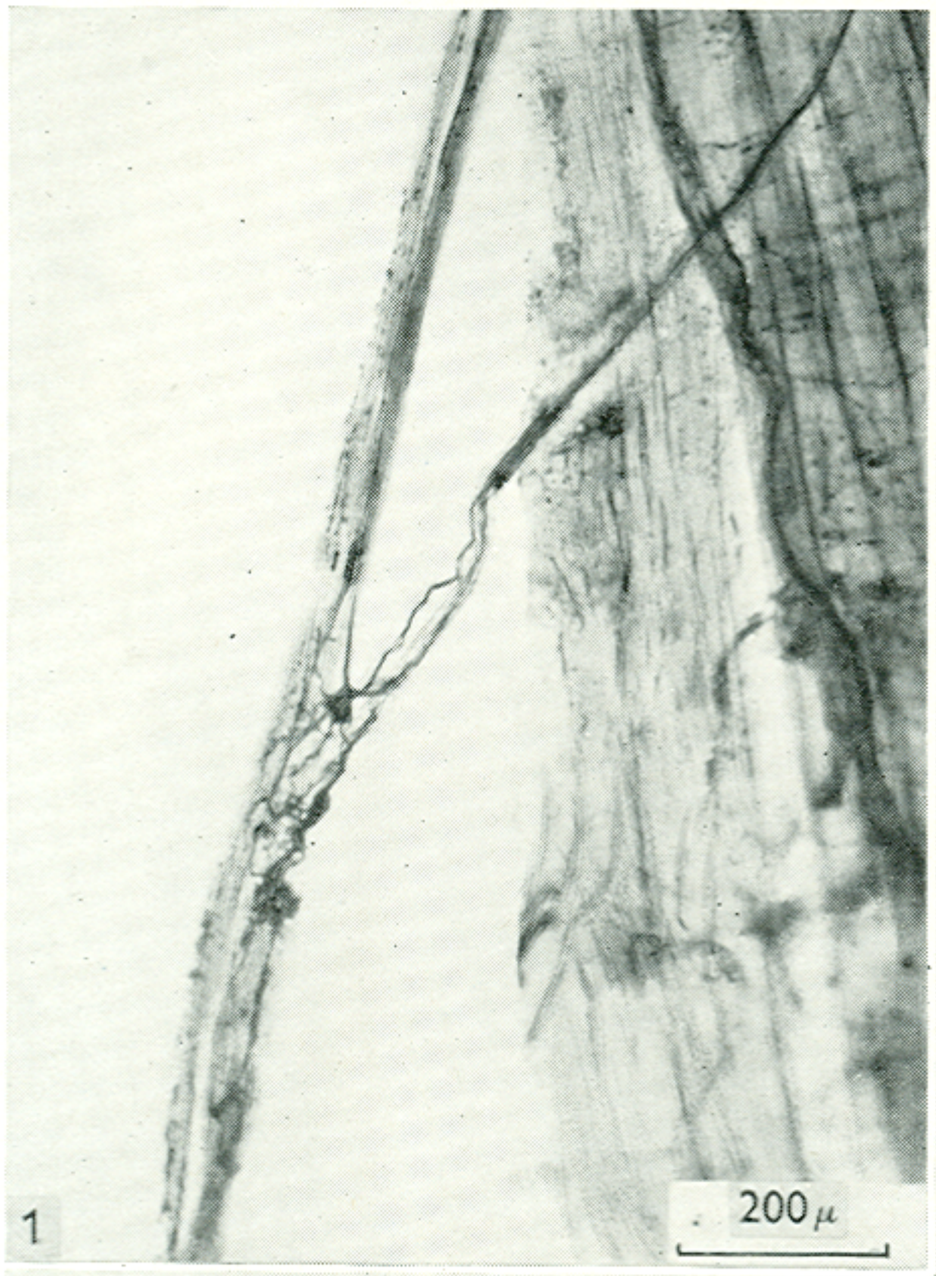
Fig. 1. *Pagurus calidus*. Middle portion of the muscle receptor organs of the 2nd abdominal segment showing their oblique course in relation to the dorsal muscles. The latter have been partly removed. Note the position of the two nerve cells, the difference of their shapes, the unequal staining of the two receptor muscles and the medial position of the darker stained RM 2.

Fig. 2. *P. striatus*. Cell 1 with several processes passing on to the muscle RM 1. *ax*, its axon joining the nerve; *b*, process arising from the axon and associating with a nerve branch to reach RM 1 at a point distant from the cell; *c*, area of distribution of the processes of cell 2, the latter being invisible.

Fig. 3. *P. calidus*. Receptor organs with the cells showing the different expansions of their processes. The unusual situation of the cells is produced artificially at fixation. *ax*, axons of both cells.

Fig. 4. *P. calidus*. Cell 1 with processes associating with the nerve-fibres of central origin.

Fig. 5. *P. calidus*. Cell 1 and the bundle of nerve fibres of central origin supplying the MRO. The branches of the nerves, most of them disintegrated in granules, are seen spread in RM 1, but not in the RM 2 (darker stained).



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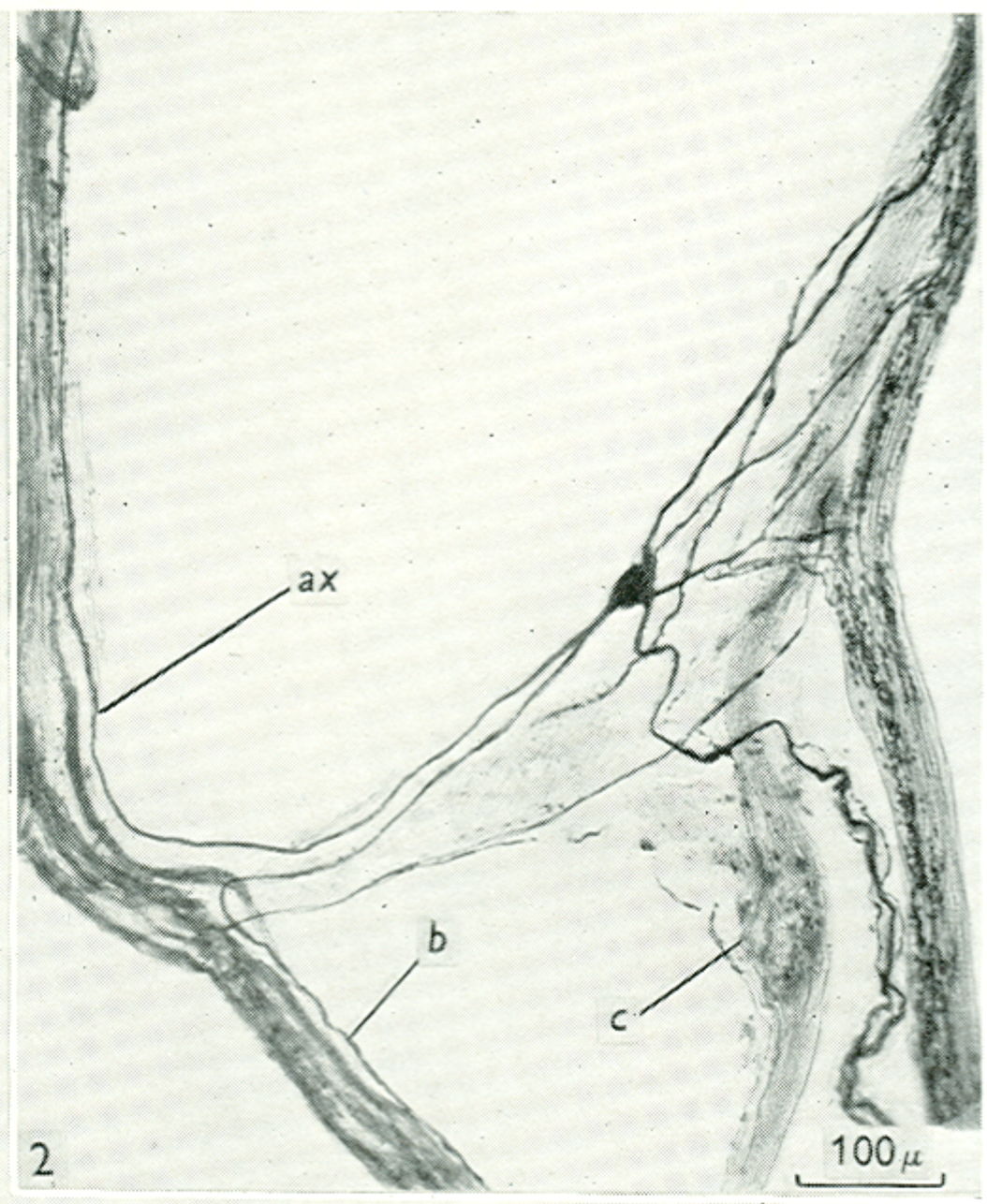

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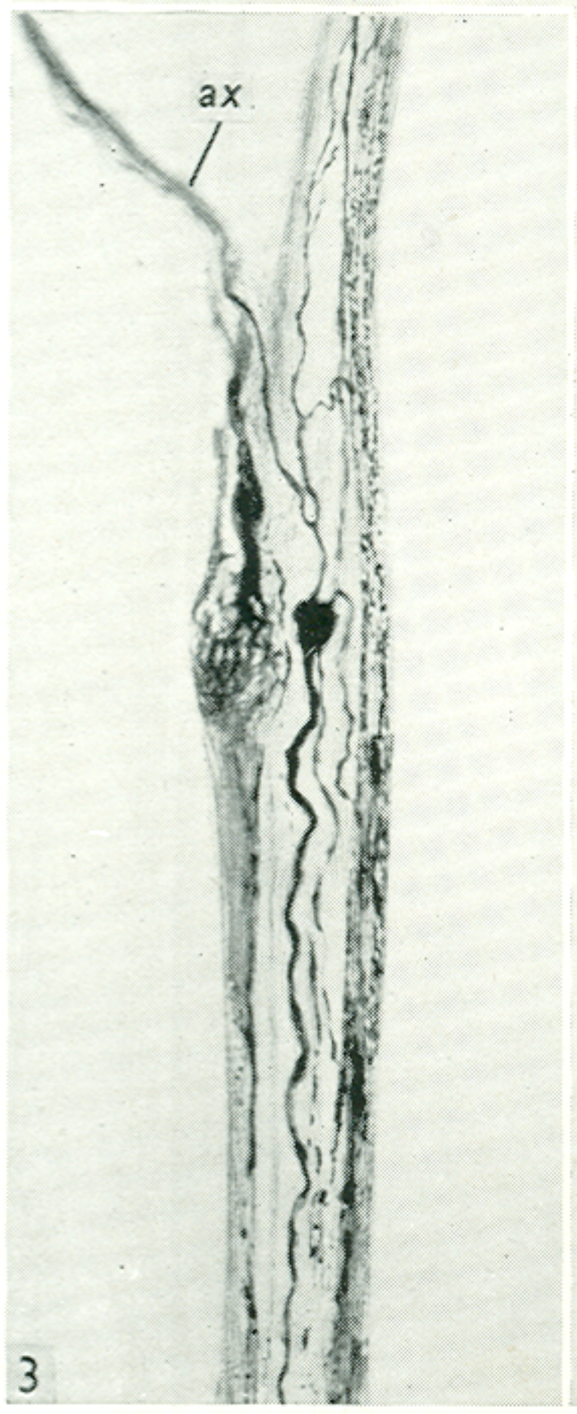

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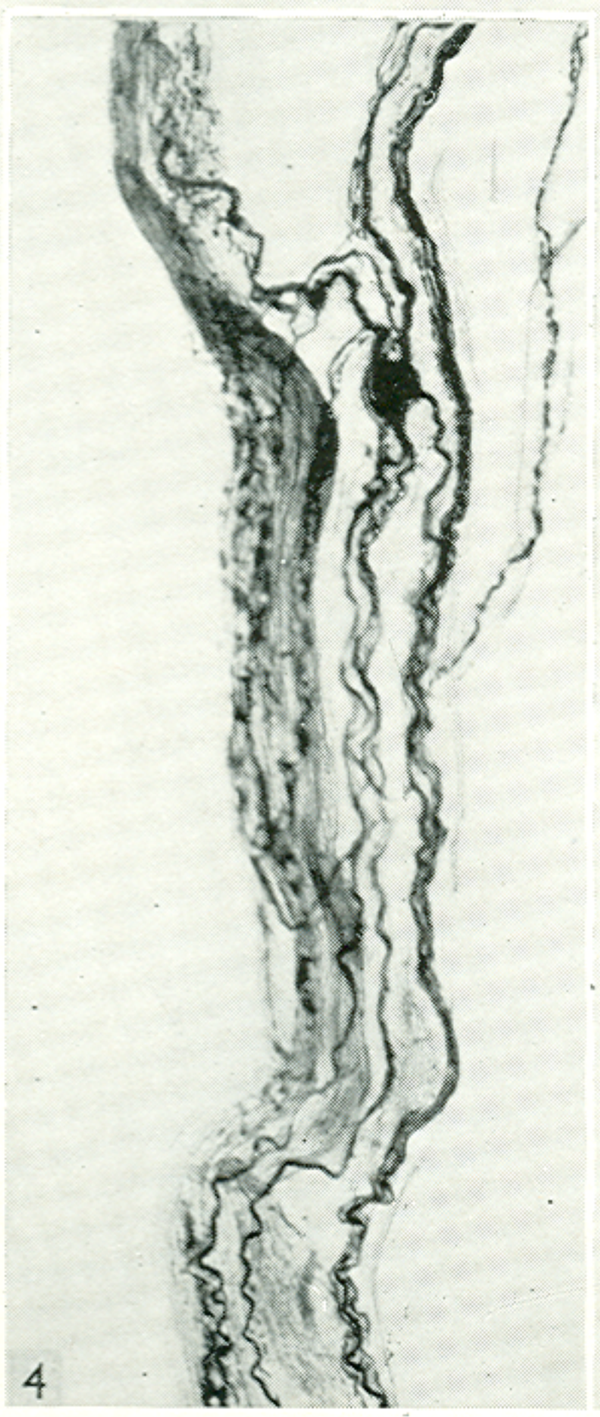

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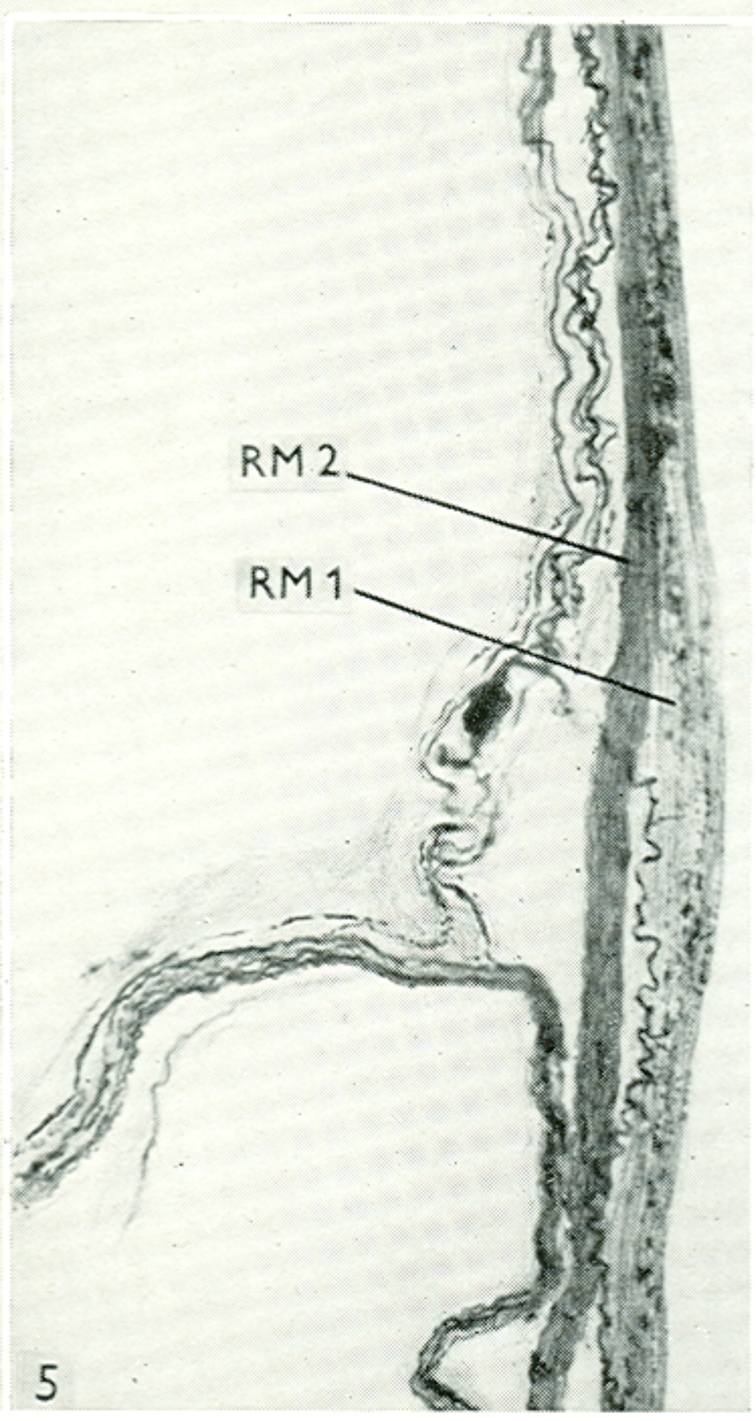

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THE RESPONSE MECHANISM IN ASCIDIANS

By Graham Hoyle

Department of Zoology, University College, London

(Text-figs. 1–14)

CONTENTS

Introduction

The responses of tunicates to stimulation have been studied principally by Jordan (1908), Polimanti (1911), Kinoshita (1910), Hecht (1918), and Bacq (1935). Jordan and Hecht established the typical responses to mechanical stimulation. A light touch on the outside of either siphon rim causes that siphon to close, the extent of the closure being proportional to the strength of the stimulus. Stronger stimulation causes closure also of the unstimulated siphon. This closure is accompanied by a shortening of the siphons. Stimulation of the body of the animal also causes closure of both siphons together. When the stimulation is still stronger, either applied to a single siphon or to the whole animal, a violent synchronous contraction of the whole musculature occurs, accompanied by the ejection of water from the branchial and atrial cavities. In addition to these simple responses 'crossed responses' occur. Gentle stimulation of the inside of a siphon-rim results in closure of the opposite siphon without affecting the stimulated one. Further stimulation in the same manner results in violent contraction of the whole animal with water ejection through the open stimulated siphon. In some ascidians there is also a reflex bending of the body to vigorous mechanical stimulation. The latter

activity depends on the presence of unequally thickened walls of the test and is probably due to this structural peculiarity.

Measurements of the siphon contractions during stimulation were made by Kinoshita and Polimanti, who both used *Ciona intestinalis*. They studied animals which had settled on pieces of rock, or used a clamp to grip the base of the test. Hooks were passed through the siphon rims and attached to levers writing on kymograph paper. The methods of stimulation employed were: (1) mechanical, touching a siphon-rim with a glass rod; (2) electrical, using induction-coil shocks applied through platinum wires. Neither method permits very accurate control and it seems desirable to re-investigate the responses using the more accurately controlled method of stimulation employed by Pantin (1935*a–c*) for the analysis of the responses of actinians.

The studies of Kinoshita show that the responses of *Ciona* become rapidly weaker with successive bursts of stimuli. He used spring levers, thereby giving the siphons unaccustomed work to do against the lever system in addition to the normal work done against the mechanical resistance of the test. The test is very weak in *Ciona*. He claimed that the latent period of the response to an electrical stimulus was about twice that to a mechanical stimulus (0·54 sec. compared with 0·28 sec.). Polimanti, using a pulley system to transfer movements from the animal to the levers, gave the siphons less work to do. He compared the responses of both siphons simultaneously and obtained a large number of records. The results were not consistent. It is clear from his records: (1) that the heights of the contractions of the two siphons are independent of each other on many occasions; (2) that factors which are not obviously related to the given stimuli affect the contractions. In fact, the whole animal cannot be regarded as a simple mechanical system always responding to similar stimuli in the same way. Uncontrollable factors affect both the height of contraction and the rate of relaxation. Other points also appear during a survey of Polimanti's records. Contraction may not start until after several stimuli have been given, although sometimes the contractions start almost immediately after the beginning of stimulation. There are several possible explanations. The latency may be variable, the electrical stimuli may sometimes be ineffective, or some form of inhibition may be present.

As in sea-anemones (Batham & Pantin, 1950) the responses of sea-squirts to stimulation must be observed against a background of spontaneous activity. Rhythmic activity of the siphons was studied by Hecht (1918) using *Ascidia atra*, and by Yamaguchi (1931) using *Styela clava*. Both these authors had to take special precautions to protect their experimental animals from external vibrations by working in isolated laboratories built on either a concrete or stone floor, because ascidians are extremely sensitive to mechanical vibrations. However, even with extreme precautions to protect the animals spontaneous contractions were apparent. The spontaneous activity described by Hecht consisted of body-contractions and siphon closures accompanied by water

ejection, at intervals of about 5 min. Yamaguchi also described spontaneous activity with 5 min. periodicity but claimed that in filtered sea water the pattern of this activity was changed to a more regular type than that observed in ordinary sea water, in which three or four small contractions alternated with larger ones.

Experimental Animals

The animal principally chosen for investigation was *Phallusia mammillata* Cuvier. Some duplicate experiments were also done on *Ascidiella aspersa* Müller. These were so exactly similar in their responses that records from both species have been chosen for use in this paper to illustrate various salient results. These animals are not as sensitive to vibrations as *Ciona* and have thick tests. *Phallusia* is especially endowed in this respect. It is available near the Plymouth Laboratory, both in estuaries, where it is exposed at very low tides, and in the Sound to considerable depths. Specimens from 13 to 15 cm. long can be obtained without damage to the test. They survive for at least a few days in Plymouth tank sea water under circulation but do not live long when transported to London. The estuarine forms are brownish in colour owing to the presence of pigmented cells in the body-wall and the test. The deeper water forms are milky white. The test is nowhere less than a quarter of an inch in thickness except at the siphon rims. It is quite firm even when the blood is drained out and shows viscous-elastic properties when stretched. Gross alteration of the form of the test takes place fairly rapidly when the animal is removed from the sea water. The original form is recovered on returning to water if the animal is still alive. The mantle, or body-wall is firmly attached at each siphon rim but elsewhere is only loosely attached to the test. Contractions of the body-wall musculature result in the expulsion of water from the branchial and atrial cavities accompanied by siphon-rim closure and withdrawal. No conspicuous movements of the whole animal occur. Hence it is possible to study siphon-rim closure as a virtually isolated system. The musculature consists of a large number of long, narrow bands of various relative size, distributed round the body-wall in a dense tangle in which only a few bands stand out. The fibres anastomose considerably, and end in fine branches which are embedded in the connective tissue of the body-wall. These muscles grade into those surrounding the siphons. The customary sharp distinction of the musculature into longitudinal and annular (Berrill, 1950) is hardly justified in *Phallusia* and *Ascidiella* where the siphon muscles appear to be just an extension of the body-wall muscle complex which is strongly concentrated in these regions so as to surround the siphons. The 'annular' muscles, principally those round the siphons, have discrete, branching ends. There are strong bands attached to the siphon rims between the lappets. Contraction of these muscles and of others attached to them brings the siphon rim inwards and downwards towards the body, the rim

being neatly folded so that complete closure results. There are few siphon-encircling muscles in close proximity to the rim, but there is a strong band with its centre about 1 cm. distant from the rim.

When the longitudinal musculature is cut near the rim on one side, that side of the rim no longer contracts, and complete siphon closure is then impossible. Cuts in the encircling muscle band affect the contraction only slightly. Hence it is inferred that the principal muscles concerned with siphon-rim closure are those which work at right angles to the rim. The encircling muscles control the diameter of the whole siphon cylinder, but principally serve to give the siphons rigidity and to provide attachment for other muscles.

Ascidiella is found in the same estuarine habitat as *Phallusia*. Average specimens are about 9 × 4 cm. The test is 3–6 mm. thick. Its general organization is similar to that of *Phallusia*.

The experiments to be reported involve the use of whole animals and are therefore subject to all the difficulties encountered when trying to investigate phenomena which are undoubtedly complex and affected by a variety of factors, largely internal to the animal, which are not subject to experimental control. Nevertheless, as a preliminary to the investigation of isolated physiological units, which may prove possible in *Phallusia*, it is hoped that given adequate control, useful information may be derived from such a study.

Methods of Recording and Experimental Procedure

Animals to be investigated were allowed to rest in their natural position on a heavy glass plate, usually being secured lightly with cotton tape. The plate was placed in a large, heavy, porcelain tank or enamel basin capable of holding several gallons of sea water. These, in turn, were supported on tables built into a concrete floor. Kymograph motors were mounted on sponge-rubber strips. Under these conditions the animals were sufficiently isolated from vibrations. The recording system consisted of long levers of dried grass writing on smoked drums. The writing points were of thin glass tubing made up to give points of the frontal type mounted at right angles to the levers (Fig. 1). Whenever the natural position of the animal permitted, a glass arm attached to the lever was allowed to touch the inside of the siphon rim, thereby transmitting movements to the lever. Alternatively, a small glass hook was bent to fit over, but not penetrate, the siphon rim, and this was connected by thread to the lever. The weight required to balance the levers when placed in the position normally occupied by the siphon rim was about 0·4 g. so work done against the lever system was small with either method and the animals were not unduly disturbed by either the contact arm or the hook.

Stimuli were derived from condenser discharges. They were applied through silver/silver chloride electrodes contained in glass tubes filled with sea water.

A potentiometer was connected across the stimulator terminals. The frequency of discharge was controlled by a metronome operating a post-office relay which also acted as stimulus marker. The electrodes were applied to the outside of the test in various positions.

With this method of stimulation results were, at first, extremely variable. During the investigations it became probable that this variation is connected in some way with the changing states of the animals associated with their

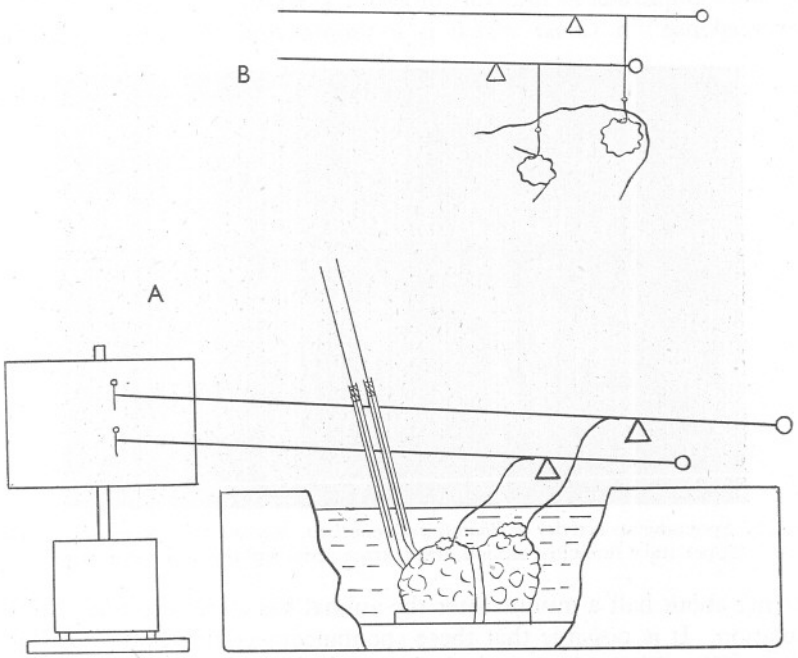

Fig. 1. Diagram of method of recording and manner of stimulation showing use of: (A) fixed glass arms; (B) glass hooks.

rhythmicity, and with the possible effect which the shocks might have on these states. Hence in *Phallusia* various experiments have been executed in an attempt to obtain an understanding of the interactions of background internal phenomena and external stimuli. The spontaneous activity shows a variety of patterns which will be discussed in another paper. The commonest pattern, that of synchronous activity of the two siphons at fairly regular intervals of 6–9 min. and continuing without interruption for several hours, is illustrated in Fig. 2. Other types of spontaneous activity may be related to external factors (cf. Batham & Pantin, 1950). In order to be able to plan experiments which will give consistent and strictly comparable results it is important to be able to distinguish two sources of variation. These are: (*a*) the variation in

response to stimulation purely as a function of the stage in the spontaneous activity cycle which the animal has reached; (*b*) the response to stimulation as a function of the previous history of the animal. It would be expected that (*a*) would show an additional variation with different test animals; (*b*) would vary likewise but probably less than (*a*).

The first type of variation is found to have two main components. Stimuli given immediately after a spontaneous contraction disturb the rhythmicity and frequently give rise to one or a series of small spontaneous contractions of variable amplitude at intervals of about $\frac{1}{2}$–1 min. Kinoshita describes an 'after response' in *Ciona* which is a spontaneous incomplete contraction

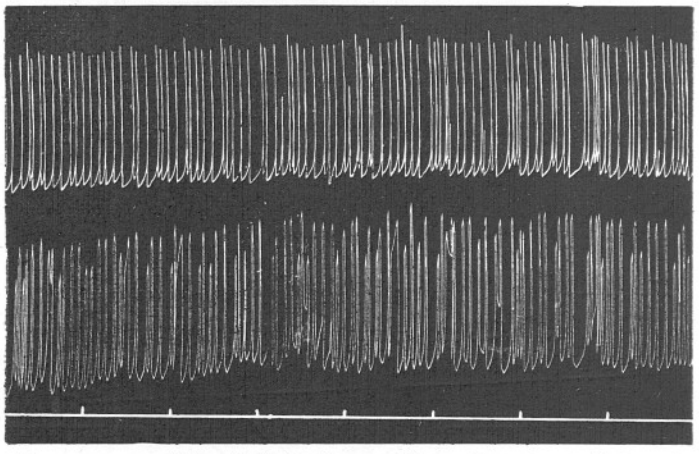

Fig. 2. Spontaneous activity of *Phallusia mammillata*. Record reads from right to left. Upper trace branchial siphon, lower trace atrial siphon. Time in hours.

occurring about half a minute after the animal has started to relax following stimulation. It is possible that these spontaneous contractions (see Fig. 12) represent Kinoshita's 'after response'. Stimuli given just before a spontaneous contraction is due are abnormally effective in eliciting responses, for single stimuli may elicit a squirt at this time. This is not the normal reaction to a single shock, as will be shown below. These results illustrate the extremes of the first component of type (*a*) variation which is variation during the interval between individual squirts. The second component of type (*a*) variation is a much slower variation which is revealed by giving pairs of shocks at 1 min. intervals over a period of several hours. Although the stimuli are kept at 20% above the initial threshold there are frequent phases, each lasting for several minutes, when these stimuli give only a small response or even none at all. This observation is in line with the variations observed by Polimanti. Fig. 3 shows the effect of stimulating a specimen of *Phallusia* in this way. At the start of the series illustrated the shocks were ineffective. Spontaneous activity was accelerated and then the animal entered a phase which lasted

for 20 min. when the stimuli were equally effective. This phase ended almost as sharply as it began, apparently without further affecting the spontaneous activity. Later, with no increase in stimulus intensity a second period of responsiveness was apparent. Now, however, the response was weaker and more erratic. These results illustrate also the type (*b*) variation referred to. The smaller size and erratic nature of the second set of responses shows the exhausting effect of the earlier stimulation.

Stimulation experiments must, therefore, be planned to avoid coinciding with the immediate pre- and the immediate post-spontaneous contraction period. They must also be conducted during phases of normal responsiveness, and they must not be executed too soon after a previous experiment. After stimulation several minutes may elapse before the same pattern of response can be re-elicited. The normal state can usually be said to be restored when the animal returns to its normal pattern of spontaneous activity.

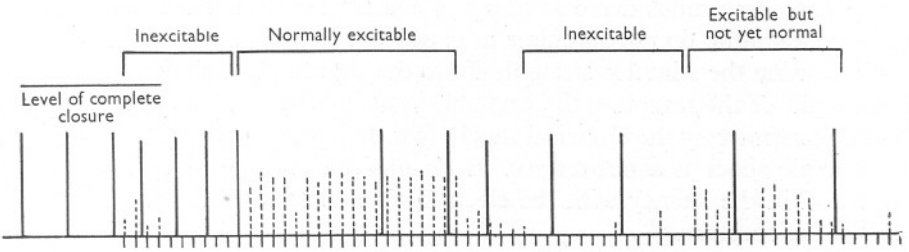

Fig. 3. The results of part of an experiment on the relation between excitability and internal phasic activity. The unbroken lines indicate spontaneous contractions, the broken lines indicate responses to electrical shocks. The marks below the baseline indicate the application of closely spaced pairs of shocks at 1 min. intervals between pairs. *Phallusia*, branchial siphon.

The experimental procedure used is therefore as follows. Only healthy specimens showing rapid movements of the siphons are used. Two equal test shocks 1 sec. apart and of suitable strength are given to the animal about 2 min. after a spontaneous contraction. If the animal gives a good response a further minute is allowed to pass and then an experiment is carried out. Immediately after the experiment the animal is allowed to rest for 10–15 min., or longer according to the length of the experiment, so that normal rhythmicity is restored. The procedure is then repeated. In about 5% of such tests the response is small or, rarely, absent, and a pair of shocks does not elicit a squirt (*vide* above types of variation). After a few minutes the response has always been normal again, further indicating that occasional phases of unresponsiveness are a normal feature of ascidian behaviour.

Results of Experiments

Stimulus Strength

The electrodes, separated by about half an inch, were placed in various positions on the test. The battery voltage and potentiometer were roughly adjusted until a pair of shocks gave a response. The potentiometer was then adjusted more carefully. The minimum strength required to produce a response varies with the position of the electrodes and the size of the animals. It is least when near the siphons. The strength required is usually large in *Phallusia*, of the order of 100 V. from an 8 μF. condenser across most of a 50 K. potentiometer. These facts are to be expected in view of the variable thickness of the test and the extent of short-circuiting of the shock. In *Ascidiella* the strength required is only about one quarter of the *Phallusia* value. The magnitude of the response to threshold stimulation does not vary with the position of the electrodes. At the least effective stimulation strength every stimulus is not always effective (Fig. 8*a*). A stimulus decrease of 0·5% makes the stimuli ineffective. Subthreshold stimuli do not summate to produce a response.

Increasing the stimulus strength above the threshold value does not affect the height of the response, the excitable system being activated in an all-or-nothing manner by the electrical shocks (e.g. Fig. 6). The latency of response to a single shock is about 0·6 sec. in *Phallusia*, and there is no appreciable variation in the latency with the electrodes in different positions using this method of recording.

The excitable system

It is not possible at present to decide what the excitable system is, although it is clear from the results of the experiments on *Phallusia* and *Ascidiella* that during electrical stimulation the muscles receive the stimuli through a rapidly conducting system which is excited in an all-or-nothing manner by the stimuli. Von Buddenbrock (1928) stated that in ascidians there is a nerve network in the body-wall, but this statement has since been strongly contested by Fedele (1937*a*). Das (1936) has described nervous elements in the test of *Herdmania*. It is possible that local stimulation of the test is brought about by these elements. Whatever the excitable system may be, the situation is remarkably similar to that found in coelenterates, especially actinians, when these are stimulated in the same way (cf. Pantin, 1935*a–c*, and Bullock, 1943).

Facilitation

Many results are, nevertheless, quite different from those given by sea anemones. A single stimulus produces a measurable response, although this is small (Fig. 4) and occasionally ineffective (Fig. 8*b*). The second of a pair of shocks at intervals of 1 sec. down to about 0·3 sec. (the smallest interval used) produces a large, fast response (Figs. 4–6). Quantitative measures of the size of this response are not of great value, but it may be stated that over this range

of interval between shocks there is no significant variation in the magnitude of the response (Fig. 7*a*, *b*). When the first stimulus is ineffective the second

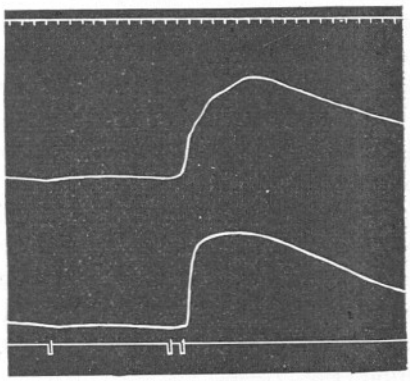

Fig. 4. Responses to a single shock and to a pair of shocks at 1 sec. interval. *Phallusia*. Upper record atrial siphon, lower record branchial siphon.

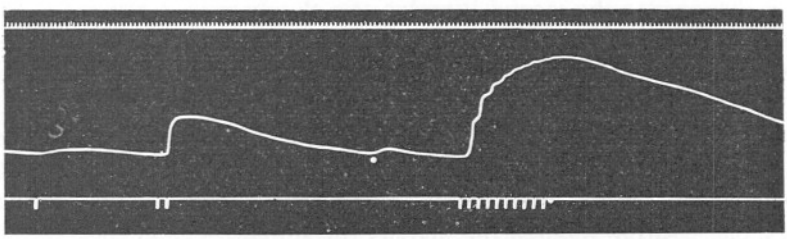

Fig. 5. Responses to a single shock, to a pair of shocks and to a consecutive series of ten shocks. *Ascidiella*. Branchial siphon. Time in sec.

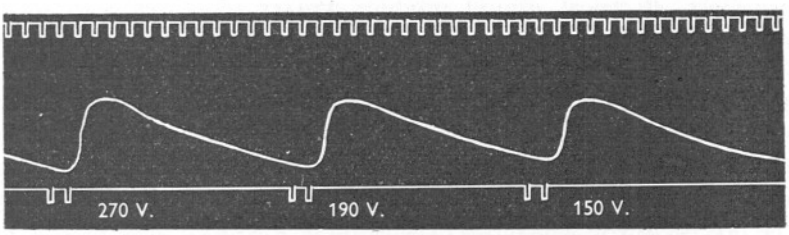

Fig. 6. Responses to pairs of stimuli at various voltages. Threshold was 145 V. *Phallusia*. Branchial siphon. Time in sec.

may act like a normal first and the large response is then given to the third (Fig. 8*b*). Occasionally, three or even four stimuli are necessary before a first effective stimulus appears.

The second of a pair of shocks in rapid succession produces a response which is so much larger than the response to the first that it looks as though a different effector mechanism has been brought into play. Lengthening the interval between a pair of shocks shows, however, that this large response is simply due to an extensive facilitation consequent upon the arrival of a first effective stimulus. At frequencies of 1 per 2 sec. and lower the height of the response to a pair of stimuli is reduced (Fig. 7*c*). There is still an enhancing effect of the first stimulus at a frequency of only 1 per 10 sec. (Fig. 7 *d*). The state of facilitation develops rapidly, as in anemones, stays at its maximum for 1·5–2 sec. and then gradually declines, becoming negligible after 10–15 sec. After a closely spaced pair of shocks the aperture is almost half-closed and subsequent shocks produce contractions which serve to close it more completely. Further stimuli after the first two produce a typical smooth-muscle-type staircase. The steepness of the staircase increases with increasing frequency of stimulation (Fig. 7*a–d*).

Functional significance

The functional significance of this type of response is fairly clear. The rapid rise in response to the second stimulus of a closely spaced pair is the characteristic squirt of the ascidians. The first stimulus simply closes the aperture slightly, the usual response to a slight mechanical vibration or light touch of the siphon. The second, effected by stronger vibration or contact, results in a rapid ejection of water through the closing aperture. This 'ejection reflex' (Jordan, 1908) has frequently been described as being of use in removing sources of irritation from the branchial cavity, ejecting sexual products or faeces, etc. During spontaneous activity the animals seldom close the siphon much further than the closure produced by two or three shocks in rapid succession. Complete closure only follows persistent stimulation. When the animal has recently been stimulated, or during periods of natural unresponsiveness, electrical stimuli produce weaker responses with increased latency and slower rate of rise of contraction (Fig. 14, and cf. also Kinoshita and Polimanti). These consequences, which are apparent after only one burst of electrical stimuli and increase progressively with further bursts until the animal is relaxed but inexcitable, are consistent with the view that the vigorous normal enhancement of the response to the second effective stimulus is due to an extreme development of facilitation, and that this mechanism is easily exhausted.

The precise way in which this exhaustion is developed must depend on the nature of the facilitation phenomenon. The indirect evidence points to the neuromuscular junction as being the site of facilitation in sea anemones. It is unlikely that direct evidence will be forthcoming. In the absence of the latter it is probably unwise to speculate, but if a junction transmitter is involved, exhaustion could be due either to its progressive depletion, a phenomenon which is not found in any known systems, or to its accumulation which is also

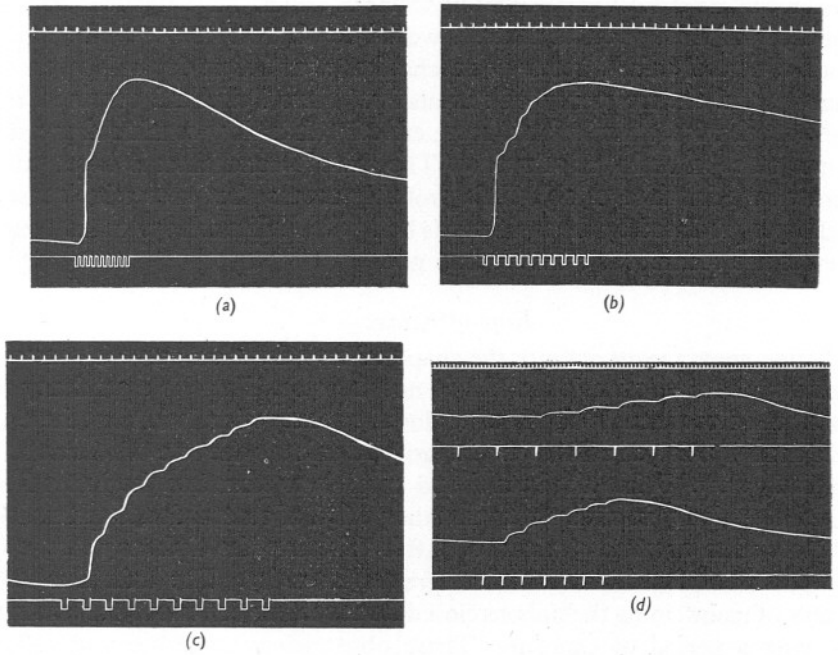

Fig. 7. Responses to: (*a*) 2 per sec.; (*b*) 1 per sec.; (*c*) 1 per 2 sec.; (*d*) 1 per 5 sec. (lower record); 1 per 10 sec. (upper record). *Phallusia*. Branchial siphon. Time in sec.

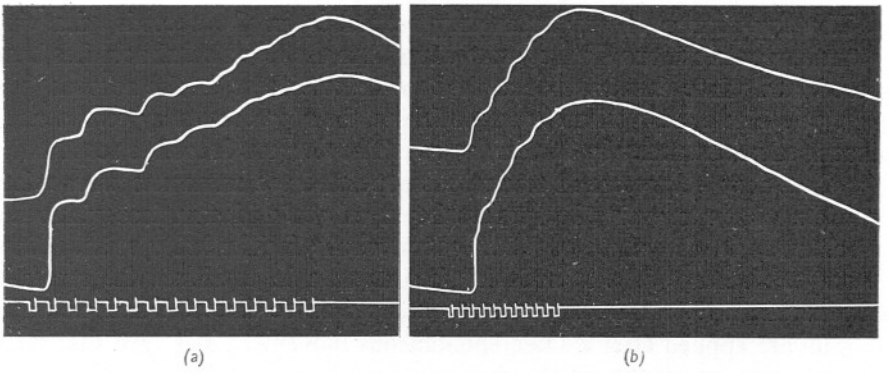

Fig. 8. Parallel behaviour of the atrial (upper record) and branchial (lower record) siphons showing also: (*a*) responses to just threshold stimulation at 1 per sec., not every stimulus is effective; (*b*) ineffective first stimulus with delayed response to the second and quick response to the third. *Phallusia*.

unlikely after such brief stimulation. An alternative possibility is that the phenomena are at least partly intramuscular in origin. Investigations into the properties of these peculiar muscles would be of great interest. The way in which a normal animal reacts to mechanical stimulation depends upon the intensity and the frequency of stimulation. Thus Polimanti observed that 'rapid mechanical stimulation is more effective than slow continued pressure for the same intensity of stimulus'. The same phenomenon is observed in anemones (Kinoshita, 1911). This probably means that successive sensory discharges produced by the rapid prods bring the facilitation system into play, whereas the continuous stimulus may not.

Rate of Relaxation

During spontaneous activity the shape of the relaxation curve is constant, but after electrical stimulation this is not the case. There is a tendency for relaxation to occur more slowly after slow frequency stimulation but there are exceptions to this generalization. In fatigued animals the rate of relaxation is extremely slow. It has not been found possible to stimulate the intact fresh animal electrically in such a way that the period of contraction is maintained for more than about five minutes. After this time the siphons relax, even though stimulation is continued at greater intensity. The animal is itself capable of maintaining the siphons closed for much longer periods, for example, following a period of exposure. These observations, together with others mentioned below in connexion with ganglion extirpation, suggest that relaxation is an active process in ascidians.

Supernumerary Responses

The appearance of supernumerary responses in the records, denoting stimulus contributions from sources other than the electrical shocks has been noted, and white dots have been used to indicate these on the records (e.g. Fig. 9*c*). These are, perhaps, comparable to the supernumerary contractions described in anemones by Pantin (1935*c*). The nervous impulses responsible for these may be present in normal unstimulated sea anemones where they would not have an overt effect unless they nearly coincided in time with other discharges, so that these together operated the facilitation system. Since a single discharge is a recordable phenomenon in ascidians the study of supernumerary contractions is there rendered more direct. When electrical stimuli are applied after a small spontaneous movement it is seen that these are effective in enhancing the response to subsequent shocks (Fig. 9*c*, *d*). Rhythmic supernumerary responses have also been observed, as mentioned above (p. 292) (see Fig. 12), although these occur at much longer intervals than those described in anemones. It seems highly probable that the events giving rise to supernumerary contractions are not a consequence of the electrical stimuli but arise independently of them, except in the case of the rhythmical

contractions which may be due in ascidians to an effect of the shocks in changing momentarily the frequency of spontaneous activity.

Ganglion Extirpation

Experiments have been carried out on deganglionated animals. These animals usually respond to electrical stimulation like slightly fatigued intact animals, but there is no great difference in the pattern of response (Fig. 11). Jordan (1908) and Hecht (1918) have studied the effect of ganglion extirpation on the responses of the siphons to mechanical contact. Before extirpation a slight mechanical stimulus to the outside of a siphon rim causes a small local

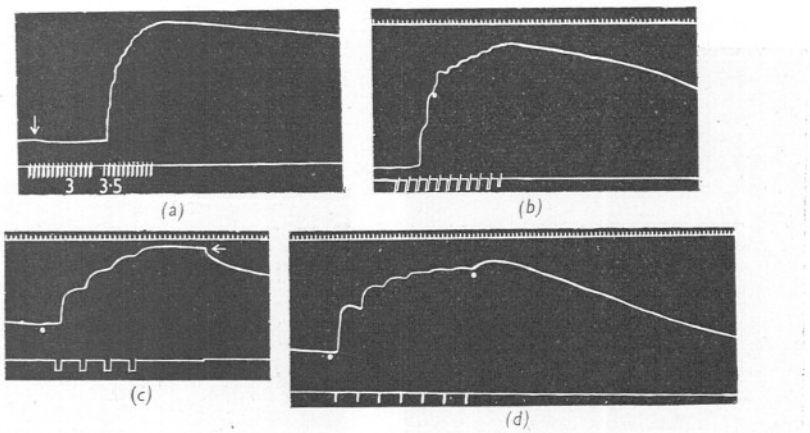

Fig. 9. Spontaneous movements and their consequences. *Ascidiella*. (*a*) Slight relaxation during subthreshold stimulation; (*b*) spontaneous movement (indicated by white dot) during stimulation experiment; (*c*) stimulus applied 2 sec. after a spontaneous movement. Drum stopped at arrow; (*d*) stimulus applied 1 sec. after a spontaneous movement.

response of the siphon. A larger stimulus causes closure of the other siphon as well as closure of the stimulated one. After ganglion extirpation the unstimulated siphon fails to respond, although the stimulated one continues to respond. Jordan described these responses as reflexes and regarded the second response as a protective reflex. If we confine the use of the term reflex to its original usage in physiology (as 'animal spirits' ascending nerves to central systems and in turn descending to effect motor activity) then these activities are better described as responses than as 'reflexes'. These responses can be studied graphically with this preparation (Fig. 10). In *Phallusia* it will be noted that in spite of the absence of the ganglion there is a slight response of the non-stimulated siphon when a single siphon is touched with a glass rod. When the containing vessel is tapped both siphons respond together. Day (1919) and Bacq (1935) agreed that the operation of ganglion extirpation reduces the general muscle tone. The fact that ganglion extirpation only

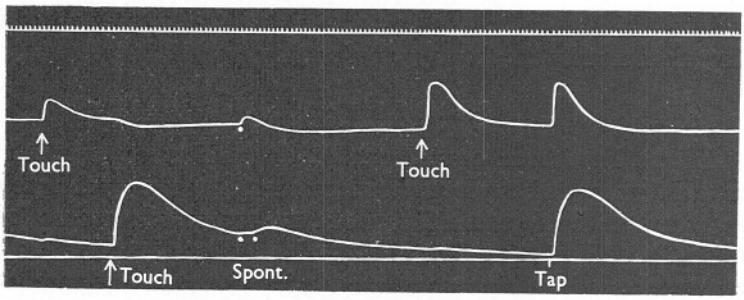

Fig. 10. Responses of a deganglionated *Phallusia* to local stimulation of the siphons and to a tap on the tank. Note the small response of the opposite siphon. Time in sec.

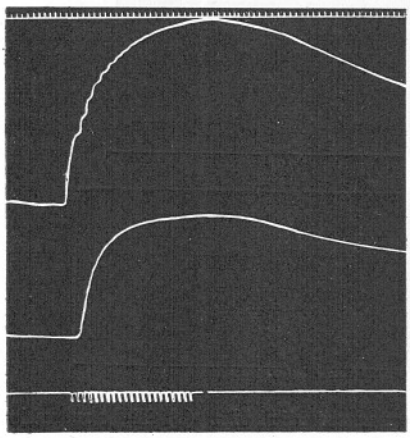

Fig. 11.

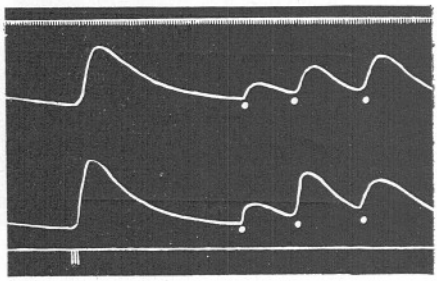

Fig. 12.

Fig. 11. Responses of a deganglionated *Phallusia* to electrical stimulation at 1 per sec. Upper record branchial siphon, lower record astrial siphon. Time in sec.

Fig. 12. Spontaneous rhythmical contractions following an electrical stimulus (three shocks) applied soon after a spontaneous squirt (not shown). *Phallusia*. Time in sec.

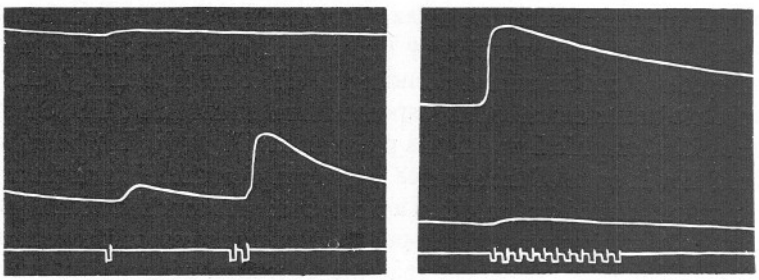

Fig. 13. Inhibition of one siphon only during stimulation experiments. Upper record atrial, lower record branchial in both records. *Phallusia*. Time in sec.

affects the pattern of response to electrical stimulation indirectly, by the effect which this operation appears to have on muscle tone, shows that augmentation by the ganglion is not normally involved in the squirting movements. Also, the results show that the electrical stimuli are not transmitted to the muscles by way of the ganglion.

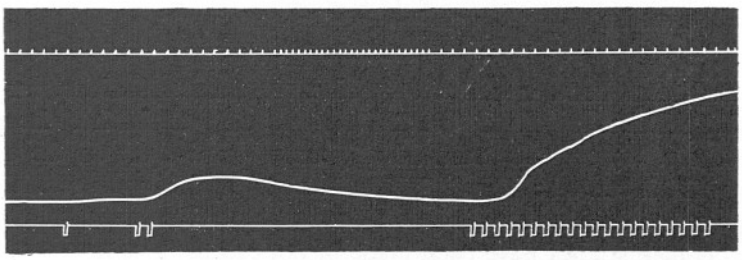

Fig. 14. Responses of *Phallusia* branchial siphon immediately following relaxation after intense stimulation before the experiment. Time in sec. The drum was slowed down in the middle of the record to include the whole of the relaxation after the second response.

Synchrony of the Siphons

When responses are recorded from both siphons simultaneously, it is seen that these act in unison. Water is ejected through both siphons simultaneously through the closing apertures. The same water movements occur during spontaneous contractions which are also synchronous. Very rarely during stimulation one siphon fails to respond. In Fig. 13 the failure of one siphon has in turn been followed by inhibition of the other siphon after this had started to contract. This failure of the siphons to act together has not been observed in deganglionated animals during electrical stimulation. Jordan and Polimanti were both of the opinion that the ganglion can regulate the 'reflexes' by either inhibition or facilitation. Occasionally, small positive openings can be seen in the records (e.g. Fig. 9*a*) which correspond to reflexing movements of the siphon rims. It is difficult to see how these movements can be brought about except by quick positive relaxation. Similar movements can be observed in some of Yamaguchi's records. These observations strongly suggest that the ganglion can maintain or reduce tone in the muscles, and that it can prevent stimuli from giving effective responses.

Test-free Animal

When the animal has had its test removed it remains in a state of contraction for several minutes and then relaxes gradually. When relaxed, spontaneous contractions appear at intervals of a few minutes, as in the intact animal. These contractions involve the whole of the muscle mass simultaneously, as far as the eye can judge. They can also be produced by stimulating the siphon rims mechanically but not by touching the body-wall. In the latter case,

a ripple of contraction travels outwards from the point of stimulation. The extent of this travel depends on the strength of the stimulus. Loeb (1901), and later Fedele (1937*b*), thought that the muscles of ascidians are capable of direct excitation, and that they are also capable of propagating this excitation. Bacq (1935) demonstrated slow ripples of contraction in the siphons of *Ciona*. There are certainly at least two different methods of transmission of stimuli in ascidians.

Discussion

Ascidians show a number of interesting physiological peculiarities. Investigation of ascidian nerve-muscle should not only help to further the general study of these systems, but should also throw some light on the adaptive changes which can take place in nerve-muscle physiology in relation to an animal's way of life. The sessile sea-squirts have free-living relatives and when adequate studies have been made of both forms a comparison will be possible. There is also a parallel between the sedentary, or free-living members of the Tunicata and the corresponding forms of the Coelenterata, the sea anemones and the jellyfish. It is now possible to carry the comparison between the sedentary forms a little further.

Although no homology of intimate mechanism is postulated, and detailed consideration must await the results of further investigations, it is remarkable that these phylogenetically unrelated groups should include sedentary representatives which have evolved independently what appears to be a similar basic method of producing a protective response from a simple muscle system. *Metridium* and *Phallusia* inhabit similar environments and are often found together. They both feed on small particles and depend on a ciliary current for both feeding and respiration. A large central cavity is in each concerned with these activities and there is a terminal opening into the cavity. Protection is important not so much against predators, although these have been described (see, for example, Yonge, 1949), as against interference with the continuity of the feeding and respiratory mechanisms by foreign bodies entering therein. The quick contractions of the longitudinal muscles of *Metridium* withdraw the animal from the source of the stimulus and produce a small current of water which helps to drive it away. Later, if the stimulus persists, the entrance to the all-important cavity is closed. In large, sedentary ascidians the facilitated quick contraction is more effective in producing a protecting jet of water than the actinian system, but as in the actinian is followed later, if the stimulus persists, by further withdrawal and by closure of the aperture.

The utilization of a single effector system which has no antagonists, to produce slow or quick contractions according to the nature of the stimulation by the development of facilitation to an extremely high degree, is an efficaceous and very economical method. The systems which have been evolved by several more highly organized animals to produce comparable effects, by the use of multiple innervation, giant fibres, etc., are not necessarily more effective.

The investigations described serve to make the variations in some of the results of previous workers, published and unpublished (personal communications), a little clearer. Ascidians have patterns of spontaneous activity which affect the properties of the nerve-muscle system so that similar stimuli may elicit different degrees of response in the same animal at different times. The pattern of spontaneous activity, and other properties of the nerve-muscle system are modified for some time after a period of stimulation. The extent of the modification is proportional to the physiological condition of the animal and the duration of stimulation.

There remain, unfortunately, large gaps in our knowledge of the phenomenon of facilitation as it appears in anemones and in ascidians. First, we do not know the nature of the excitable system (this applies especially to ascidians) and the way in which it is activated by electrical shocks; whether, for instance, it gives trains of impulses or a single impulse for each condenser discharge. Secondly, we do not know anything about the physical phenomena occurring in the muscles during stimulation. There are several suggestions that intramuscular factors are involved. Thirdly, we have no notion as to the chemical nature of the junction transmitter. None of these problems can be solved until isolated physiological units are available for investigation.

The work was done at the Plymouth Laboratory; to the Director and staff of which most grateful thanks are extended. The writer occupied the London University table during parts of the spring and autumn of 1951. Gratitude is also expressed to Miss P. Kott and Dr J. A. C. Nicol for helpful discussion during my stay at Plymouth, and to Prof. O. Lowenstein, Dr G. P. Wells and Prof. P. B. Medawar for carefully reading the draft and offering valuable cirticism.

Summary

A method is described for investigating the reactions and spontaneous activity of two species of ascidian, *Phallusia mammillata* and *Ascidiella aspersa*, which does not disturb the animals unduly. The method can be used for obtaining graphic records of the so-called 'reflexes' of ascidians.

If due attention is paid to certain factors which affect the state of the animals, they can be made to respond to electrical stimuli applied to the outside of the test in a way which can be observed repeatedly in the same animal, in other animals of the same species and in at least two genera of ascidian.

Electrical stimuli applied to the test affect the excitable system of the whole animal in an all-or-nothing manner.

Response to graded electrical stimulation reveals a facilitation mechanism which gives enormous enhancement to the size and speed of response to the second of a close pair of effective stimuli. It is suggested that this mechanism

is responsible for the production of the rapid squirt of the large sedentary ascidians.

A possible cause of the very rapid fatigue of ascidians to all kinds of stimulation is fatigue of the facilitation mechanism following a period of stimulation.

A parallel is drawn between the responses of *Metridium* and the responses of *Phallusia* and *Ascidiella*. The responses have some common features and the response mechanism appears to serve a similar purpose in the life of the animals.

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ECOLOGICAL AND NON-ENVIRONMENTAL CONSTITUTIONAL RESISTANCE OF THE PROTOPLASM OF MARINE ALGAE

By Richard Biebl, Ph.D.

Institute for Plant Physiology of the University of Vienna and the Plymouth Laboratory

For some years workers on cell physiology have made a practice of investigating the tolerance, or, as perhaps more correctly expressed, the 'resistance', of the protoplasm of plant cells to variations in the environment, both natural and artificial. Weber (1929) and Höfler (1932) have contributed valuable results in their description of the properties of the cytoplasm of plant cells, showing how greatly these may vary among different plants or different cells and tissues of one plant. Experiments have been recorded on the resistance of various plant cells to heat, cold, desiccation, various acids and alkalis, poisons and other chemicals, various radiations, and, for marine algae, to salinity changes in the water.

A closer examination shows that these resistances are not of equal value in the discernment of different types of protoplasms.

Through adaptation to the requirements of the habitat all organisms within a certain biological area show a characteristic resistance to desiccation, exposure to strong light, cold, heat, and other factors. This we shall call the 'ecological resistance'. Although essentially determined by heredity, it varies to a certain extent under external influences.

On the other hand, there is the 'non-environmental constitutional resistance', i.e. the resistance to substances or influences which, under natural conditions, never become so strong that a resistance to them might play an important part in the life of the plant. This includes resistance to acids, alkalis, certain chemicals, X-rays or other short waves. Such differences, often rather obvious, seem to be quite independent of environmental relations; and are particularly suited for characterization of different types of protoplasm or of protoplasmic states. If non-environmental resistance changes during the development of the plant we may interpret it, like changes in the permeability of the cell (Höfler, 1937; Hofmeister, 1938), as an indirect indication of a change in the general condition of the protoplasm.

Ecological Resistance

Marine algae of various depths from coastal regions show characteristic differences in their resistance to desiccation, temperature, light, pH, and other factors. The plasmolytic behaviour and osmotic resistance of some red

algae have been previously observed by Höfler (1930, 1931); the resistance to desiccation and other adverse conditions of the habitat by Baker (1909), Johnson & Skutch (1928) and others; the pH-resistance by Gail (1918), Atkins (1922*a*, *b*) and Kylin (1927); and the resistance of marine algae to cold by Kylin (1917) and others. An excellent summary of the ecology of marine algae and numerous references are to be found in Fritsch (1945).

The ecological resistances for many marine algae have already been investigated (Biebl, 1937, 1938, 1939*a*, *b*). The variations in resistance to different ecological factors establishes three definite ecological groups: (1) algae from the intertidal zone, (2) algae from low-water level and tide-pools, and (3) sublittoral algae.

The osmotic resistance can be found by placing portions of algae in dilute and in concentrated sea water for a period of 24 hr. The osmotic value is determined by plasmolysis.

The algae from the intertidal zone show an average resistance to 0·1–3·0 sea water (i.e. 10–300 % normal sea water), algae from the low-water level and the tide-pools a resistance to 0·4 (0·5)–2·0 sea water, and algae from the sublittoral zone, to only 0·5 (0·6)–1·5 sea water. Such ranges in resistance have been observed in algae from Plymouth and also from Heligoland and Naples. Table I shows the osmotic resistance of algae from various levels at Naples.

The same ecological groups were found when examining the resistance to desiccation. The algae were placed, for 13 hr., in small, closely sealed jars over a saline solution of varying concentration under atmospheres of relative humidity varying from 83 to 100 %. Table II shows the results of such experiments with algae from the rocky shores off Heligoland.

In the summer of 1951 I made some informative experiments at Plymouth on the influence of direct sunlight on algae from both the intertidal and sublittoral zones.

On 21 September pieces of algae from the intertidal zone and tide-pools, *Porphyra umbilicalis* (L.) Kütz. f. *laciniata* (Lightf.) J. Ag., *Cladophora utriculosa* Kütz., *Plumaria elegans* (Bonnem.) Schmitz, *Callithamnion tetragonum* (Wither.) Ag., *Griffithsia flosculosa* (Ellis) Batt., *Phycodrys rubens* (Huds.) Batt., *Sphondylothamnion multifidum* (Huds.) Näg., and from the sublittoral zone, *Dictyota dichotoma* (Huds.) Lamour., *Neomonospora pedicellata* (Sm.) G. Feldm. & Meslin, *Polyneura hilliae* (Grev.) Kylin and *Antithamnion cruciatum* (Ag.) Näg., were placed in shallow dishes of white porcelain filled to a depth of 1·5 cm. with sea water and exposed to direct sunlight on the roof of the laboratory for 2 hr. from 11.30 a.m. to 1.30 p.m. G.M.T. The daylight recorder of the laboratory showed that the light received had been 107 kilolux-hours for that time with a maximum vertical illumination of 61·1 kilolux and a minimum of 19·9. At the end of the experiment the water temperature was 17·8° C.

TABLE I. RESISTANCE TO DILUTE AND CONCENTRATED SEA WATER

	Osmotic resistance (sea water concentration)	Osmotic value (sea water concentration)
Intertidal zone		
Cladophora spinulosa Grev.	0·1–3·0	1·6
C. bertolonii Kütz.	0·1–3·0	1·5
C. hamosa Kütz.	0·1–3·0	1·6
C. laetevirens Kütz.	0·1–2·8	—
Bangia fuscopurpurea (Dillw.) Lyngb.	0·1–3·0	—
Porphyra leucosticta Thur.	0·1–3·0	—
Polysiphonia pulvinata J. Ag.	0·2–3·0	2·4
Low-water level		
Chaetomorpha linum (Mull.) Kütz.	0·0–2·4	1·4
Cladophora utriculosa Kütz.	0·1–2·4	1·5
Ceramium berneri Schffn.	0·3–1·9	1·5
Callithamnion granulatum (Wucluz.) Ag.	0·4–2·6	—
Antithamnion cruciatum (Ag.) Näg.	0·4–1·9	1·7
Sublittoral zone		
Cladophora prolifera (Roth) Kütz.	0·1–2·0	1·5
C. ramellosa Kütz.	0·5–1·7	1·6
Taonia atomaria (Good. & Wood.) J. Ag.	0·8–1·5	—
Griffithsia furcellata J. Ag.	0·7–1·4	1·5
G. flosculosa (Ellis) Batt. (=*setacea*)	0·6–1·5	1·6
G. schousboei Mont.	0·6–1·4	1·5
Aglaeothamnion scopulorum (Ag.) G. Feldm.	0·6–1·5	1·6
Ceramium diaphanum (Lightf.) Roth var. *strictum* (Kütz.) G. Feldm.	0·4–1·4	1·4
Pleonosporium borrerii (Sm.) Näg.	0·7–1·5	1·5
Plocamium coccineum (Huds.) Lyngb.	0·7–1·4	1·7
Nitophyllum punctatum (Stackh.) Grev.	0·7–1·4	—
Acrosorium uncinatum (Turn.) Kylin	0·6–1·5	—

TABLE II. RESISTANCE TO DESICCATION

Algae exposed to air of the stated percentage humidity for 13 hr. The figures show the minimum humidity tolerated.

	Humidity (%)
Intertidal zone	
Porphyra umbilicalis (L.) Kütz. f. *laciniata* (Lightf.) J. Ag.	83·0
Rhodocharton floridulum (Dillw.) Näg.	88·0
Elachista fucicola (Vell.) Aresch.	86·0
Ulva lactuca (L.) Le Jol.	83·0
Enteromorpha linza (L.) J. Ag.	83·0
Cladophora rupestris (L.) Kütz.	83·0
C. gracilis (Griff.) Kütz.	86·0
Low-water level	
Polysiphonia nigrescens (Sm.) Grev.	86·0
Membranoptera alata (Huds.) Stackh.	94·6
Plumaria elegans (Bonnem.) Schmitz	94·6
Dictyota dichotoma (Huds.) Lamour.	94·6
Sublittoral zone	
Plocamium coccineum (Huds.) Lyngb.	98·8
Antithamnion plumula (Ellis) Thur.	98·4
Trailliella intricata Batt.	98·4
Halarachnion ligulatum (Woodw.) Kütz.	96·8

The sublittoral algae were killed completely by the irradiation; the algae from the intertidal zone and tide-pools, however, showed little or no injury. Among the algae from the tide-pools only *Sphondylothamnion multifidum* and *Phycodrys rubens*, which grow in especially shaded places, were killed.

Under light of injurious intensity the necrotic cells of the red algae first changed to a raspberry red but quickly bleached entirely under more extensive light exposure in contrast to other lethal injuries.

If continuously exposed to two lamps of 350 W. each at a distance of 31 cm. the difference in the reaction of the intertidal algae and the sublittoral algae can be readily seen after 5 days. After such a long exposure some of the algae from the intertidal zone—*Ulva lactuca* (L.) Le Jol., *Cladophora utriculosa* Kütz., *Ceramium ciliatum* (Ellis) Ducluz, *Callithamnion tetragonum* (Wither.) Ag., *Plumaria elegans* (Bonnem.) Schmitz and *Polysiphonia furcellata* (Ag.) Harv.—were bleached intensively but were still living, as shown by staining with neutral red, while the sublittoral algae and the algae from shady tide-pools—*Acrosorium uncinatum* (Turn.) Kylin, *Dictyota dichotoma* (Huds.) Lamour., *Heterosiphonia plumosa* (Ellis) Batt., *Bonnemaisonia asparagoides* (Woodw.) Ag. and *Neomonospora pedicellata* (Sm.) Feldm. & Meslin—were killed.

The resistance of the protoplasm to light of high intensity therefore also shows the typical characteristics of an 'ecological resistance'.

Non-environmental Constitutional Resistance

Experiments made in recent years have shown that the resistance of the cells of various plants to minute quantities of various elements, such as boron, zinc, manganese and vanadium, differs widely (Biebl, 1947, 1949, 1950). If moss leaves or slices from the epidermis of phanerogams are brought into graded solutions of salts of the above substances we find that the death-point of the various plants differs rather widely.

Such experiments were made with a series of solutions, of boric acid (H_3BO_3), manganese sulphate ($MnSO_4$), zinc sulphate ($ZnSO_4$), and vanadium sulphate ($VOSO_4$), of concentrations 3, 1, 0·1, 0·01, 0·001, and 0·0001 %. The material was immersed and examined 48 hr. later. Table III, giving the results, shows the resistance of the epidermal cells of some dicotyledons and the leaflets of some mosses and liverworts to the solutions mentioned. Sulphates were chosen for the experiment, since the sulphate radicle is known to be least harmful to protoplasm.

The picture which emerges shows not that some plants are very sensitive to all these substances while others are resistant, but rather that a given plant may be relatively resistant to one substance and relatively sensitive to another. Therefore, each separate 'combination of resistances' can be used as a differentiating characteristic for the various kinds of protoplasm.

Table III shows that the resistance of the phanerogams to boron, zinc and vanadium is relatively small and varies but little, while the resistance to manganese differs widely.

On comparing the resistance limits of those phanerogams with that of some mosses and liverworts we find that the latter behave quite differently. Some mosses can stand H_3BO_3 or $ZnSO_4$ in solutions of as much as 3 %, and the death-point in $MnSO_4$ lies generally above 20 % and in $VOSO_4$ at 5–10 %.

Among the marine algae it was interesting, on the one hand, to find out whether the chemical resistance of the protoplasm holds a similar exceptional position like that of the mosses when compared with phanerogams. On the other hand, the marine algae are excellent objects for deciding experimentally whether there is any relationship between 'non-environmental' chemical resistance and 'ecological' resistance.

TABLE III. RESISTANCE TO BORON, ZINC, MANGANESE AND VANADIUM OF SOME DICOTYLEDONS (EPIDERMAL CELLS) AND MOSSES (LEAFLETS)

The tissues were in each case exposed to the following strengths of solution: 3, 1, 0·1, 0·01 0·001, and 0·0001 %. The strengths given are of the strongest solution which the tissues resisted.

	H_3BO_3	$ZnSO_4$	$MnSO_4$	$VOSO_4$
Beta vulgaris (mangel-wurzel)	0·1	0·01	3·0	0·01
Beta vulgaris (beet-root)	0·1	0·01	3·0	0·001
Brassica oleracea (kohlrabi)	0·1	0·001	0·001	0·001
Brassica oleracea (cabbage)	0·1	0·001	0·001	0·001
Raphanus sativus	1·0	0·001	0·001	0·001
Solanum tuberosum	0·1	0·001	3·0	0·0001
Daucus carota	0·1	0·001	0·01	0·001
Pisum sativum	0·1	±0·001	0·1	—
Phaseolus multiflorus	0·1	0·001	0·001	—
Mnium punctatum	3·0	0·1	3·0	3·0
M. rostratum	0·1	0·001	3·0	3·0
Bazzania trilobata	0·1	3·0	3·0	3·0
Plagiochila asplenioides	3·0	0·1	3·0	3·0

Algae from the intertidal zone, from tide-pools and from the low-water level on the rocky shore at Wembury (east of Plymouth), and sublittoral algae collected at Plymouth (mostly near the Mewstone) were placed in sea-water solutions of H_3BO_3, $ZnSO_4$, $MnSO_4$ and $VOSO_4$ and examined 48 hr. later.

All four substances are soluble in sea water, but the 3 % solutions of $ZnSO_4$ and $MnSO_4$ show a slight deposit at the bottom of the bottle. The experiments were made with algae which, owing to the size of their cells, were especially suited for microscopic examination.

Death in almost all the green and the red algae was accompanied by a strong swelling of the membranes. This was most prominent in *Callithamnion tetragonum* when placed in lethal solutions of boron and vanadium, and less so if placed in $ZnSO_4$ and $MnSO_4$. Moreover, in the species of *Cladophora* the complex chloroplasts within the dead cells were destroyed and

frequently decomposed into lumps of a dark green colour. This destruction of the normal structure of these algae was especially obvious when they were placed in strong solutions of manganese. The majority of red algae change to a red-violet colour when dead. This and the white colour of the swollen membranes, even of the small cells of *Plumaria elegans*, made dead tissues easily recognizable. In death the plastids of most red algae are displaced, rounded off, or occasionally stuck together. In this way also the dead cells of *Dictyota dichotoma* can be distinguished from the living. In this alga the living, homogeneously coloured plastids are, as a rule, distributed close to the cell wall in the cytoplasm; in the dead cell they are displaced, stick together, and have a dark contour.

Especially difficult to recognize are the dead cells of *Ulva lactuca*, but staining with neutral red helps (6 drops of a 1 % solution of neutral red in distilled water to 50 c.c. of sea water). The living cells show red vacuoles, while the dead cells remain colourless. The same is true of *Porphyra*, but the cell sap of the living cells is not stained homogeneously and one can see dark red globules in the protoplasm. Similar globules are also to be found in the vacuoles after neutral red staining in *Callithamnion tetragonum* and in the species of *Polysiphonia*. On the other hand, *Ceramium ciliatum* shows a homogeneous red colour of the cell sap. But if a subsequent plasmolysis is made small red globules appear. This biological reaction of *Ceramium ciliatum* was of especial value for experiments in the resistance to light as described earlier in this paper, where the first injury from light was a strong bleaching of the plastids so that it was often only possible to recognize the cells as living through vital staining with neutral red. The neutral red staining of the living cells of *Dictyota* is characterized by a granulated deposit. *Neomonospora* and other red algae, on the other hand, show a diffused red staining of the cell sap. In the species of *Cladophora* plasmolysis in sea water of double or treble concentration is a good test for living cells.

The results of experiments on the resistance of some algae from various habitats to boron, zinc, manganese and vanadium are given in Table IV.

Table IV gives a clear answer to our two initial questions. (1) The resistance limits and the combination of the resistances against the chemicals used are similar to those of the phanerogams. The difference in resistance to boron, zinc, manganese, and vanadium between phanerogams and marine algae is far smaller than that between phanerogams and mosses. (2) There is no relationship between the ecological resistance of marine algae to sea water of various concentration, to desiccation or light exposure, on the one hand, and the chemical resistance to boron, zinc, manganese and vanadium, on the other. It differs within an ecological group, but is typical for the species.

In the above experiments the survival of the protoplasts offered an indication of the resistance of the cell. The death of the protoplasts indicates that the resistance limit has been exceeded, and this allows a sharp definition of

the range of resistance. The fact that injurious influences which are not quite lethal affect the physiological processes within the cells can also be observed occasionally by cytological methods through changes in the protoplasm viscosity, and through permeability or the effects of vital staining. But the examination of the internal conditions of the cell under the stress of extremely strong but not quite lethal conditions is another question. It can be better answered by examining the progress of certain physiological processes such as respiration or assimilation (Montfort, 1936, 1937; Montfort & Hahn, 1950; Stocker & Holdheide, 1937).

TABLE IV. RESISTANCE TO BORON, ZINC, MANGANESE AND VANADIUM OF ALGAE FROM VARIOUS HABITATS

The algae were placed in solutions of the same strength as in Table III, the strongest solution which they survived being recorded. Figures in brackets show that the alga was partially killed. At concentrations lower than this the tissues survived.

	H_3BO_3	$ZnSO_4$	$MnSO_4$	$VOSO_4$
Intertidal zone				
Cladophora ramosissima (Drap.) Kütz.	(1·0)	(0·1)	0·1	0·01
C. rupestris (L.) Kütz.	1·0	0·1	3·0	0·01
Ulva lactuca (L.) Le Jol.	0·1	0·01	(1·0)	0·01
Ceramium ciliatum (Ellis) Ducluz	0·1	0·01	(3, 1)	0·01
Low-water level and Tidepools				
C. utriculosa Kütz.	1·0	(0·1)	(0·1)	0·01
Plumaria elegans (Bonnem.) Schmitz	0·1	(1, 0·1)	3·0	(0·01)
Callithamnion tetragonum (Wither.) C.Ag.	0·01	(1·0)	(1·0)	(0·01)
Polysiphonia elongella Harv.	(1·0)	(0·1)	1·0	0·001
Polysiphonia sp.	0·1	0·1	1·0	0·001
P. furcellata (Ag.) Harv.	(1·0)	(0·1)	(1·0)	0·01
Sublittoral zone				
Dictyota dichotoma (Huds.) Lamour.	0·01	0·1	1·0	(0·01)
Dictyopteris membranacea (Stackh.) Batt.	0·01	0·01	3·0	(0·0001)
Antithamnion cruciatum (Ag.) Näg.	0·1	0·1	0·1	(0·01)
Heterosiphonia plumosa (Ellis) Batt.	1·0	(0·1)	(3·0)	(0·01)
Neomonospora pedicellata (Sm.) G. Feldm. & Meslin	0·1	(0·1)	(3·0)	0·001

I am sincerely grateful to the Director, Mr F. S. Russell, F.R.S., and to Dr W. R. G. Atkins, F.R.S., Head of the Physiological Department, for my kind reception at the Marine Biological Laboratory at Plymouth and for all the facilities provided.

SUMMARY

Marine algae supply good examples of the difference between 'ecological' and 'non-environmental constitutional' resistance of the protoplasm of their cells to variations in the environment. The resistance to ecological factors such as diluted or concentrated sea water, to desiccation, or to light exposure is very similar among algae occupying the same habitat. On the basis of the

degree of resistance shown, three ecological groups can be distinguished: (1) algae from the intertidal zone; (2) algae from the low-water level and tide-pools; and (3) sublittoral algae.

On the other hand, there is no similarity in the resistance to chemical substances (H_3BO_3, $ZnSO_4$, $MnSO_4$, $VOSO_4$) of algae within a given ecological group. It is characteristic for a given species.

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STUDIES ON THE PARASITES OF *CARDIUM EDULE* L.: *CERCARIA FULBRIGHTI* N.SP., A *GYMNOPHALLUS* LARVA WITH A FORKED TAIL

By Robert F. Hutton

From the Plymouth Laboratory

(Plate I and Text-figs. 1–2)

An examination of 420 specimens of *Cardium edule* L., collected at Millbrook, Plymouth, England, revealed a species of marine cercaria differing from any other larval trematode which has been described. This parasite was present in five of the 420 specimens. The name *Cercaria fulbrighti* is given to this species in honour of U.S. Senator J. William Fulbright of Arkansas.

This work was carried out at the Plymouth Laboratory of the Marine Biological Association while the author was holding a Fulbright Scholarship.

I am grateful to Dr V. Fretter and Dr B. Dawes for reading and criticizing the manuscript. In addition to thanking Dr J. S. Alexandrowicz for reading and offering valuable criticism for the improvement of my manuscript, I am indebted to him for taking the photomicrographs.

The Trematode Parasites of *Cardium edule* L.

Table I contains a summary of the trematode parasites which have been recorded from the cockle. In the table there is some doubt as to whether *Cercaria dichotoma* Müller and *C. fissicauda* La Valette St. George are different species: they may represent, as Lebour (1912) considered them, only one; or, if two, they are closely related. Pelseneer (1906), reporting

Table I

Parasite	Author	Reported by	Encystment or Sporocyst
Bucephalopsis gracilescens = *Bucephalus haimeanus*	(Rudolphi, 1819) Lacaze-Duthiers, 1854	Lebour, 1912; etc.	Sporocyst
Cercaria dichotoma	Müller (according to La Valette St. George, 1855)	Pelseneer, 1906; etc.	Sporocyst
C. fissicauda	La Valette St. George, 1855	Johnstone, 1904	Sporocyst?
Parorchis acanthus = *Cercaria purpurae* sp.inq.	(Nicoll, 1906) Lebour, 1912	Lebour & Elmhirst, 1922	Encystment
Himasthla leptosoma = *Echinostomum secundum*	(Creplin, 1829) Nicoll, 1906	Lebour, 1912?	Encystment
Cercaria mytili sp.inq.	Lebour, 1912	Lebour, 1912	Encystment
C. strigata	Lebour, 1908	Rees, 1939	Sporocyst
Lepidapedon rachion? = *Lepodora rachiaea*?	(Cobbold, 1858) (Cobbold, 1858)	Lebour, 1912	Sporocyst
Cercaria margaritae sp.inq.	Lebour, 1912	Lebour, 1912	Sporocyst
C. cambrensis	Cole, 1938	Cole, 1938	Sporocyst

C. dichotoma from *Cardium edule* (and from several other bivalves), and believing but one species to be involved, gives the following evidence as to why the name *Cercaria fissicauda* should be suppressed in favour of *C. dichotoma* for this larval trematode.

C. dichotoma a été trouvé libre, en mer, à Nice (3). C'est de cette espèce, que notre forme se rapproche le plus; Villot était aussi de cet avis dans sa communication préliminaire (4); mais dans son travail définitif, il donne au parasite de '*Scrobicularia tenuis*', le nom de *C. fissicauda* (5). Or *C. fissicauda* (6) en diffère bien plus et est parasite dans un Gastropode pulmoné d'eau douce: *Limnaea stagnalis*.

(3) De La Valette St. George, *loc. cit.*, pl. II, fig. 1.
(4) Villot. Sur les migrations et les métamorphoses des Trématodes. *Comptes Rendus Acad. Paris*, t. LXXXI, 1875, p. 475.
(5) Villot. *Ann. d. Sc. nat.* (*Zool.*), sér. 6, t. VIII, p. 37.
(6) De La Valette St. George, *loc. cit.*, pl. II, fig. 6 et H.

Materials and Methods

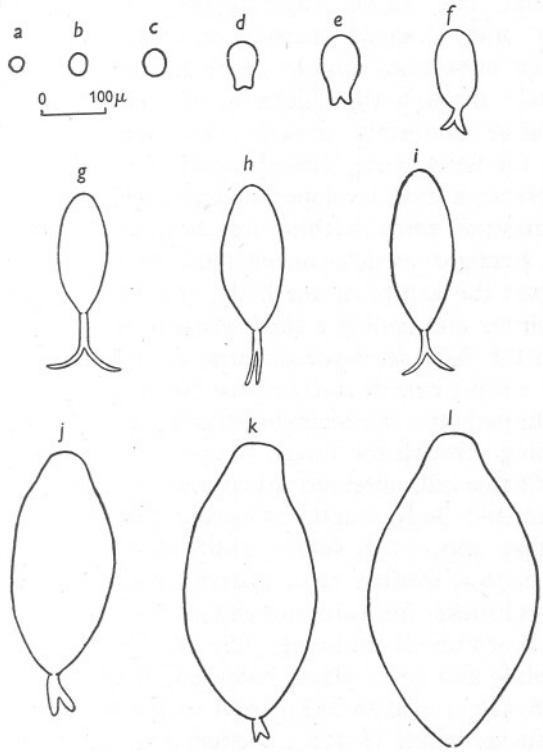
Living material was used to study the excretory system. Measurements were made on living specimens compressed between a glass slide and a cover-glass, as well as on whole mounts fixed in sublimate, stained with Giemsa, and mounted in Canada balsam. Tissues of infected specimens of *Cardium edule* were fixed in Bouin's solution. Serial sections (6μ) were stained with Ehrlich's haematoxylin and eosin.

Observations

The development of *Cercaria fulbrighti* n.sp. within the sporocyst differs from that of any other larval trematode yet recorded. In young developing cercariae forked tails appear (Text-figs. 1 *d–k* and 2 A, B; Pl. I, figs. 1, 4), while *fully developed* cercariae (Text-figs. 1 *l* and 2 A, C; Pl. I, figs. 1, 2 and 4), although still within the sporocyst, never exhibit tails. Throughout the paper, the term '*fully developed* cercariae' is used to designate cercariae, still enclosed within the sporocyst, which have had, in the course of their development, forked tails, but which no longer possess these structures. The tail of this larval trematode may degenerate completely while it is still within the sporocyst. The development and subsequent degeneration of the tail is illustrated in Text-fig. 1; the drawings were made with the aid of a camera lucida using the same magnification. Both tailed and tail-less forms may be present within a sporocyst at the same time, with five being the maximum number of *fully developed* cercariae. Fork-tailed cercariae, capable of active swimming (provided the tail has not started to degenerate), may be liberated from the sporocyst. However, the free-swimming tailed forms, thus far observed, were not as well-developed as compared with cercariae whose tails had degenerated and which were still within the sporocyst. From these observations the possibility of two types of life-history arises; namely, one type in which the free-swimming or tail-less larvae enter a second inter-

mediate host, and a second type in which the tail-less larvae are transferred directly to the final host.

Of the 420 cockles collected at Millbrook, five (1·2 %) were found to contain sporocysts of this species, and in four of these cockles, sporocysts of at least one other cercaria were found. There were two double (Pl. I, fig. 1) and two triple infections. In addition to *C. fulbrighti*, both double infections contained '*Bucephalus haimeanus*', while '*B. haimeanus*' and *Cercaria cambrensis* were included in the two triple infections.



Text-fig. 1. *Cercaria fulbrighti* n.sp.; development and subsequent degeneration of the tail which occur within the sporocyst (camera lucida drawings made at the same magnification).

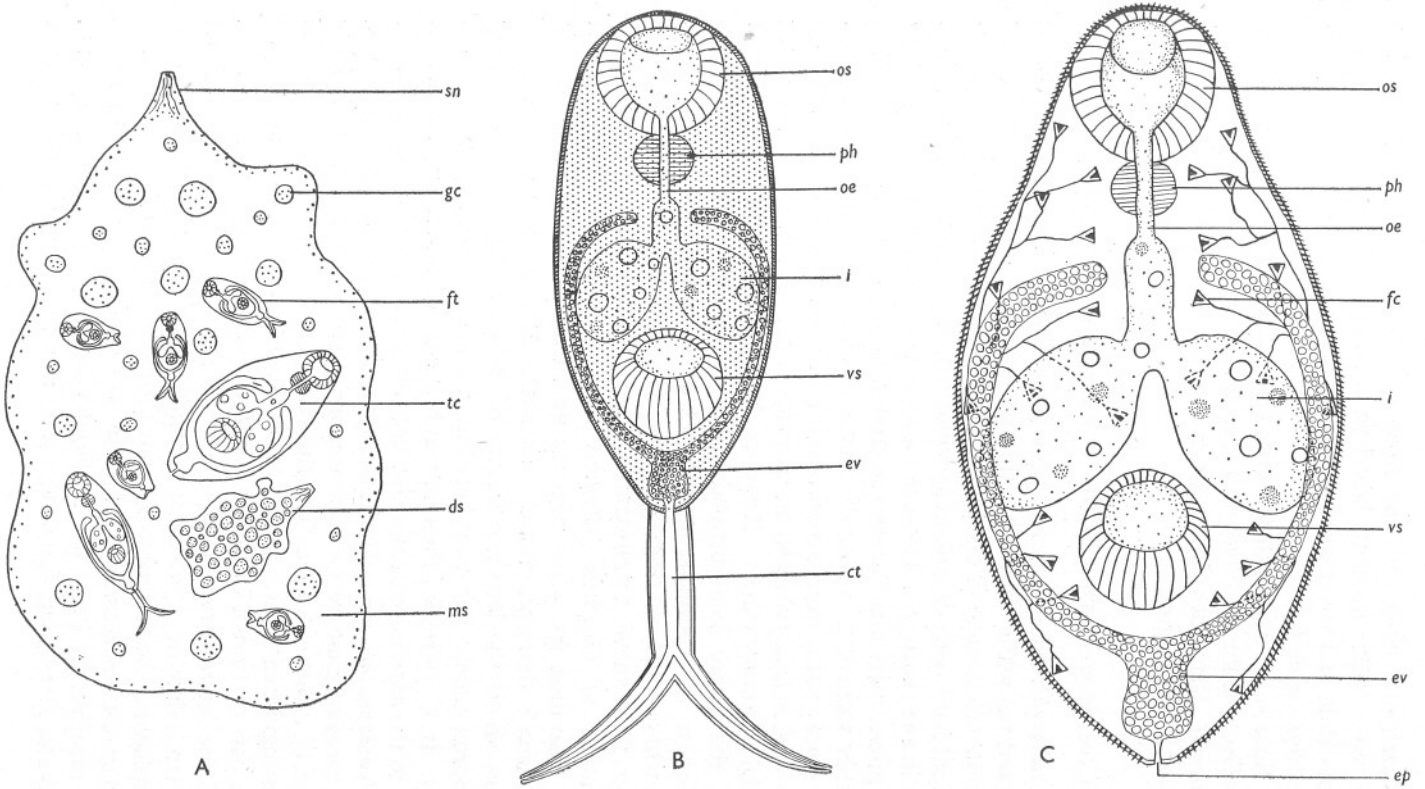
The sporocysts of *C. fulbrighti* are capable of movement by means of simultaneously expanding and contracting parts of the body-wall. The entire body-wall, with the exception of a snout-like structure (Pl. I, fig. 1), is involved in such movements. The snout-like structure is pierced by an opening leading into the body cavity. Sporocysts of this species are very numerous, but never quite so concentrated within the individual *Cardium* as those of '*Bucephalus haimeanus*' (Pl. I, fig. 1); the latter trematode, the most common in the cockles examined, occurred in 26·4 % of the specimens.

Cercariae fulbrighti n.sp.

(Text-figs. 1 and 2; Pl. I)

Specific diagnosis. Marine, nonoculate, distome cercariae developing within irregularly ovoid sporocysts. Partially developed cercariae having distally forked-tails (Text-figs. 1 *d–k* and 2 A, B; Pl. I, figs. 1, 4); *fully developed* cercariae tail-less (Text-figs. 1 *l* and 2 A, C; Pl. I, figs. 1, 2 and 4) while still within the sporocyst; sporocyst liable to contain both tailed and tail-less forms at the same time. Cuticle covering the body of the fork-tailed forms showing small dots arranged densely and regularly (Pl. I, figs. 2, 3), this pattern seen in sections appears to be the surface view of fine striae passing obliquely through the thickness of the cuticle; cuticle of *fully developed* cercariae uniformly spined. Oral sucker slightly larger than ventral sucker, the latter being located posterior to the centre of the body. Prepharynx absent; a well-developed pharynx present leading into a wide oesophagus; intestinal caeca reaching just beyond the anterior edge of the ventral sucker. Excretory vesicle conspicuous, the lateral branches extending forward well past the centre of the body, converging before reaching the level of the pharynx and ending a short distance from the mid-point of the oesophagus; in the *fully developed* cercaria, the terminal vesicle opening to the exterior by a short narrow duct; in the tailed form, the caudal excretory tube passing through the tail stem bifurcating at its distal end with each branch continuing through the furcae to open to the exterior at their tips; thirteen pairs of flame cells observed. Measurements based on five fixed, *fully developed* specimens: body length 258–408 μ, median 328 μ; body width 152–196 μ, median 160 μ; oral sucker width 68–82 μ, median 72 μ; ventral sucker width 62–76 μ, median 70 μ; pharynx width 20–24 μ, median 22 μ; distance of ventral sucker from anterior end of body 124–208 μ, median 164 μ. Measurements based on eleven living, *fully developed* specimens compressed between glass slide and cover-glass: body length 440–596 μ, median 536 μ; body width 248–320 μ, median 288 μ; oral sucker width 100–132 μ, median 120 μ; ventral sucker width 88–126 μ, median 104 μ; pharynx width 28–36 μ, median 32 μ; distance of ventral sucker from anterior end of body 268–356 μ, median 312 μ. Measurements based on three tailed specimens: body length 100–124 μ, median 120 μ; body width 60–80 μ, median 64 μ; oral sucker width 28–34 μ, median 32 μ; ventral sucker width 28–32 μ, median 30 μ; tail-stem length 40–52 μ, median 44 μ; tail stem width 12–18 μ, median 16 μ; furca length 44–80 μ, median 48 μ.

Sporocyst. Sporocysts numerous and somewhat irregularly ovoid; capable of independent movement by means of projecting parts of the body-wall; a definite snout-like structure present (Text-fig. 2 A, *sn*); relatively few *fully developed* cercariae in any one sporocyst, five being the maximum number observed; both cercariae and daughter sporocysts developing within the mother sporo-



Text-fig. 2. *Cercaria fulbrighti* n.sp. A, sporocyst containing daughter sporocyst and cercariae in various stages of development. B, cercaria before degeneration of tail begins. C, cercaria after degeneration of tail is completed. The excretory system is incompletely shown as the granules within the excretory vesicle obscured parts of some of the flame cell canals. (All figures are semi-diagrammatic.) *ct*, caudal excretory tube; *ds*, daughter sporocyst; *ep*, excretory pore; *ev*, excretory vesicle; *fc*, flame cell; *ft*, furcocercous cercaria; *gc*, germ cell; *i*, intestinal caecum; *ms*, mother sporocyst; *oe*, oesophagus; *os*, oral sucker; *ph*, pharynx; *sn*, snout; *tc*, tail-less cercaria; *vs*, ventral sucker.

cyst. Measurements based on one fixed specimen: body length 1416 μ; body width 768 μ. Measurements based on one living specimen compressed between glass slide and cover-glass: body length 1250 μ; body width 880 μ.

Host. *Cardium edule* L.

Habitat. Sporocysts in gonad, digestive gland, and upper part of foot.

Type locality. Millbrook, Plymouth, England.

Type material. Reference No.: 1952, 6, 26, 1/2, British Museum (Natural History), South Kensington.

Comparisons with Previously Described Cercariae

Cercaria fulbrighti differs from all previously described cercariae in that it loses its forked tail while still within the sporocyst. It was first thought that either the fork-tailed stage (Text-fig. 2B), or the *fully developed* stage (Text-fig. 2C), might have been described previously by a worker who failed to find both forms in the sporocyst. However, a search of the literature revealed no such description: there is no larval trematode which corresponds in structural detail to either stage of *C. fulbrighti*. But, *C. dichotoma* Müller, as described by Lebour (1908, 1912) from *Scrobicularia tenuis*, appears to be very like the tailed form of *Cercaria fulbrighti* in its proportions and in the arrangement of the caudal excretory canals. However, because of certain morphological differences, the author feels justified in separating these forms specifically. Lebour refers to the sporocyst stage of *C. dichotoma* as 'structureless', an impression which could not be given by the sporocyst of the species described in this paper, for it shows a well-defined snout-like projection (Text-fig. 2A), and the cuticle of *Cercaria fulbrighti* shows the characteristic pattern previously described (p. 320), whereas no mention of such markings is made in Lebour's description of *C. dichotoma* Müller. Lebour's figure of *C. dichotoma* shows the lateral branches of the excretory vesicle diverging laterally approximately half-way between the anterior and posterior ends of the body. In *C. fulbrighti* these lateral branches extend nearly two-thirds of the way to the anterior end and converge almost to touch the oesophagus.

Three *Gymnophallus* cercariae, in the sporocyst stage, have been reported from *Cardium edule*; namely, *Cercaria margaritae* sp.inq. of Lebour, *C. strigata* Lebour, and *C. cambrensis* Cole. The fully developed cercaria of *C. fulbrighti* can be distinguished quite readily from each of these. *C. margaritae* possesses a pair of brown eye-spots while *C. fulbrighti* does not. Also, in the former, the lateral branches of the excretory vesicle reach to the level of the pharynx, while in *C. fulbrighti* they never extend beyond the mid-point of the oesophagus. According to Lebour (1912), the ratio of the oral to the ventral sucker of *C. margaritae* is 2 : 3, but, as Cole (1938) pointed out, this is probably a misprint for 3 : 2. In *C. fulbrighti* this ratio is approximately 9 : 8. For *C. strigata*, Rees (1939) gives this ratio as 9 : 5. Also, she reported the

flame-cell formula to be $2[(2+2)+(2+2)]=16$, while in *C. fulbrighti* the total number of flame cells observed was 26. However, it should be mentioned that the granules within the excretory vesicle obscured parts of the excretory system and prevented the tracing of all the canals of the flame cells. Specimens of both *C. cambrensis* and *C. fulbrighti* were observed in the same cockles and they are surely different species. The two species can be separated easily by the size and shape of their excretory vesicles: the lateral branches of this vesicle of the former larva occupy most of the body and extend to the level of the pharynx. In the tailed *Gymnophallus*, the lateral branches of the excretory vesicle are much smaller and never extend beyond the mid-point of the oesophagus. Also, the latter is much the larger and has (1) a longer oesophagus, and (2) larger suckers, which can be seen by the following measurements comparing the sucker widths with the body length. The measurements for *C. cambrensis* are Cole's (1938):

	C. cambrensis		*C. fulbrighti*			
			Tailed stage		Tail-less stage	
	(μ)	Ratio	(μ)	Ratio	(μ)	Ratio
Body length	300	*10*	120	*4*	536	*5·15*
Oral sucker width	40	*1·33*	32	*1·1*	120	*1·15*
Ventral sucker width	30	*1*	30	*1*	104	*1*

Discussion

Lühe (1909) placed those forms in which a tail is not developed in the Cercariaea group. He described the Furcocercous cercariae in the following words:

> Distome Cercarien mit langem, an seinem freien Ende gegabeltem Schwanze, in welchen der schlanke Körper nicht zurückgezogen werden kann.[1] Entwickelung meist in sehr langgestreckten Sporocysten, welche (ob bei allen Arten?) selbständig beweglich sind, nur bei einer Art angeblich in Redien.
>
> [1] Vgl. hierzu auch die vorstehende *C. mirabilis*.

Lebour (1912), reviewing the British marine cercariae, placed the tail-less forms in the *Gymnophallus* group and defined them as follows:

> Cercaria tail-less, developed (in the only species in which the sporocysts are known) in more or less spherical sporocysts in Pelecypoda. Oval body covered with spines. No prepharynx, conspicuous pharynx: short and broad intestinal caeca seldom reaching beyond ventral sucker. Ventral sucker always behind centre of body. Excretory vesicle large, forked, reaching far forward anteriorly.

She assigned the fork-tailed form (*Cercaria dichotoma* Müller) to a separate group and stated that in structure this group was closely allied with the *Gymnophallus* group.

Sewell (1922), modifying Lühe's scheme of classification somewhat, placed those forms 'in which development occurs in rediae or in simple sporocysts, and in which all trace of a tail is absent' in the Cercariaea group. He revised and extended the three groups of Furcocercous cercariae created by Cort (1917), placing in group 1 the apharyngeate, brevifurcous cercariae and in group 2 the pharyngeate, longifurcate cercariae (with the exception of *C. indica* XXII which he included in the 'Baiswan' subgroup of group 2, although it had certain characteristics in common with the brevifurcous cercariae). Group 3 includes those forms which Sewell believed to have originated from a monostome stock and in which the acetabulum was extremely small and rudimentary or completely absent.

Miller (1926), in his monograph on Furcocercous cercariae, modified Sewell's scheme of classification and considered the presence or absence of a pharynx to be of more significance than the presence or absence of a ventral sucker in determining a natural scheme of classification. He subdivided the pharyngeal cercariae into 'brevifurcate' and 'longifurcate' larvae, the former with 'furcae usually less than one-half the tail-stem length' and the latter with 'furcae longer than one-half the tail-stem, sometimes exceeding it'. He made a comparison of the characteristics of the brevifurcate and the longifurcate larvae known at that time.

At one stage in its development *C. fulbrighti* has many characteristics in common with Miller's 'pharyngeal longifurcate distome cercariae', but differs from this group in certain respects, the most notable difference being that in this cercaria the excretory openings are at the tips of the furcae while in Miller's longifurcate larvae the openings are typically mid-furcal. In a later stage, when the tail disappears and spines develop, *C. fulbrighti* has all the characteristics of Lebour's *Gymnophallus* group. These characteristics were quoted previously.

Cort (1918), discussing the tail-less cercariae, points out that the provisional *Cercariaeum*, based only on the absence of the tail in the fully developed cercaria within the sporocyst or redia, is evidently an unnatural group. It may yet be assumed that members of this group, however unnatural, have evolved from cercarial ancestors which possessed tails. As shown above, the forked tail of *Cercaria fulbrighti* degenerates while still within the sporocyst. The tail-less cercaria cannot therefore have a free-swimming stage. This much is evident, even though information is lacking on the further stages of this species.

Since *C. fulbrighti* presumably develops into a member of the genus *Gymnophallus* Odhner (1900), there appears to be sufficient evidence to suggest a phylogenetic relationship between this group and certain of the furcocercous cercariae.

As was already noted, the adult stage of *Cercaria fulbrighti* is almost certainly a species of *Gymnophallus*. It is interesting to note the remarkable similarity between this larva and the adult stage of *G. choledochus* Odhner

which Nicoll (1923) recorded from the gall-bladders of three British birds: the common sheld duck, *Tadorna tadorna* (L.); the eider duck, *Somateria mollissima* (L.); and, the king eider, *S. spectabilis* (L.).

Summary

A summary of the trematode parasites which have been recorded from the cockle is given.

A furcocercous, *Gymnophallus* larva, *Cercaria fulbrighti* n.sp., from the marine bivalve *Cardium edule* L., is described from Plymouth, England. The tail of this larva may degenerate completely while the cercaria is still within the sporocyst.

Simultaneous development of more than one species of cercaria has been recorded in four out of 420 specimens of *C. edule* L. Two double and two triple infections were found.

Available evidence suggests a phylogenetic relationship between the *Gymnophallus* group and certain of the Furcocercous cercariae.

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EXPLANATION OF PLATE I

Cercaria fulbright n.sp.

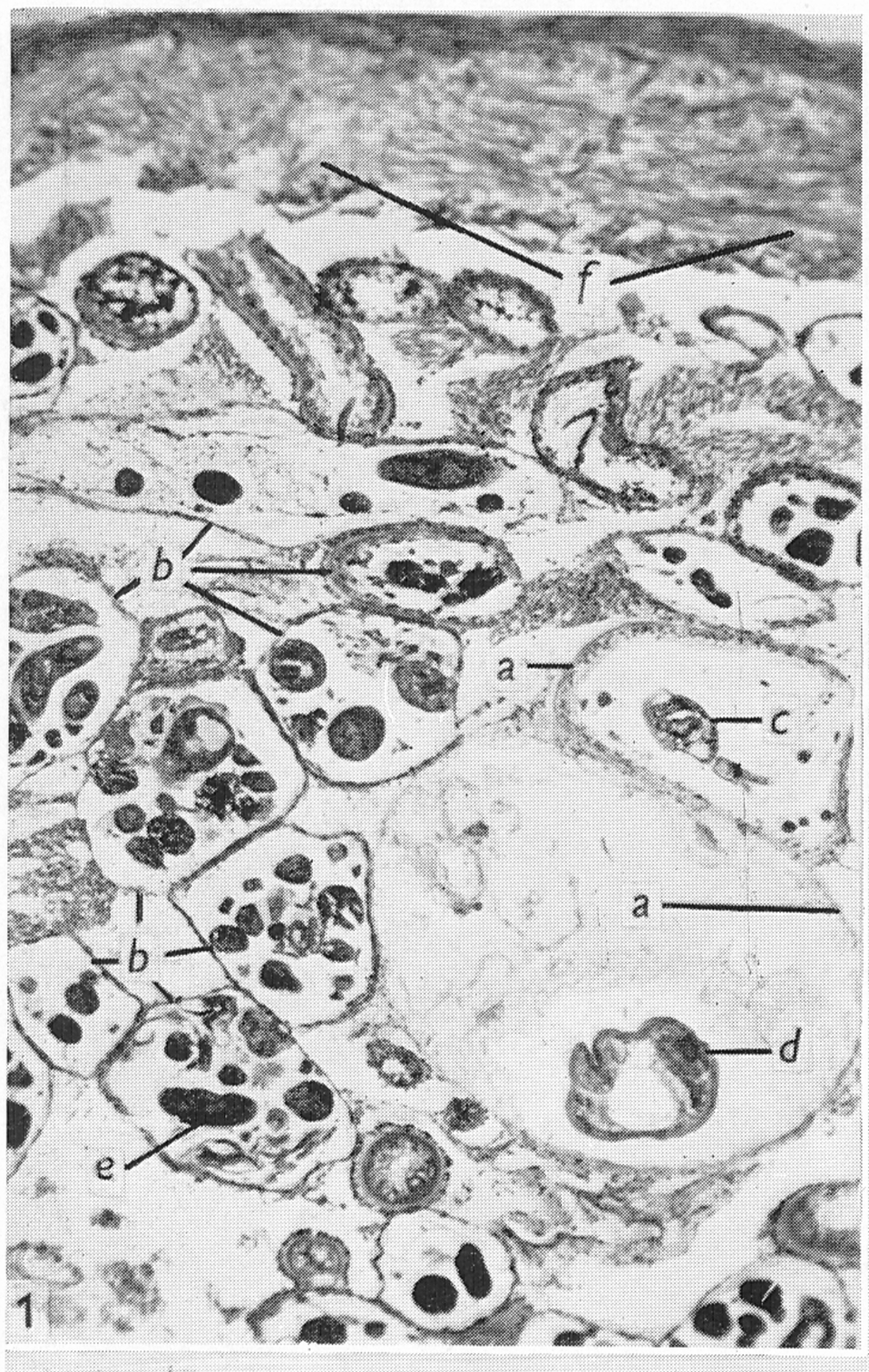
Fig. 1. Section through the upper part of the foot of *Cardium edule* L. showing double trematode infection; *a*, sporocyst of *Cercaria fulbrighti*; *b*, sporocyst of '*Bucephalus haimeanus*'; *c*, fork-tailed stage of *Cercaria fulbrighti*; *d*, *fully developed* stage of *C. fulbrighti*; *e*, cercaria of '*Bucephalus haimeanus*'; *f*, muscle layer of foot.

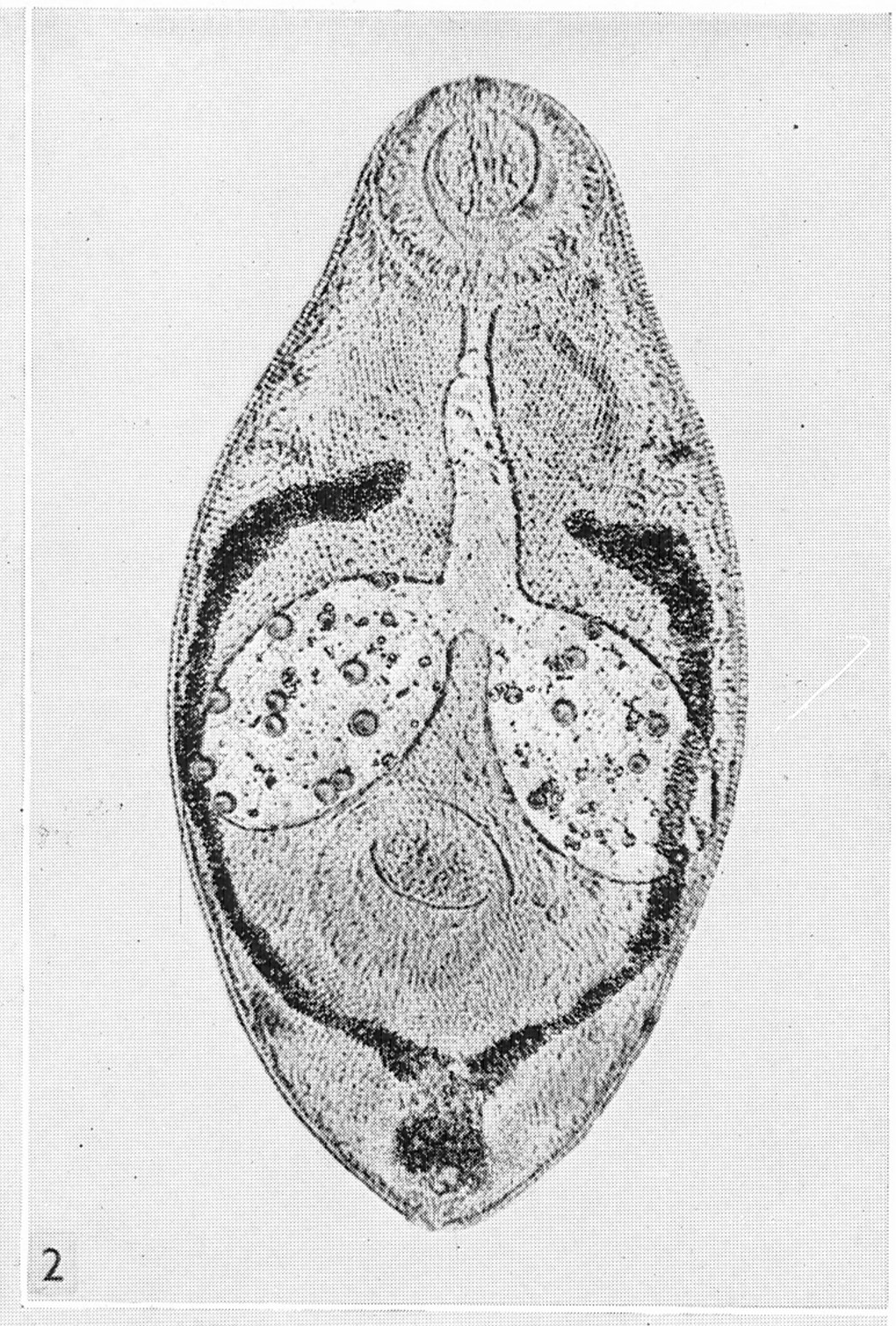
Fig. 2. Tail-less cercaria before spines develop.

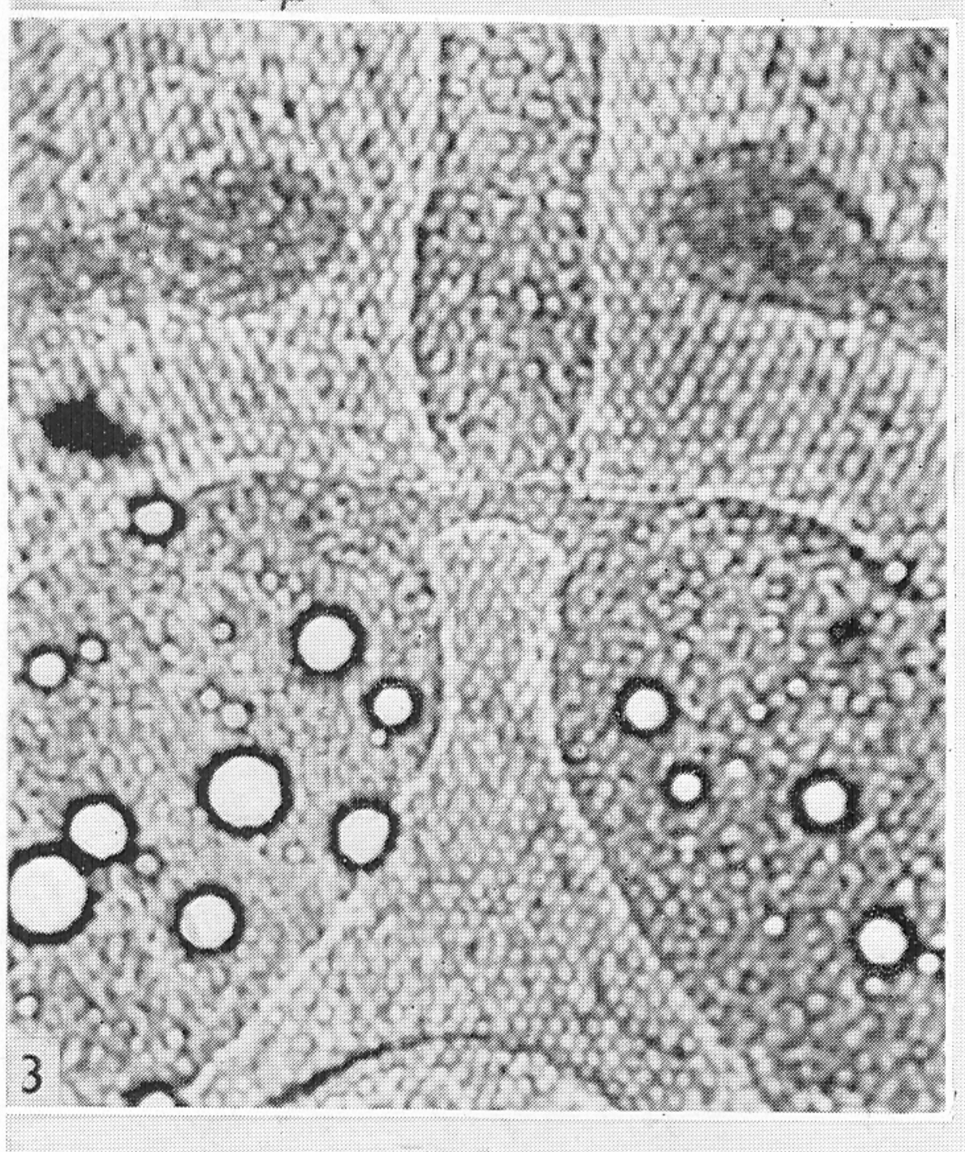
Fig. 3. Characteristic markings on body of cercaria before spines develop.

Fig. 4. Part of sporocyst showing both tailed (*a*) and *fully developed* (*b*) cercariae.

Figs. 1 and 3 have been made from sections stained with Ehrlich's haematoxylin and eosin. Figs. 2 and 3 were made from living material compressed between glass slide and cover-glass with Fig. 3 being made under oil immersion ($\frac{1}{12}$).


f
b
a
c
a
b
d
e
1
150 μ


2
50 μ


3
50 μ


a
b
4
100 μ

NOTE ON SEA TEMPERATURES IN THE ENGLISH CHANNEL, 1921 TO 1949, AND PLYMOUTH SUNSHINE AND LIGHT

By W. R. G. Atkins, F.R.S. and Pamela G. Jenkins

From the Plymouth Laboratory

(Text-figs. 1–3)

International hydrographic station England no. 1 (E1) has been visited regularly for many years, and since 1921 the periods have been (nominally) once a month, or more frequently. Much work has been done on the plankton and chemical changes in the water, but no biological use has been made of the temperature-depth observations, which are primarily of hydrographic importance. The aim of this paper is to render the sea-temperature observations over this long period readily available and to place beside them observations on air temperature, sunshine and light. Such comparisons may be expected to give information upon the causes of variations in temperature, but the adequate investigation of this very difficult problem is outside the scope of this note. The subject is worthy of fuller treatment on the lines suggested by Harvey (1925), based on data for the years 1921 to 1924, and has been considered on broad lines by Sverdrup, Johnson and Fleming (1942).

The Sea-temperature Observations

These are made with standardized thermometers in a Nansen-Petterssen water-bottle at 5 m. intervals down to an almost constant reading, and thereafter at 10 or 20 m. intervals to 70 m. with the usual precautions. Surface samples are also taken with a wooden bucket, the bottle observations at the surface being termed 0·5 m., but these two are here grouped together. Mean column temperatures are based on means for 2·5, 7·5...67·5 m. The observations are thus for single days, or possibly means for 2 or 3 days, in each month.

The Air-temperature Observations

These are got from the Meteorological Office publications. In 1921 until the end of 1922 the figures for daily temperature taken were those of the Borough Meteorologist, which were based on observations at 9, 15 and 21 hr. The station is on the Hoe, close to the Marine Biological Laboratory, and is at about 30 m. above sea-level. From January 1923 the Hoe records were based on mean values of the daily maximum and minimum readings taken at

21 hr. Accordingly, we took those read at 7, 13 and 18 hr. at the Cattewater station, Mount Batten, which is about 22 m. above sea-level. These continued until after the end of our 1938 period. For 1947 until August 1948 they were taken at Mount Wise, also about 22 m. above sea-level, and from September 1948 till now they have been again at Mount Batten. Our post-war period means are based on observations at 3, 9, 15 and 21 hr. The series is not therefore entirely concordant, though the resultant change is probably unimportant.

It is obvious that temperatures obtained, as monthly means, on land are not truly comparable with observations made over 20 miles to the south, at sea. But they are the only ones available and with the slower changes met with at sea as compared with on land, the less frequent readings at sea still give a tolerably accurate representation.

The Sea and Air Temperatures

The minimum sea temperature for the 21 years, 7·4° C., was on 27 February 1947, and the warmest winter minimum was in 1949, 9·9° C., on 13 April. Excluding the exceptional value for 1947, ten winter minima lay between 8·2 and 9·0° C., mean 8·55° C., and ten between 9·0 and 9·9° C., mean 9·41° C. The mean for the twenty is 8·98° C. There was no indication of any regular movement in the value of the minimum temperature which occurred once in January, twice in February, sixteen times in March, once in April and once in December.

In winter, surface and column temperatures are almost identical. The column had become isothermal by October in 13 years, and was nearing this condition in eight Septembers. In 1922, it was reached on or before 11 July and again by 22 September. The vertical mixing indicated is important in bringing up the nutrient salts.

The air temperature monthly mean minima were never in January, but nine occurred in February, four in March, one in November and seven in December, arranged quite irregularly.

The lowest maximum of the sea column was 13·12° C., and 5 years were below 14·0° C. Thirteen lay between 14 and 15° C., three 15° C. or over, with maximum 15·8° C. The mean column maximum is 14·34° C.

The maximum column temperatures occur when the column becomes isothermal or nearly so, usually late in September or early in October. The maximum surface temperature was observed fifteen times in August, four times in July and twice in September, such figures being influenced by the dates on which it was possible to make cruises. Mean monthly air maxima were twice in June, nine times each in July and August and once in September.

Table I shows the observations from which Fig. 1 has been constructed. Fig. 2 shows the mean temperatures of the water column at E 1 for selected years which include the warmest and the coldest.

Fig. 3 shows the column maximum and minimum temperatures for each year. The greatest range was for 1947, 7·02° C., and the least, 4·32° C., for 1923. Out of the 21 years the order of difference was: 1923, 21; 1925, 20; 1922, 19; 1924, 18; 1926, 17; 1927, 16, and in all these years the phosphate content of the water was relatively high.

Values for sunshine and light are also shown in Fig. 3.

TABLE I. COMPARISON OF SEA AND AIR TEMPERATURES

	Air temp., °C., monthly mean			Station E 1, column temp., °C.			Station E 1 Surface max.
	Coldest	Warmest	Mean	Coldest	Warmest	Mean	
Jan.	4·2	9·5	7·3	9·0	11·3	10·2	11·2
Feb.	0·9	8·5	6·4	7·4	10·2	9·3	10·2
Mar.	5·9	9·5	7·4	8·3	10·0	9·0	10·1
Apr.	7·9	10·7	8·9	8·2	10·0	9·4	10·6*
May	10·5	14·5	12·0	9·25	11·4	10·4	13·5
June	13·8	17·4	14·9	10·5	12·4	11·5	15·7
July	14·7	19·9	16·3	12·1	13·8	12·8	18·4
Aug.	14·8	19·2	16·5	12·7	14·5†	13·6	19·4‡
Sept.	13·1	17·0	15·1	12·8	15·2	13·8	18·3
Oct.	10·6	15·1	12·2	13·1	15·8	13·8	16·4
Nov.	5·8	11·1	9·0	11·9	15·0	13·0	14·6
Dec.	3·5	10·5	7·4	10·0	13·1	11·5	12·9

* Surface 11·2, 30 April 1930.

† Column temperature for 29 August 1947 was 15·3° C. and the September and October maxima were for 1947 also. For 1921, October, November and December gave respectively 15·4, 15·0 and 13·1° C.

‡ 29 August 1949.

Hours of Sunshine

The values are those for Plymouth Hoe, as published by the Meteorological Office, in hours daily. The yearly means vary from 5·54 in 1949, followed by 5·25 in 1929, 5·17 in 1933, 5·13 in 1921, 5·00 in 1948 to 4·03 hr. in 1931, other low values being 4·16 for 1927, 4·19 for 1924, 4·21 for 1947, and 4·25 for both 1937 and 1938. The period covered was 1921–40 inclusive and 1947–49. The mean value for 23 years is 4·63 hr. a day. It is obvious that the heat received from the sun is not linearly proportional to the hours of sunshine, since the intensity is influenced by solar altitude, which varies throughout both year and day.

Illumination

Since light falling on and penetrating the sea is absorbed and converted into heat, the illumination affects the temperature. What is measured is the daylight, from sun and sky, received on a horizontal surface on the laboratory roof in an almost unobstructed position. The photoelectric cell used is more sensitive to the short than to the long wave part of the spectrum, so that the effect of cloud in obscuring the sun is less than with a thermopile, which is approximately uniformly sensitive throughout the spectrum. The current is measured with a Cambridge thread-recorder galvanometer and the illumination is got from the area of the daily chart, in kilolux-hours, which for the

year may be conveniently given in megalux-hours. The details of the measurements and results are given by Poole & Atkins (1935, 1936), Atkins (1938),

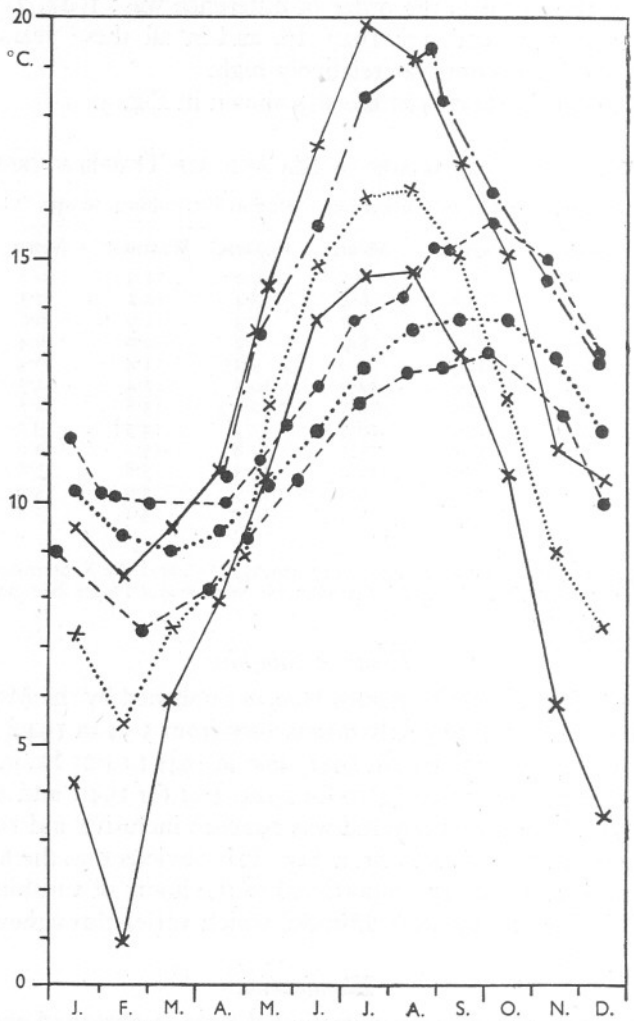


Fig. 1. Air temperature at Plymouth, monthly means (crosses). The continuous lines show the warmest and coldest months of the period studied, plotted as if for single hot and cold years. The dots show the mean values. Sea temperatures at station E 1 (dark circles) are shown by broken lines for the water columns, warmest and coldest, as for air; the dots and dashes denote the warmest sea surface temperatures encountered each month. The dots show the mean values for the water column over the 21 years.

Atkins & Ellison (1947), Atkins & Jenkins (1952). The observations cover 14 years, 1930–40 inclusive, also 1947–49. The value for 1930 proved to be exceptionally high, 150 megalux-hours, but all efforts to show that this was

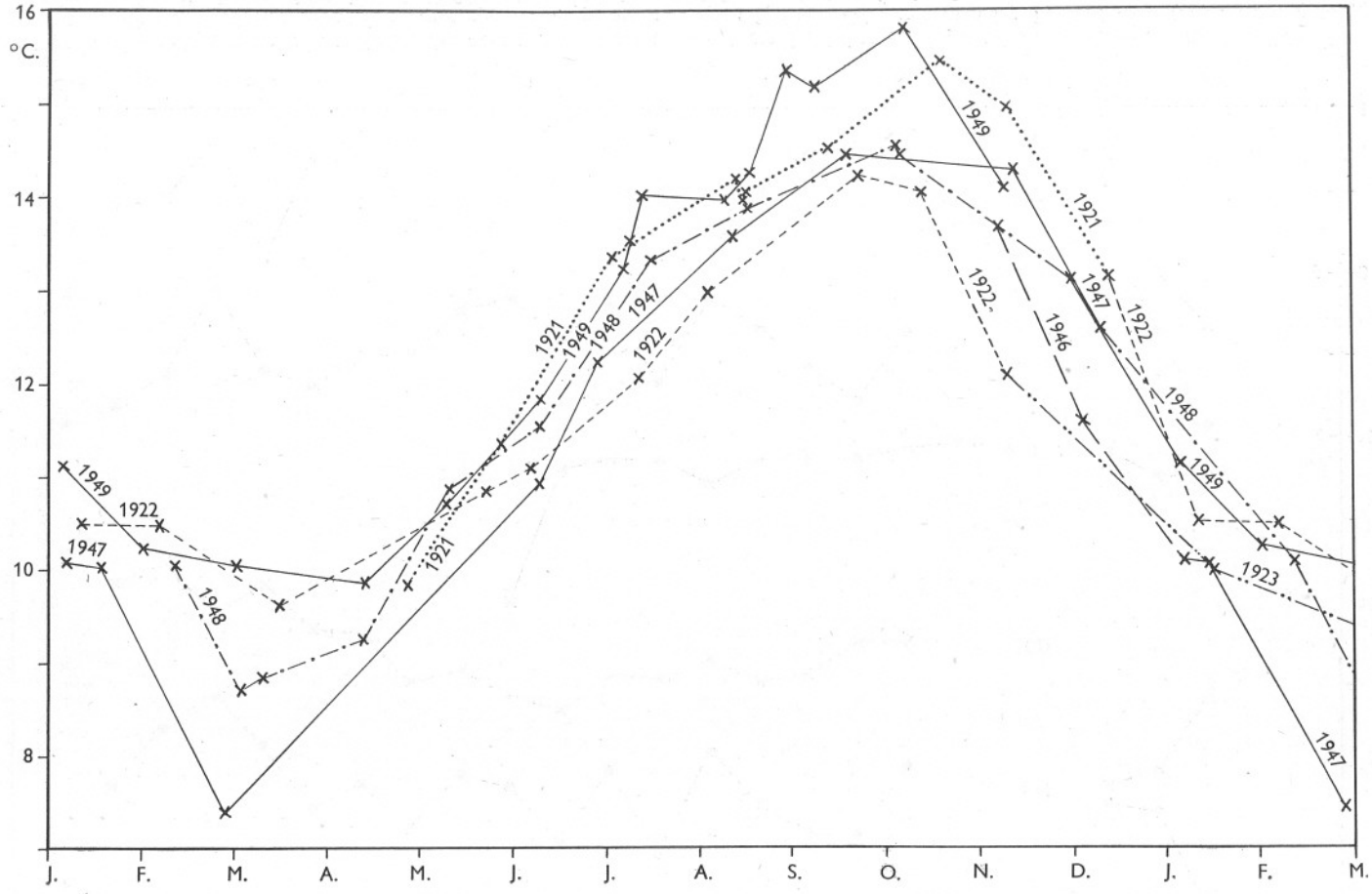


Fig. 2. Mean temperatures of the water column at E 1 for warm, cold and intermediate years.

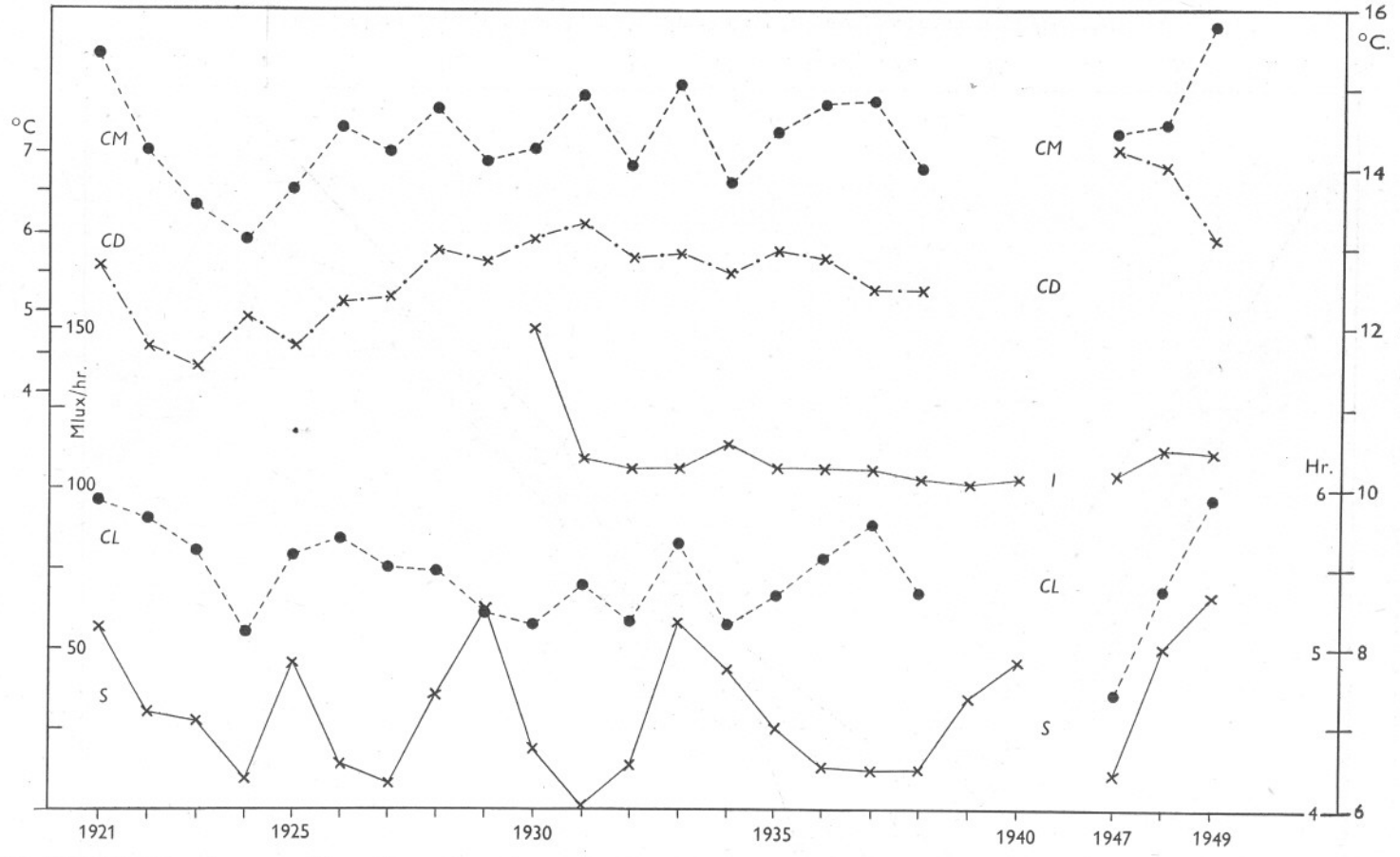


Fig. 3. The abscissae show years. The ordinates show the water column temperatures, from 6 to 16° C., for the warmest month (broken line *CM*) and coldest month (*CL*), of each year. The differences in temperature between *CM* and *CL* are shown by dot and dash (*CD*), from 4 to 7° C. The line *S* gives the hours of sunshine daily for each year, 4–6; while *I* denotes the illumination for each whole year in megalux-hours, 0–150.

due to a subsequent loss of cell sensitivity have failed, and between highest and lowest values for daylight Aurén (1933, 1939) got a similar high range near Stockholm in a series between 1928 and 1937. The minimum was in 1939, with 103 megalux-hours and the 14-year mean is 116 megalux-hours.

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FURTHER EXPERIMENTS ON BIOLOGICAL DIFFERENCES BETWEEN NATURAL SEA WATERS

By Douglas P. Wilson, D.Sc., F.R.P.S. and F. A. J. Armstrong

From the Plymouth Laboratory

(Text-fig. 1)

In a previous paper it was shown that the eggs and larvae of a sea-urchin and of two species of polychaetes 'developed abnormally, or were in poor health, in sea water collected from the English Channel in the region of the Eddystone, although in water collected from the Celtic Sea development was generally normal and healthy' (Wilson, 1951, p. 18). It was suggested that the Channel water lacked some constituent necessary for normal healthy development which was present in water from the Celtic Sea. In a mixture of the two waters the larvae did almost as well as in the Celtic Sea water alone.

It had been planned to continue experimental work on the properties of these two waters when it became evident that further cruises to the westward to obtain Celtic Sea water would not be possible for some time to come. As an alternative to using Celtic Sea water it was thought that water from the Firth of Clyde, which like that from the Celtic Sea is generally characterized by the presence of *Sagitta elegans* (Russell, 1939; Barnes, 1950), might show similar properties, and be equally suitable for the purpose. Through the kind co-operation of the staff of the Marine Station at Millport, and particularly of Dr H. Barnes, it has been possible to undertake some preliminary experiments using water from the Firth of Clyde. In these experiments the responsibility for the chemical work was undertaken by F.A.J.A. who has prepared an account of the technical details (see pp. 336–8). The form of the experiments, especially the second and third, was agreed upon after discussion in which Dr L. H. N. Cooper and Dr C. P. Spencer sometimes took part.

General Methods

Methods followed closely those already described for the earlier experiments with *Echinus esculentus* L. (Wilson, 1951, p. 5). The concentration of larvae was less than in most of the previous experiments, but more were used than for the thin cultures of Exp. 8B (Wilson, 1951, p. 12). Decanting, to separate swimming blastulae from undeveloped eggs, was unnecessary, as in 1950.

Pyrex crystallizing dishes of 7 cm. diameter were again used, the quantity of water tested in each being equal at about 100 ml.

The Clyde water was collected in carboys cleaned at Plymouth and was sent by passenger train.

Chemical Work

Cleaning of Apparatus

We think that the attention given to this matter has been justified by the uniformity of larval growth in each set of dishes, and that space may properly be given to a detailed description of the methods used.

The 5-gallon glass carboys in which the sea water was collected and kept until filtered were cleaned beforehand by thorough scrubbing inside with a bottle brush, followed by rinsing with 1 : 1 sulphuric acid as hot as seemed safe (about 60° C.). The acid was removed by repeated washing with tap water. Finally, the carboys were washed three times with distilled water, and allowed to drain upside down. The criterion of cleanliness for these carboys and all glassware used in these experiments was that on draining there should be no 'water-break', i.e. that the film of water on the glass spread evenly and did not gather into drops as on a greasy surface. If any article showed a 'water-break' the cleaning was repeated.

Crystallizing dishes, except those cleaned with chromic acid, were immersed completely for about 5 min. in 1 : 1 sulphuric acid at about 120° C., and then rinsed successively with hot tap water and distilled water. They were allowed to drain and dry while inverted on an arrangement of glass plates and rods. During cleaning they were held in a fork of glass rod, and were not touched by hand.

The dishes cleaned with chromic acid cleaning mixture were allowed to stand in the cold mixture for 3 days, after which they were washed in running tap water until the yellow colour disappeared. They were then allowed to stand in clean tap water for 2 days, rinsed with tap water and distilled water and dried in the same way as the other dishes.

Other glassware used was cleaned in hot 1 : 1 sulphuric acid and rinsed with tap and distilled water, contact with the hands being always avoided. The larger beakers and vessels used for collecting and treating sea water were cleaned on the inside only.

The Berkefeld filter candles and the rubber and glass tubing used with them had been used for earlier experiments. They were washed as thoroughly as possible with hot tap water and distilled water, sterilized at low pressure in an autoclave, and re-washed with boiling distilled water. The first litre or so of sea water filtered was always discarded.

Measurement of Hydrogen-ion Concentration

In the first experiment, pH was measured with a glass electrode and the Cambridge Instrument Company's portable pH meter. For the later experiments this method was inconvenient, and pH was estimated by visual colour comparison with Palitzsch buffers, using cresol red and thymol blue as indicators, applying the appropriate salt error corrections given by Buch & Nynäs (1939). When examining the dishes containing larvae it was found to be quite easy to remove 2 ml. with a pipette without much disturbing the water.

Alteration of Hydrogen-ion Concentration of Sea Water

This was done empirically by adding acid or alkali to portions of the filtered Clyde water, and aerating to bring the water into equilibrium with the carbon dioxide of the atmosphere.

The reagents used were 0·1 N solutions of hydrochloric acid and sodium carbonate made from analytical grade chemicals; the quantities used were so small as to make it unlikely that the small changes brought about in salinity or trace elements are significant. Aeration was by means of air filtered through cotton-wool and passed rapidly through the water with a sintered glass gas distribution tube.

On adding acid to lower the pH, equilibrium with the CO_2 in the air, i.e. removal of CO_2, came about after some 10 min. aeration. Trial experiments in raising pH with sodium hydroxide showed that the reverse process (absorption of CO_2) was much slower, equilibrium not being obtained after an hour's aeration, and that it was better to use sodium carbonate as the alkali. Even so, equilibration was slow, and had to be assumed to be complete when 30 min. aeration failed to cause any change in pH.

The filtered, but not specially aerated, water was at approximately pH 8·0. Solutions of suitable hydrogen ion concentrations were made by using the quantities of acid and alkali listed in Table I.

TABLE I

Acid or alkali added	pH after aeration
6 ml. 0·1 N HCl/l.	7·82
1 ml. 0·1 N HCl/l.	8·02
2 ml. 0·1 N Na_2CO_3/l.	8·14
4 ml. 0·1 N Na_2CO_3/l.	8·18
6 ml. 0·1 N Na_2CO_3/l.	8·28
8 ml. 0·1 N Na_2CO_3/l.	8·45

Treatment of Sea Water with Carbon

The procedure was suggested by the successful method used by Braus, Middleton & Walton (1951) to extract organic substances from drinking and river waters with active carbon. The particular make ('Nuchar C 190' unground) of carbon used by these workers does not seem to be obtainable in this country. On the advice of Messrs Sutcliffe, Speakman and Co. Ltd., we tried their own carbon 207B, 12–22 mesh, a generous sample of which this firm supplied without charge.

20 l. of the sea water to be treated was driven by air pressure at the rate of 1 l./hr. first through a Berkefeld filter candle and then upward through a glass tube (length 30 cm., int. diam. 11 mm.) containing 10 g. of the carbon. This almost filled the tube. Fine particles of the carbon were retained by a plug of cotton-wool at the top. The treated water was collected and kept.

Preparation of Extracts

The carbon through which the sea water had passed was washed by passing 50 ml. of distilled water through the tube to remove some of the salt and was then spread on a large clock glass and dried at 60° C. for 4–5 hr. It was then put into a porous alundum thimble previously ignited and extracted with acetone, and was extracted for 6 hr. in a Soxhlet apparatus with 100 ml. of reagent grade acetone. This solvent was used in the hope that it would extract more water-soluble material than would ether, which was used by Braus *et al.* (1951).

A pale greenish yellow acetone solution was obtained. Some partially charred material was seen at the liquid level of the extraction flask where it had obviously been decomposed by the heat of the heating mantle used for the apparatus. After filtration through an acetone-washed No. 43 Whatman paper to remove particles of carbon, the extract was evaporated to dryness at low temperature in a 100 ml. beaker and dried in an oven at 60° C. and weighed. A blank extraction was also performed on a 10 g. portion of the carbon. The weights and appearance of the extracts are given in Table II.

20 ml. of distilled water was added to each beaker, and the mixture warmed to 30–40° C. to help to break up the residues. That from the E 1 water dispersed almost at once to give a cloudy pale yellow-green solution, a small amount of greenish brown matter remaining on the bottom. That from the Clyde water did not disperse so readily, and left a larger amount of the greenish brown matter on the bottom of the beaker; the supernatant liquid was a clear yellow green, but paler than from the E 1 water. The film of residue from the blank extraction did not appear to dissolve in water.

By rubbing the undissolved residues with a glass rod they were dispersed in the liquid as quite small particles, and the extracts were allowed to stand for 3 hr., stirred, and each divided into equal portions of 10 ml. On adding these to the E 1 and Clyde waters, markedly turbid solutions were given by the E 1 extract, slightly turbid ones by the Clyde extract and clear ones by the blank extract. They were used without further filtration.

TABLE II. RESULTS OF ACETONE EXTRACTS

	E 1 water	Clyde water	Carbon blank
Vol. water used (l.)	20	20·5	—
Wt. of extract (g.)	0·0282	0·0222	0·0007
Appearance	Waxy greenish yellow solid with feathery brownish cystals together with some whitish opaque matter	Waxy greenish brown solid with feathery brown crystals together with some whitish opaque matter	Thin film of whitish deposit

Addition of Ascorbic Acid to Sea Water

The contents of a 1 c.c. ampoule of 'Celin' Vitamin C, Glaxo, stated to contain 100 mg. of ascorbic acid B.P. were diluted to 100 ml. with distilled water. 10 ml. of this solution were added to 1 l. each of filtered Clyde and E 1 waters. At the time of preparation these solutions should therefore have had an addition of 10 mg./l. of ascorbic acid.

EXPERIMENTAL RESULTS

Experiment I

Designed to test three waters, namely water from the international hydrographical station E 1, about 10 miles W.S.W. of the Eddystone, water from close inshore, and Clyde water. The first would come into the category 'Outside water' as used in the previous paper. In this paper it will be referred to by its international station number.

E 1 water collected from the sea surface by means of a wooden bucket. Strained through 200-mesh bolting silk.

Position: 50° 02′ N., 4° 22′ W.

Date: 17. iii. 52.

Ship: M.F.V. *Sula* with Dr L. H. N. Cooper.

Salinity: 35·25‰ pH (on 21. iii. 52) 8·28.

Inshore water collected by the same method and on the same day as E 1 water.

Position: ½ mile W.S.W. Rame Head.

pH (on 21. iii. 52) 8·25.

Clyde water collected from sea surface by means of a glass breffit on string handle. Strained through 200-mesh bolting silk.

Position: approx. mid-channel between Keppel and Fairlie.
Date: 17. iii. 52. Time 15.00 G.M.T. (high-tide 15·26 G.M.T.).
Small boat, with Dr H. Barnes.
Salinity: 32·59‰ pH (on 21. iii. 52) 8·17.

The sea-urchins were trawled on 20 March 1952 and kept under circulation overnight. A fertilization from a selected specimen of each sex was made in a mixture of E 1 and Clyde water at noon the next day. The fertilization was divided equally into three beakers, and each portion washed with six changes of each of the three waters. Five dishes of each water, and five each of equal volumes of Clyde water with E 1 and with Inshore waters were tested.

The results are summarized in Table III. The larvae in the Clyde water did much better than in the E 1 or Inshore waters, and although the difference was not as spectacular as in some of the earlier experiments it was none the less well marked by the end of the experiment. The difference was, indeed, perceptible as early as the first day and by the third day was unmistakeable. On that day (24. iii. 52) the larvae in the Clyde water had longer arms and were larger and finer looking than those in the E 1 and Inshore waters. It should be emphasized that up to this time in any one set all five dishes were identical one with another. Afterwards there were slight variations between dishes in a set but they were only of small magnitude. In any dish of Clyde water the larvae were always much better than in any dish containing E 1 or Inshore water, though one E 1 dish in particular had from 25 March onwards rather better larvae than the other four.

On 24, 25 and 26 March larvae were removed from some or all of the dishes for closer examination after fixation, and for photographic recording. Careful comparison of the photographs fully confirmed the result already arrived at by examination alive. Three of the photographs are reproduced here (Fig. 1). They were obtained by the following method. With a glass dipper each dish of a set of five was thoroughly stirred and one dipper-full withdrawn. The samples from all five dishes were mixed and the larvae then killed by the addition of a small volume of 5 % neutral formalin in sea water. The mixed sample was poured into a boiling tube and allowed to settle. When all the larvae were on the bottom they were withdrawn in a pipette and transferred to a glass dish. A crowded group was chosen at random and photographed. In comparing these photographs it should be borne in mind that the group from the E 1 water looks better than it should do. Many larvae had already died and decayed leaving little trace, and the photograph is therefore biased in favour of the living and the partially decayed dead. Most of the better-looking larvae in this E 1 group came from one particular dish, mentioned above. The other photographs are a fairer assessment of the conditions, for very few larvae had died in the Clyde, or the mixed Clyde and E 1 waters.

After 26 March, the last day recorded in the table, there was greater variation between dishes, but for another 3 days, until the experiment was

TABLE III. EXP. I. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 21 MARCH 1952

	Clyde water	E 1 water	Inshore water	Mixture of Clyde and E 1 waters	Mixture of Clyde and Inshore waters
22. iii. 52	Most blastulae swimming strongly at or near surface	Blastulae dispersed downwards a little more than in Clyde water with more on the bottom	Blastulae swimming a little more strongly than in E 1 water	Similar to blastulae in Clyde water	Similar to blastulae in Clyde water
23. iii. 52	Larvae a little more finely developed than in E 1 water	Larvae again dispersed downwards a little more than in Clyde water	Larvae still swimming a little more strongly than in E 1 water	Larvae a little more finely developed than in E 1 water	Larvae a little more finely developed than in E 1 water
24. iii. 52	Larvae larger and better formed than in E 1 water	Fewer at the surface and more on the bottom than in Clyde water	Similar to larvae in E 1 water	—	—
25. iii. 52	Well-formed plutei swimming well. Very few dead or abnormal	Plutei shorter-armed than in Clyde water, mainly swimming well. A moderately large number dead or abnormal	Plutei closely resemble those in E 1 water, but there are fewer dead or abnormal	Well formed plutei swimming well, like those in Clyde water. Very few dead or abnormal	Good plutei swimming well, like those in Clyde water. Very few dead, a few abnormal
26. iii. 52	A fair number of long-armed plutei swimming in mid-water and at surface but majority on bottom, some of these becoming short-armed. A very few dead	A small number of medium-armed plutei swimming, but majority dead on bottom, mostly well decayed. Those still living mainly short-armed	Similar to E 1 water but not so many dead. Plutei mostly short-armed and slightly inferior to those still living in E 1 water	A fair number swimming but majority on bottom. Larvae in structure similar to those in Clyde water. A very few dead	A fair number swimming but majority on bottom. In structure similar to those in Clyde water. A very few dead

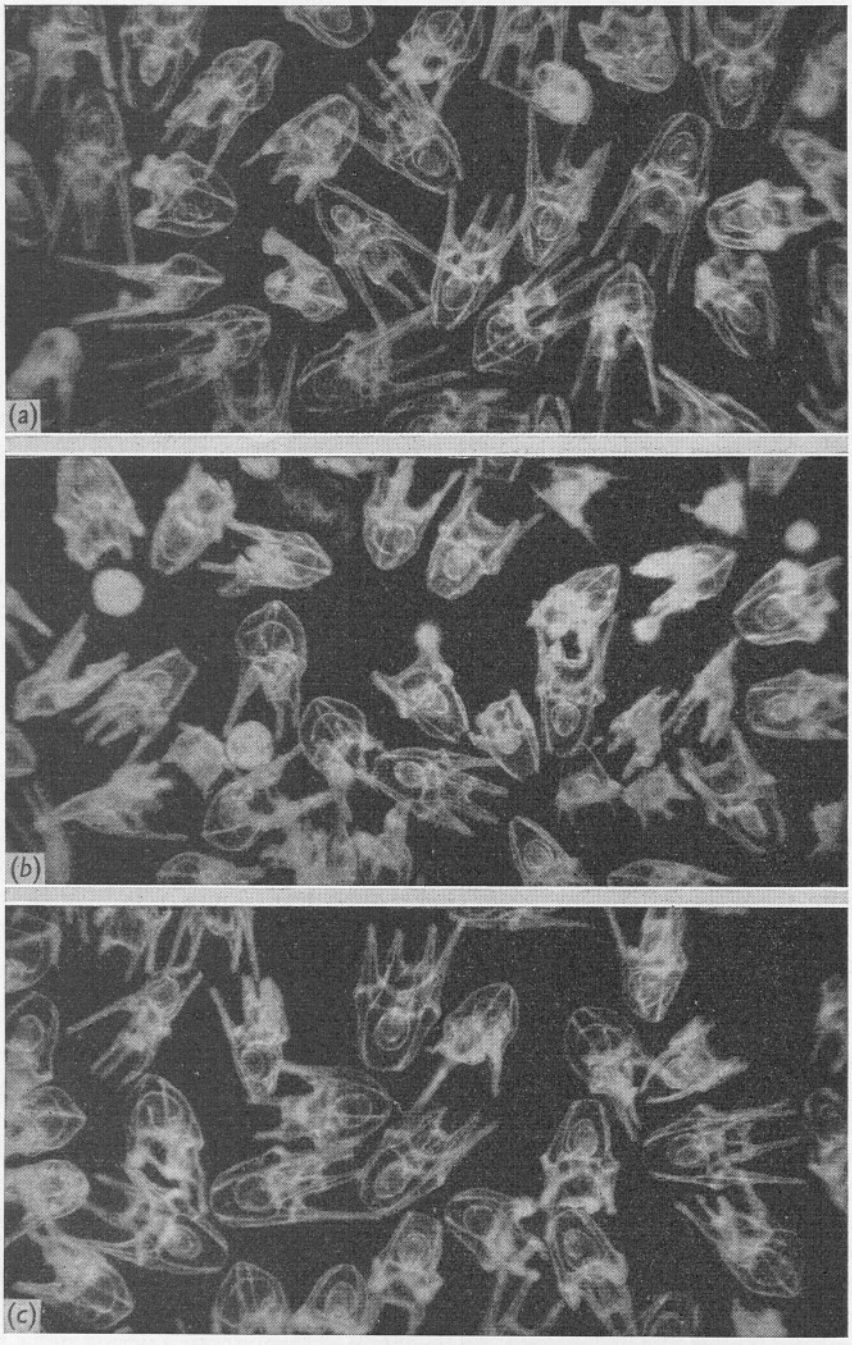

Fig. 1. Photomicrographs of larvae from Exp. I. Taken on 26 March 1952, a few minutes after fixation with dilute neutral formalin. ×35. (*a*) larvae from five dishes of Clyde water; (*b*) larvae from five dishes of E 1 water; (*c*) larvae from five dishes of Clyde and E 1 waters mixed in equal proportions.

ended, the larvae in the Clyde dishes and in the mixtures were better than those still living in the E 1 water, where almost all were dead.

The larvae which survived in Inshore waters were, on the whole, better in the end than those in E 1 water (except for one dish of the latter) but were not as good as in the other waters. Throughout this experiment the room temperature varied between 15·1 and 16·6° C.

Subsidiary Experiment concerning Method of Cleaning Glassware

Before the experiments began it was suggested to us that the cleaning of the glassware with hot sulphuric acid was unnecessarily dangerous. Arguments were advanced in favour of using potassium bichromate and strong sulphuric acid in the cold—a method commonly adopted for culture glassware. We ourselves agreed that this method of cleaning would be safer and easier to carry out, but we thought that there was a risk that some chromium compound might be left adhering to the glass, even after thorough washing, and that the results might thereby be affected. There was therefore added to Exp. I a set of dishes cleaned in this way to see whether there was, in fact, any difference between the two methods of cleaning.

Six bichromate-cleaned dishes were used, three for Clyde water and three for E 1. They were filled in the same manner as those cleaned with pure acid and stood alongside them. Within 24 hr. it was seen that the larvae in Clyde water in bichromate-cleaned dishes were swimming less strongly than in Clyde water in pure acid cleaned dishes. On 25 March one of the bichromate dishes contained well-formed plutei similar to those in the five pure acid cleaned dishes, but in the other two the plutei were very malformed and a considerable number were dead. The larvae in E 1 water in bichromate-cleaned dishes differed little in appearance from the abnormal short-armed plutei in the other E 1 dishes, but by 25 March a higher proportion had died. From these results it may be concluded that it is definitely unwise to use a bichromate cleaning mixture for glassware in which delicate larvae are to be kept.

The Influence of Hydrogen-ion Concentration

In the earlier work little attention had been paid to the pH of the sea water used. On one occasion, when there was a marked difference between larvae in waters of different kinds, the pH had been checked and found to be that of normal sea water in all dishes (Wilson, 1951, Exp. 5, p. 7). Among various suggestions put forward after publication of this earlier work was that the results obtained might have been due to initial pH difference of the waters concerned. Smith & Clowes (1924—we are indebted to Mr F. R. H. Jones for this reference) have shown that with *Arbacia* and *Asterias* eggs the velocity of cell division is reduced in sea water adjusted to abnormally high or low pH and that some retardation occurs even at pH 7·6 and 8·5. 'It is doubtful if normal development can be obtained throughout a period of 24 hr.

in solutions more acid than pH 7·8 or more alkaline than 8·4' (Smith & Clowes, 1924, p. 331). Although these figures are almost outside the limits likely to be obtained for normal sea water it was obviously desirable that the influence of pH be considered.

For Exp. I, described above, the initial pH of the waters after filtration and the pH of the waters in the dishes after some days was determined with the following results:

	pH	
	21. iii. 52	25. iii. 52
Clyde water	8·17	8·08
E 1 water	8·28	8·06
Inshore water	8·25	8·06
Clyde + E 1 water	8·20	8·07
Clyde + Inshore water	—	8·07

It will be observed that there were initial differences between the various waters, but that later on these differences were not so great. Although they were relatively small, they none the less underline the desirability for a more precise investigation.

Experiment II

This was devoted solely to testing the influence of pH within the range likely for natural sea water.

Clyde water (collected 17. iii. 52) was adjusted (see pp. 336–7) to six different alkalinities. A fertilization from one male and one female sea-urchin, newly trawled, was made at 6 p.m. on 31 March in water of pH 8·09, and washed with four changes of the same water. The eggs were distributed in the usual

TABLE IV. pH OF EXPERIMENTAL DISHES

Set	31. iii. 52	1. iv. 52	2. iv. 52	3. iv. 52	4. iv. 52
I	7·82	7·80	7·80	7·74	7·76
II	7·94	7·92	7·86	7·80	7·84
III	8·09	7·99	7·94	7·86	7·87
IV	8·16	8·02	7·98	7·91	7·94
V	8·28	8·05	8·04	7·98	7·99
VI	8·38	8·17	8·10	8·05	8·04

manner, there being five dishes of water of each alkalinity. After distribution 2 ml. of water were pipetted from each dish and the pH of the combined five dishes determined. This was also done on the following days. Table IV gives the results.

It will be observed that in all instances the pH dropped more or less steadily and that the drop was most pronounced in the higher alkalinities. On the last day some of them showed a slight rise.

Between 4 and 5 p.m. on 1 April blastulae swam up in all dishes and no differences could be detected. At 10 a.m. on 2 April, however, it was noticeable that in set VI more larvae were on the bottom than in any of the others,

while in set I there were slightly more larvae at the surface than in the others. Sets II–V appeared identical, with most larvae at the surface. The next day, 3 April, no distinctions could be observed, all thirty dishes were alike with about half the larvae at the surface, the others distributed in mid-water and over the bottom. Similarly, on 4 April all dishes seemed equally healthy, with well-formed normal plutei all very much alike. There were hardly any abnormal specimens to be seen. At noon on that day larvae were removed, fixed and photographed from all five dishes of sets I and IV–VI, the method used being that already described (p. 339) for Exp. I. Careful examination of these negatives, as well as of the fixed material with a microscope, revealed no great distinction between any of them. The larvae from sets IV–VI appeared identical, but those from set I had slightly shorter arms and were a little less developed than the others. The difference was very small and could scarcely be observed in living moving plutei.

On 5 April the larvae in all dishes were dying, the flesh of the arms shrinking and the naked rods protruding, and by 6 April most of them were dead.

Throughout this experiment the room temperature varied between 14·9 and 16·5° C.

It is obvious that the pH differences had had no fundamental effect on early development either as regards speed of the development or the structure of the early pluteus, or on the time of death. In future work slight differences of pH between sea waters can probably be ignored.

Attempted Extraction of a Growth Factor: Experiment III

In pursuance of the hypothesis that waters which are favourable to development contain some substance or substances lacking in those which are not, an attempt has been made to extract, with the aid of active carbon, materials from the Clyde water and to add them to E 1 water. Details of the method used are given above (pp. 337–8); it is only necessary to repeat here that in order to ensure complete control a similar extract was prepared from the E 1 water and a blank extract from the active carbon alone. Water which had passed through the carbon was also tested. In all, ten tests with a set of five dishes for each test were made. These are listed below, together with the pH, recorded on 24 April from samples of the original waters stored in glass containers:

Set		pH
I	E 1 water	7·96
II	E 1 water + E 1 extract	7·94
III	E 1 water + Clyde extract	7·94
IV	E 1 water + blank extract	7·99
V	Clyde water	7·94
VI	Clyde water + E 1 extract	7·92
VII	Clyde water + Clyde extract	7·92
VIII	Clyde water + blank extract	7·87
IX	E 1 water through carbon	7·99
X	Clyde water through carbon	7·99

The waters used were newly collected as follows:

E 1 *water* collected from sea surface with wooden bucket. Not strained.
Position: 50° 02′ N., 4° 22′ W.
Date: 16. iv. 52.
Ship: R.V. *Sabella* with F. A. J. A.
Salinity: 35·26‰.
Clyde water collected from sea surface by dipping with a glass breffit. Strained through 200-mesh bolting silk.
Date: 16. iv. 52. Time, 11.00 G.M.T. (high tide 16·07 G.M.T.).
Position: mid-channel between Keppel Pier and Fairlie.
Small boat with Dr H. Barnes.
Salinity: 32·75‰.

The sea-urchins were trawled on 22 April and a fertilization from one male and one female was made at 5 p.m. the same day. A mixture of equal parts of Clyde and E 1 waters was used, the fertilized eggs being divided equally and each half washed in six changes of one or the other water. The eggs which were transferred to the waters which had been passed through active carbon were further washed in the carbon-treated water before being put into the dishes. The glass dipper method of transference (Wilson, 1951, p. 5) ensured that very nearly the same numbers of eggs were put into each of the fifty test dishes.

At the first examination on the following day (23 April) it was at once evident that in all dishes to which Clyde or E 1 extracts had been added (sets II, III, VI and VII) the eggs had cleaved irregularly and had died in early cleavage. The extracts had proved poisonous.

In all the other sets the embryos were alive. At 9.30 a.m. the blastulae were still within the fertilization membrane and motionless. It was observed that almost 100 % of the eggs had fertilized but that about 10 % had developed somewhat abnormally and it appeared that the fertilization was not quite as good as those for Exps. I and II. Shortly after noon the blastulae, free from the membrane, were beginning to swim up, noticeably more so in some sets than in others (see Table V). At this early stage the blastulae in the E 1 water, especially in that which had been passed through carbon, lagged behind all the others, although those in the E 1 water to which the blank extract had been added were reasonably active. The blastulae in the Clyde water with blank extract led all the rest. After this early stage there was from time to time some variation, first one set taking the lead and then another. It was very noticeable how all five dishes in any one set presented a uniform appearance. By the fourth or fifth day there was relatively little to choose between sets I, IV, V and VIII, although IV and VIII (the waters to which blank extracts had been added) seemed to be slightly inferior to the other two. The distinction was too subtle to indicate in the table. On 24 April the pH of one dish in each set was determined and is recorded in the table. On 26 April the larvae were mostly good four-armed plutei, but they were not quite so well developed in any of the dishes as those in the Clyde water of Exp. I of

TABLE V. EXP. III. FERTILIZATION OF *ECHINUS ESCULENTUS* MADE ON 22 APRIL 1952

		Set I E 1 water	Set IV E 1 + blank extract	Set V Clyde water	Set VIII Clyde + blank extract	Set IX E 1 through carbon	Set X Clyde through carbon
23. iv. 52	12–10 p.m.	Blastulae rising, but none at surface	Blastulae rising well, a few at surface	Blastulae well up, a fair number at surface	Blastulae well up, a fair number at surface	Blastulae all on the bottom	Blastulae rising well, a few at surface
	5 p.m.	Almost all at surface, few in mid-water or on bottom	Many at surface and in mid-water, fair number on bottom	Almost all at surface, few in mid-water or on bottom	Many at surface and in mid-water, fair number on bottom	A few at surface and in mid-water, majority on bottom	Most in mid-water and up to surface, many on bottom
24. iv. 52	4 p.m.	Many at surface, some in mid-water, many on bottom	Fair number at surface and in mid-water, many on bottom	Many at surface, some in mid-water, many on bottom	Fair number at surface and in mid-water, many on bottom	A few abnormal larvae swimming, almost all dead	A few at surface or in mid-water, majority on bottom, some abnormal
		pH 7·84	pH 7·84	pH 7·90	pH 7·84	pH 7·94	pH 7·89
25. iv. 52		Majority at surface and in mid-water, mainly normal, a few dead				A very few abnormals living. All others dead	A few in mid-water, all others on bottom, abnormal
26. iv. 52		No change				No change	No change
27. iv. 52		Majority on bottom becoming abnormal				No change	No change
28. iv. 52		Almost all on bottom very abnormal, some dead				Some of the few still living regenerating arms	A few dead, otherwise little change
29. iv. 52		No change				A few apparently normal plutei in all dishes, mainly on the bottom	A fair number dead, but majority still alive on bottom, abnormal

the same age and of which photographs were available for comparison. There was more variation in form and there was a greater proportion of plutei abnormal in varying degree. By the next day all were becoming abnormal, flesh was shrinking down the arms and exposing the rods, which eventually broke off. Not many larvae had died after another 2 or 3 days.

The main interest of this experiment derives from the condition of the larvae in the waters which had been passed through the active carbon, which was known (see pp. 337–8) to have extracted substances from them. In the carbon-treated E 1 water larvae showed little vigour and soon most of them were dead. In carbon-treated Clyde water, on the other hand, the larvae showed more vigour in keeping up off the bottom, although after a few days most of them were lying on it. They failed to develop long arms but most remained alive, stunted in their growth. Towards the end of the experiment some of the few larvae still surviving in set IX, a few in each dish (one dish had more than the others), unexpectedly grew arms which they had not had previously and to all appearance were normal plutei. Others had partially grown arms. This occurred, it should be noted, at a time when in all the other dishes the larvae had lost the arms which they had previously possessed. These newly formed plutei, however, were very lethargic, lying on the bottoms of the dishes and rarely swimming. The water in the dishes was slightly milky, probably from bacterial growth.

The temperature of the room throughout the experiment was very uniform, varying between 15·0 and 15·7° C.

Subsidiary Experiment with Ascorbic Acid

Collier, Ray & Magnitzky (1950) of U.S. Fish and Wildlife Service found a correlation between the pumping rate of *Ostrea virginica* and a factor naturally present in minute amounts in sea water which they designated as 'carbohydrate' or some other compound quantitatively associated with the carbohydrates responding to the test.

In a letter to Dr L. H. N. Cooper, dated 12 March 1952, Dr John Lyman stated that U.S. Fish and Wildlife Service investigators now believe that this substance is ascorbic acid (vitamin C) and Dr Lyman suggested that the growth factor lacking in the Channel water might possibly be ascorbic acid. In order to test this suggestion there were included in Exp. III a set of five dishes of E 1 water to which 10 mg./l. of ascorbic acid had been added (see p. 338 for details) and another set of five containing Clyde water with ascorbic acid. Except that the blastulae in the E 1 dish with ascorbic acid swam up off the bottom a little earlier than in the untreated E 1 water the behaviour and development of the larvae in these waters dosed with ascorbic acid was closely similar, throughout the experiment, to the larvae in the untreated waters.

This experiment cannot be considered conclusive. It was tried out in E 1 water which proved better than usual and with a batch of eggs which may have been of inferior quality (see p. 345).

Discussion

It has now been shown that sea waters from two distinct localities, namely the Celtic Sea and the Firth of Clyde, are sometimes more suitable for laboratory rearings of *Echinus esculentus* than is sea water from the English Channel in the neighbourhood of Plymouth. Both of the better waters come from sea areas known to be normally characterized by a *Sagitta elegans* plankton, whereas the poorer Channel water supports only a less abundant *S. setosa* community. No doubt the relative merits of the two sorts of water vary from time to time. This seems to be indicated by those earlier experiments in which the larvae failed to develop properly in both types of water, and by Exp. III of the present series. In this latter experiment the larvae in the E 1 water were practically indistinguishable from those in the water from the Clyde, although in neither was the rearing one of the best. The plutei showed a greater variation of structure than usual, about half being to greater or lesser degree subnormal. This may have been due to variability in the condition of the eggs, but on this aspect the experiment was not controlled. Nevertheless, the larvae in the E 1 water did better than previously, implying that at times the water occupying this Channel station will be fairly favourable for developing *Echinus esculentus*. That the larvae of this species do develop somewhere in the region is obvious from the numbers of adults present on the trawling grounds (but see Wilson, 1951, p. 18). Late larvae of the species were seen in plankton catches taken off Plymouth in May and June 1951, but in that year no laboratory tests of the sea water were made.

The results of mixing waters (Exp. I) are most instructive. They are probably most easily explained by assuming that the poor condition of the larvae in the E 1 and Inshore waters was due to deficiency of something which was present in the Clyde water. In previous experiments Celtic water had appeared to supply some necessary ingredients to similar mixtures. This conjecture that the better waters contain some essential material which is deficient in the poorer waters seems to be supported by the results of Exp. III where the larvae did so badly in both good and bad waters after they had been passed through activated carbon. Although there is no definite proof, it would seem more probable that the carbon removed needed subtances from the water than that it added something deleterious. Indeed it is known that the carbon extracted a considerable quantity of matter which was recovered with acetone (see p. 337). The acetone extracts from the carbon alone, on the other hand, had little or no effect on the larvae in the waters to which they were added.

The much delayed outgrowth of arms on some of the few surviving larvae in the carbon-treated E 1 water (set IX of Exp. III) is of particular interest. It raises the question whether the early death and decay of the majority of the larvae in these dishes had restored to the water, perhaps by bacterial action, the material needed. Alternatively, perhaps, the larvae had obtained it in particulate form by way of the mouth.

Summary

In one experiment sea water from the Firth of Clyde yielded better cultures of *Echinus esculentus* larvae than did sea waters from two positions in the English Channel.

From the Clyde water materials of unknown composition were extracted, using active carbon and acetone. The addition of these materials to both Clyde and Channel waters resulted in the death of the *Echinus* eggs during early cleavage. A similar extraction from Channel water had the same effect. The Clyde and Channel waters from which these materials had been extracted gave poor abnormal cultures, especially the Channel water in which most larvae died early. A few, however, survived, and later on some of these grew into almost normal plutei.

It is shown that alkalinities between pH 7·82 and 8·38 have little or no effect on the growth and form of early *Echinus* larvae.

The addition of ascorbic acid to both Clyde and Channel waters produced little or no improvement, but the experiment was in the main inconclusive.

Some evidence is advanced that English Channel water is not always an unfavourable medium for the development of sea-urchin larvae.

Some glass dishes which had been cleaned with a cleaning mixture consisting of potassium bichromate and sulphuric acid gave rise to abnormal and unhealthy larvae, while similar dishes cleaned with hot sulphuric acid did not.

Details of the chemical methods used in these investigations are given.

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THE BOAR FISH, *CAPROS APER* (L.), AS A POSSIBLE BIOLOGICAL INDICATOR OF WATER MOVEMENT

By L. H. N. Cooper, D.Sc., F.R.I.C.
Chemist at the Plymouth Laboratory

(Text-fig. 1)

Capros aper (L.) is sporadic in its occurrence in the English Channel; for many years near Plymouth it has been scarce or absent. Between 3 June 1948, when Capt. C. A. Hoodless began to keep exact records of all fish trawled by R.V. *Sabella*, and 29 June 1949 no *Capros* were taken by that ship. From 30 June 1949 to September 1951 odd fish were trawled in the summer months, never more than three in a haul, and in October 1951 two more fish were caught separately. Then on 30 October two hauls by R.V. *Sabella* about 5 miles south-west of the Eddystone brought up 1000 and 300 fish, followed by 50 on 13 November, 100 on 10 December and 50 on 17 December. In the same area on 1 November M.F.V. *Sula* in two hauls caught 200 and 50, a further 50 near Station E 1 on 14 November and 9 on 17 March 1952. All these catches were in hauls of 45–90 min. duration. Single fish were taken by each ship in February 1952.

A hypothesis to explain the introduction of a considerable fresh stock of *Capros* into the English Channel late in the year has been developed from an earlier hypothesis (Cooper, 1952*a*) concerning 'submarine eagres' in canyons in the continental slope.

On a number of occasions between July and October inclusive the post-larval stages of *Capros* have been recorded by Russell (1930–47) and Corbin (1948–51) from the 2 m. ring-trawl catches taken weekly 2 miles east of the Eddystone. In all years in which young *Capros* occurred, except 1937, the species of the siphonophore, *Muggiaea*, occurring at about the same time was *M. kochi* and not *M. atlantica*. *M. kochi* was the species present (Corbin, private communication) on 24 October 1951 at International Station E 1, a few miles from the position where the large hauls were made a few days later. There are reasons, as yet unpublished, for suspecting that *M. kochi* in the English Channel may indicate deeper water brought up over the continental slope lying to the south-west. These events therefore suggested that *Capros* might also indicate water from the continental slope.

In the Plymouth aquarium *Capros*, by means of gentle fin movements, may remain poised almost stationary in the water or make slow excursions around

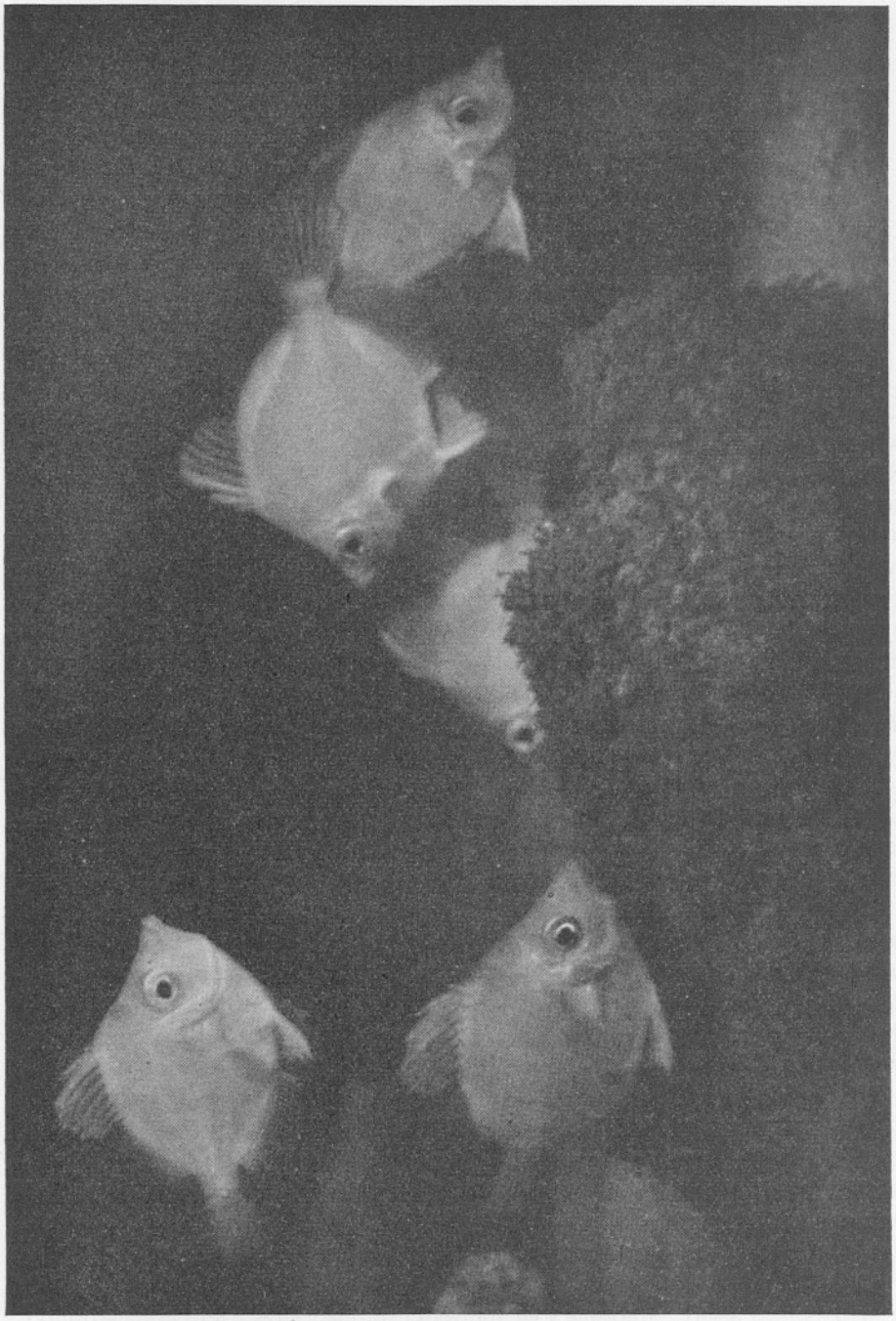

Fig. 1. *Capros aper* in the Plymouth Aquarium. Photograph by D. P. Wilson. Two-thirds natural size.

the tank. Occasionally it may make short random darts through the water. Since it does not appear the sort of fish to make far-reaching migrations by swimming, the illusion of migration may be due to travel from some distant source of the water mass in which it occurs. If so it might be of value as a biological indicator of water movement.

Records of its distribution have been summarized by Cornish (1868), Gatcombe (1879) and Legendre (1934). The latter took eighteen examples from the stomachs of germon or white tunny (*Germo alalunga*) caught in the Bay of Biscay north-west of Concarneau. *Capros* has often been found in the stomachs of tunny. Apart from records near Plymouth or off Cornwall, all others are near to the western European or Mediterranean continental slopes. All authorities agree on a distribution epitomized by Holt & Calderwood (1895) who said that 'it is known to frequent rather deep water, although in the neighbourhood of Plymouth it is tolerably abundant in depths of less than 30 fathoms during summer months'. In 1879, Gatcombe was told that within a few years *Capros* had become a pest, so much so that trawlers had been obliged to change their fishing grounds to avoid them. So great was the weight of the fish that the fishermen had to cut large holes in their nets to let them escape.

Collett (1896) stated that it occurs along coasts in great numbers only after storms. He was writing mainly of the Mediterranean where continental shelves are narrow and either 'submarine eagres' or 'capsizing of water masses' would introduce *Capros* directly into coastal waters.

Le Danois (1913) said that it is a deep-water fish and that only accidentally does it rise to the shallow banks of the English Channel. Later (1943, p. 142) he suggested that the group containing *Capros* has evolved around coral reefs. In his constructive broad survey of the fauna of western European waters he (1948, p. 278) classes *C. aper* as an inhabitant of the 'bordure continentale' and Atlantic slope and associated there with the coralline facies. The corals he divides into yellow and white (or flesh pink, *rose chair*). According to Le Danois the yellow coral, unlike the white, does not thrive in mud and prefers hard steep rocks. It is most often found on parts of the Atlantic Slope which are *tourmenté et chaotique*. It would be the species of coral most likely to occur on the steep sides of submarine canyons. This association should mean that *Capros* is indigenous in submarine canyons encrusted with yellow coral. In clear well-illuminated water the yellow or straw colour of *Capros* should provide camouflage amongst such yellow coral, but it probably has little value in the almost dark waters below 200 m. depth.

However, Day (1880) described fish which when first received in the Westminster aquarium from Mevagissey were of a rich red hue changing in the course of a few days to straw colour. Their colouring may be banded or plain. Evidently, if it so wished, *Capros* could adapt itself to match either of the coralline environments described by Le Danois, if sufficiently illuminated.

Our present interest will be centred on the population of *Capros* which may occur associated with yellow coral in the upper and narrower parts of submarine canyons between about 200 and 500 m. in depth.

A hypothetical submarine eagre, arising from vertical oscillations in stratified water following on-slope strong winds, has been suggested (Cooper, 1952*a*) as running up a submarine canyon like a bore or eagre in the Rivers Severn or Trent. In the upper, more constricted, part of the canyon this submarine eagre is considered likely to become quite violent, sufficiently so to dislodge *Capros* from its environment against the coral encrusted walls, to which the fish would be unable to return. It is scarcely credible that the momentum of such an eagre could carry the water and the fish in it the 200 miles from the continental slope to the neighbourhood of the Eddystone nor is that necessary. It is necessary only to believe that the eagre projects the water sufficiently far on to the continental shelf for it to get caught up in the general cyclonic circulation of the Celtic Sea. The eagre would inject a limited mass, a 'bubble' or 'eagre spurt' of canyon water into shelf water which could have quite different properties but which, none the less, would become effectively labelled by the considerable population of *Capros*.

To be of value as a biological indicator *Capros* would need to be exceedingly abundant in its coralline home. However, it is not postulated that there is always a dependable uniform stock available to colonize submarine eagres. The continental slope would seem likely to be an exacting environment for species largely restricted to it, so that the population of *Capros* against the slope may fluctuate widely.

A canyon wall swept clean of *Capros* by a submarine eagre would be slowly re-colonized either by adults moving in from neighbouring less dissected areas of the slope, including the muddy areas inhabited by 'white coral', or by metamorphosis in the right place of larvae spawned from such areas. There may be a difference in age composition of *Capros* populations in submarine canyons and in the Celtic Sea and English Channel, on the one hand, and over the muddy white-coralline areas on the other.

A submarine eagre would introduce on to the continental shelf a compact population of *Capros*, but the water introduced with the fish might be of two kinds. An eagre spurt is visualized as having a compound structure. After a persistent strong on-slope wind a homogeneous water-mass is likely to be present, not only within submarine canyons to several hundred metres depth, but also for some miles inward over the continental shelf. As the wind dies down the water in the canyon may oscillate. The upper part which would sweep out the stock of *Capros* on to the shelf need not be distinguishable from the neighbouring shelf water. The event could not be followed by measurements of chemical properties or temperature but only by current meters or biological indicators. However, towards the end of a large and deep oscillation, when the canyon walls have been swept clean of *Capros*, deeper water

of markedly different properties and richer in nutrients should follow. The result may be compared with a comet, the head of the eagre spurt being characterized only by *Capros* and any accompanying biological indicators, the tail containing few *Capros* but distinguishable chemically.

The subsequent history of an eagre spurt on the continental shelf would depend on the general circulation, tides, bottom topography and weather. When, as often, the general circulation is cyclonic, *Capros* from the southern edge of the Celtic Sea would be carried towards Ushant, the English Channel and Land's End.

Sometimes, but not always, eagre-spurt water would be slightly heavier than water over the shelf where it would tend to fill the troughs in the sea bed. There *Capros* would be expected to be trawled in large numbers more often in the troughs than on the banks. Such a distribution would be due to the topography and not to the nature of the sea-bed.

All currents are zero in immediate contact with the bottom and increase in strength upwards and the strongest currents are tidal. According to van Veen's formula (1936) the current at 4 m. off the bottom will be about twice that at 10 cm. so that tidal currents will tend to spread any dense population of truly demersal fish. In the southern Celtic Sea the major and minor axes of the tidal ellipses are almost equal so that there a circular shoal of fish would, as it spreads, remain almost circular. But in the English and Bristol Channels, the tidal streaming is almost linear, flood and ebb currents each flowing in almost the same directions for several hours. The major axis of the tidal ellipse much exceeds the minor. In these waters a dense demersal shoal will not spread radially as in the Celtic Sea but into an elongated band. Strongly swimming fish, such as the gadoids, may well choose to reform a compact shoal if this better suits their way of life but it is unlikely that *Capros* could do so. If the present hypothesis is correct shoals of *Capros* in the western English Channel, but not in the Celtic Sea, are likely to occur as elongated bands, aligned along the major axis of the tidal ellipse.

This theorem is worth investigation for a practical reason. All strictly demersal shoaling fish are likely to respond to this effect of the tide in some degree. If therefore a trawler detects on its echo-sounder a shoal of fish near the bottom, it is likely in the English Channel to make better catches by towing its trawl in or against the direction of the main tidal stream than by towing across it.

An eagre spurt containing *Capros* in numbers will be subject not only to spreading due to differential bottom currents but to attrition due to bottom friction of all kinds. Odd fish would become distributed over a much wider area than that of the eagre spurt which may be identified only while the population remains dense.

Submarine eagres can arise only in stratified water and stratification over the continental slope, as elsewhere, is most strongly developed in summer.

Consequently, only then would shoals of *Capros* be injected on to the continental shelf to arrive off Plymouth some weeks later. Again, in shallow homogeneous water wind causes vertical and lateral mixing right to the bottom. In winter strong winds should disperse shoals of *Capros*. Although beneath a thermocline, strong winds may produce more mixing than has been hitherto realized (Mortimer, 1952), nevertheless, the forces tending to disrupt shoals will be much less in summer.

TABLE I. STRONG WINDS IN THE CELTIC SEA, SEPTEMBER 1951

		Scilly Observatory Wind observed			Position 48° 30′ N., 9°–10° W. Estimated wind	
Date	Hours	Direction	Knots	Force Beaufort	Direction	Force Beaufort
13 Sept.	06	200	27	6	300	6
	12	290	31	7	280	6
	18	280	21	5	270	6
14 Sept.	00	260	17	5	250	5
	06	260	19	5	240	4
	12	220	16	4	220	6
	18	220	18	5	230	7
15 Sept.	00	200	26	6	220	7
	06	220	22	6	310	5
	12	320	21	5	300	4
	18	290	12	4	300	3
16 Sept.	00–18	250–300	6–8	2–3	—	—
23 Sept.	00	**180**	**22**	**6**	**260**	**6**
	06	270	13	4	**280**	**6**
	12	240	13	4	**270**	**6**
	18	**260**	**23**	**6**	**270**	**6**
24 Sept.	00	**260**	**23**	**6**	**270**	**6**
	06	240	20	5	**240**	**7**
	12	**220**	**23**	**6**	**240**	**7**
	18	**220**	**22**	**6**	**260**	**7**
25 Sept.	00	**210**	**29**	**7**	**260**	**6**
	06	230	18	5	270	5
	12	240	13	4	260	5
	18	240	12	4	280	5
26 Sept.	00	250	13	4	290	5

There is a critical wind speed at about 7 m./sec. (14 knots, Beaufort Force 4) (Rossby & Montgomery, 1935; Munk, 1947). Above this speed the effect of wind becomes 'hydrodynamically rough'. Only such winds can get hold of the water sufficiently to produce the conditions which must precede submarine eagre formation. The effect of wind of Beaufort Force 4 will be trivial.

A minimum Force 6–7 (22–33 knots; 11–17 m./sec.) was visualized as necessary to produce the cushion of light water against the slope, the upward swing of which would produce a submarine eagre when the wind dropped. Winds of this strength were recorded on 13, 15, 23 and 24 September 1951 (Table I).

The nearest British Meteorological Station is at Scilly (St Mary's) about 150 miles from the area where information is required. Every 6 hr. in the Daily Weather Reports the anemometer readings there are reported for direction and strength in knots. These exact records have been extracted. From the further reports from merchant and weather ships (including the French vessels at 45° N., 16° W.) and the 6 hr. synoptic isobaric charts, assessments of wind direction and speed in knots at 48° 30′ N., 9–10° W. have been made. They are printed in Table I as Beaufort numbers which correspond better to their probable accuracy.

In submarine canyons facing into the wind, submarine eagres could have been created on 14, 15 and 25 September when the strong winds dropped. The lull of about 12 hr. on 14 September may not have been long enough to be effective while any dense shoal of fish ejected on to the shelf then or on 15 September would probably have been dispersed by the strong wind on 23 and 24 September. It is suggested that on the following day, 25 September, when the wind dropped to 13 knots at Scilly and did not exceed 18 or perhaps 20 knots near the slope, an eagre spurt was injected on to the continental shelf from a submarine canyon and that this brought up the population of *Capros* which was found near the Eddystone on 30 October and subsequently. Such spurts were possible in a number of the canyons depicted by Beaugé (1934).

The continental slope concerned runs from south-east to north-west, and the axes of most of the reputed canyons point south-west or south. In these, south-westerly or southerly winds should be most favourable for creating eagres. However, one of the largest canyons at 48° 22′ N., 9° 30′ W., named by the French Fisheries Department 'la Machoire du Sud' has an almost straight axis pointing west by south. Its southern wall has been defined by H.M.S. *Dalrymple* also. In this canyon, and in this alone, westerly winds could create considerable submarine eagres. On 25 September a large eagre was more likely to occur there than in any other canyon. The winds most likely to have been responsible for the eagre spurt which brought in the *Capros* shoal are printed in heavy type.

Once this was achieved quiet weather was needed to allow the shoal of *Capros* to reach the neighbourhood of the Eddystone intact. For the remaining 5 days of September force-4 winds were consistently recorded at Scilly. Thence, until 30 October, of 120 records of wind at Mount Batten, Plymouth, only 12 were in the range 11–16 knots (force 4) and but one reached 17 knots. Such light winds would have little power to disperse an eagre spurt travelling up-Channel. The meteorological records were therefore precisely what the theory demands. If this view is correct, the shoal of *Capros* was carried about 200 miles in the eagre spurt in 35 days, or about 6 sea miles per day.

Water containing *Capros* in an eagre spurt may be heterogeneous. Only if the water can be sampled in the middle of the shoal could distinctive

hydrographical results be expected. Trawling does not generally enable one to know exactly where such a shoal was placed. Even if the centre of the shoal could be found, a high salinity characteristic of slope water is to be expected only under very favourable conditions. Let us consider an unmixed eagre spurt, fresh from a canyon, containing 10,000 *Capros* per standard trawl haul and having a salinity of 35·6 ‰ and a total phosphorus content of 0·9 μg.-atom/l. Let us consider its admixture with enveloping water containing no *Capros*, a salinity of 35·20 ‰ and total phosphorus amounting to 0·5 μg.-atom/l. The mixed waters would have the properties set out in Table II.

In October and November 1951 there was no change in the chemical properties of the water at the nearby station E 1 which could be associated with the incursion of *Capros*. Thus, if the hypothesis can be proved, *Capros aper* would provide a far more sensitive indicator of the presence of continental slope water near Plymouth than would any chemical determination.

TABLE II

Percentage of		Number of *Capros* per standard trawl haul	Salinity (‰)	Total phosphorus (μg.-atom/l.)
Eagre spurt water	Enveloping water			
100	0	10,000	35·60	0·9
10	90	1,000	35·26	0·54
1	99	100	$35{\cdot}20_6$	$0{\cdot}50_4$
0	100	0	35·20	0·50

A criticism may be made that a density of fish in an eagre spurt as high as that assumed in Table II is improbable since, for lack of food, deep-water fish are rarely in sufficiently dense concentration. This may be especially true of a species that remains in much the same place. What would it eat? The rain of food from above would support a certain number but surely not so many? In the open ocean this criticism would be pertinent, but further investigation may show that it is not true against a continental slope where food may arrive by means other than 'raining down'. There is abundant evidence (*inter alia* Cooper, 1952*a*, fig. 3, Station 51; and 1952*b*) that in winter vertical homogeneity of water against the slope, which must be due to vertical mixing, extends at least 3 to 5 times deeper than it does in the open ocean to the westward. This vertical homogeneity is a fact and not dependent on the hypotheses of cascading, capsizing and submarine eagres which have been erected to explain it. The vertical movement or mixing of the water, whatever its cause, will carry downwards some of the organisms which cannot swim. The population of these in the 200–400 m. strata against the slope is likely to be comparable with that in the surface layers. Again, there are numbers of strongly swimming vertical migrants near the slope, such as *Sagitta serratodentata*, which feed near the surface at night and make diurnal vertical migrations to several hundred metres depth. In the ocean against

a continental slope—and only there—reserves of food for fish comparable with those over continental shelves are likely to be present at considerable depths. Probably, therefore, dense populations of fish at depth in these submarine canyons may find adequate food at any season, and abounding food during cascading or after southerly storms. On this view the postulated catch of 10,000 *Capros* thrown up by a submarine eagre and caught in a standard trawl haul does not seem so unreasonable.

Since trawls and dredges are very inefficient instruments to sample fish sheltering against the rugged walls of a submarine canyon, the only hope of obtaining evidence of abundance in such a place would seem to be with an under-water camera, protected by a cage and triggered to take a photograph when the cage strikes a canyon wall.

It would be unreasonable to assert that eagre spurts similar to that here discussed did not occur in the nineteen-thirties. If they occurred they brought few *Capros*. Consequently, the present hypothesis is acceptable only if we further assume that the stock of *Capros* over the continental slope underwent a decrease in numbers comparable with that undergone by many fish and invertebrates near Plymouth at the same time. Catastrophes to adults or eggs and larvae due to excessively violent capsizing might provide an explanation of short-period changes but are unattractive to explain long-period fluctuations. It is more probable that the water of the Atlantic Ocean bathing the continental slope has been subject to vicissitudes similar to those in the English Channel. We should then have to seek an understanding of local events in terms of changes in the fundamental circulation of the Atlantic Ocean.

Within the English Channel *Capros* would find conditions resembling its postulated indigenous home only on rocky declivities from which tidal currents and breaking seas would tend to detach it. If a stock of the fish were carried into the Hurd Deep, there against the steep walls it might find food and shelter and thrive for a while. The Hurd Deep would then provide a centre of dissemination of *Capros* eggs. Again, a passing shoal might attempt a lodgement amongst the rocks of the Eddystone where they may live undetected for some while. Eggs spawned there would be sampled at the standard young-fish-trawl station 2½ miles to the eastward. In similar vein, Couch (1863) mentioned that a Penzance trawler in July 1844 in a few days caught about 200 close into the Runnelstone. He says: 'These fish may always be found within half a mile of this well-known rock, where they are probably induced to assemble by congenial food; but they are scarce, or not to be found beyond that distance.' Care would be needed that such local and possibly temporary populations do not upset a picture dependent on recruitment from the south-west.

Corroboration

Mr J. Taylor and Mr L. Cunnington, skipper and mate of M.F.V. *Jago*, later reported that between 25 June and 3 July 1947 near the Lizard they took an exceptionally large haul of *Capros*. The gear for heaving the cod-end in board was pulled down several times. The trawl in use was brand new, otherwise it would not have stood up to the great weight without splitting. Buried amongst the *Capros* and scarcely visible were twenty-two baskets of hake.

After 1 May the only winds as strong as Beaufort Force 6–7 occurred on 4 and 6 June (Table III) and these were westerly. In La Machoire du Sud, and in this canyon only, could these winds have created the considerable submarine eagre on 7 June believed to have introduced the dense shoal of

Table III. Strong Winds in the Celtic Sea, May–June 1947

		Scilly Observatory Wind observed		Position 48° 30′ N., 9°–10° W., Estimated wind*	
Date	Hours (G.M.T)	Direction	Force Beaufort	Direction	Force Beaufort
4 June	18	W.N.W.	6	W.'N.	6
6 June	00	W.'S.	6	W.	6
	06	W.	7	W.N.W.	6 or 7
	12	W.'N.	6	W.	6
	18	W.S.W.	5	W.S.W.	4
7 June	00	S.W.'S.	4	W.S.W.	4

* Assessed from observations by British Observing Ships in the area between 45° and 50° N., and between 7° and 13° W., supplied by the Marine Superintendent, Meteorological Office, Harrow.

Capros. The shoal would have been carried by the current about 200 miles in 18–26 days at an average speed of 7–11 miles a day. The evidence is scarcely strong enough to assert that the associated hake, a slope fish, came from the same source.

There appears to be a neighbouring canyon, La Machoire du Nord, which for much of its length runs west-south-west but in its upper and shallower course it turns for 5 miles to face south by west. Creation of eagres there in westerly winds is less likely.

We now have two events to support the real existence of submarine eagres, and both times La Machoire du Sud canyon is indicated as the site. Of necessity the argument has had to be based on the coincidence of large catches of *Capros* with the occurrence a few weeks earlier over the continental slope of westerly or south-westerly winds of Beaufort Force 6–7. These are prevailing winds so that the coincidences may be due to pure chance. Whereas one failure to find a fit will kill the hypothesis, certainty will come only by accumulating many such coincidences. The author would therefore appreciate news from fishing skippers of the time, position and quantity of all catches

of *Capros* (zulus) exceeding, say, 1000, together with information as to the gear used and the duration of the haul.

Evidence for the hypothesis of submarine eagres could be sought by trawling at the right time on the fine sandy bottom which exists at 48° 23′ N., 9° 20′ W., inshore of the heading of La Machoire du Sud. Some hours after strong winds (Beaufort Force 6–7) from between south-west and west have died down, *Capros* in very large numbers may there be introduced by an eagre from the canyon.

The writer is indebted to Mr A. D. Mattacola, who drew attention to the notable hauls of *Capros* and has helped in many ways and to Lieut.-Cmdr. C. A. Hoodless, D.S.C., R.N.R., for his exact records of catches.

Summary

Notable catches of boar fish (*Capros aper*) were taken near the Eddystone on 30 October and in early November 1951. From what is known of the distribution of boar fish and from the hypothesis on the genesis of 'submarine eagres' in canyons on the continental slope, a further hypothesis has been derived to explain this occurrence. It is suggested that strong west to south-westerly winds on 24 September created conditions to produce a submarine eagre the following day, and that this swept a shoal of boar fish from the yellow-coral encrusted walls of a submarine canyon in the southern edge of the Celtic Sea on to the continental shelf. Thence during quiet weather the shoal was carried by currents to the neighbourhood of the Eddystone at about 6 miles a day. Further deductions which lead to means of checking the present hypotheses have been drawn.

An exceedingly large catch of *Capros* taken by M.F.V. *Jago* in the summer of 1947 is attributed to a shoal ejected on 7 June in a submarine eagre from a large canyon at 48° 22′ N., 9° 30′ W.

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ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

THE EGG AND LARVAL STAGES OF *NYCTIPHANES SIMPLEX*, A EUPHAUSIID CRUSTACEAN FROM CALIFORNIA

By Brian P. Boden

Proc. Zool. Soc. Lond., Vol. 121, 1951, pp. 515–27

The female of *Nyctiphanes simplex* carries her eggs in an egg-sac. The eggs hatch in the nauplius stage and remain in the egg-sac throughout that stage. The larva emerges from the sac as a pseudo-metanauplius and moults immediately into the metanauplius stage. This is followed by three calyptopis stages and the furcilia stages. There are probably nineteen types of furcilia larvae. Since six of these are numerically dominant, it is probable that the larvae 'jump' stages in the furcilia series. The six dominant types are described as the six furcilia stages. A key to the furcilia stages is included. B.P.B.

MICRO-DETERMINATION OF NITROGEN IN ORGANIC MATTER WITHOUT DISTILLATION

By H. W. Harvey

The Analyst, Vol. 76, 1951, pp. 657–60

It was required to determine the quantity of organic nitrogen in small quantities of unicellular algae, which can be separated from suspension by centrifugation, and to complete six to eight analyses within 3 hr.

A method is described by which 5–30 μg. quantities of nitrogen are estimated in test or centrifuge tubes without distillation. After digestion with sulphuric acid and hydrogen peroxide, in presence of a mercury catalyst, the resulting ammonium sulphate is treated with an excess of hypobromite. The residual hypobromite is determined by titrating the iodine, liberated on addition of potassium iodide and acetic acid, with standard sodium thiosulphate solution.

In order to test the accuracy of the method, analyses of acetanilide were made and yielded the following results:

Nitrogen taken (μg.)	Nitrogen found
10·32	10·1, 10·2
20·65	19·2, 20·6
41·3	40·7, 41·4
20·65	20·7 as mean of four analyses.

H.W.H.

The Swimbladder and the Vertical Movements of Teleostean Fishes. I. Physical factors

By F. R. Harden Jones

Journ. Exp. Biol., Vol. 28, 1951, pp. 553–66.

The vertical movements of a teleostean fish may be restricted by the presence of the swimbladder which will increase or decrease in volume when the fish moves up or down in the water. The restriction that the swimbladder imposes to vertical movements involving a reduction in pressure will depend on physical factors such as: (1) the resistance that the bladder and body-wall offer to the expansion of the bladder gas; (2) the percentage volume of the swimbladder and the density change of the fish when it is subjected to a reduction in pressure; (3) the pressure reduction that leads to the rupture of the bladder wall.

Various experiments were made on the perch, *Perca fluviatilis*, the wrasse, *Crenilabrus melops*, the rockling, *Onos mustela*, and the dragonet, *Callionymus lyra*. The results showed that there was a relation between the relative size of the swimbladder and the change in the density of a fish when it was subjected to a pressure reduction; that the bladder and body-wall of the perch offer little resistance to the expansion of the bladder gas; and that the danger of the bladder wall rupturing might restrict the extent of rapid movements made by the perch. F.R.H.J.

A Larval Hoplophorid (Crustacea) from Bermuda

By Marie V. Lebour

Proc. Zool. Soc. Lond., Vol. 121, 1952, pp. 753–7

An interesting larva is described belonging, probably, to the genus *Notostomus*. No larva of this genus is so far known and it is probable that the usual habitat is in deep water. The suggestion is offered that the normal larva is small and thin-skinned and that the present large form which was found at a lesser depth may have been delayed in metamorphosing or not been able to metamorphose at all owing to the uncongenial surroundings. M.V.L.

The Induction of Regeneration in the Hydroid *Cordylophora lacustris*

By Janet Moore

Journ. Exp. Biol., Vol. 29, 1952, pp. 72–93

Reconstitution masses of the hydroid *Cordylophora lacustris*, made by chopping up unspecialized tissue and piling the fragments into heaps, may regenerate hydranths 'spontaneously'. An oral cone grafted into a mass

induces, at the point of grafting, the development from mass tissue of hydranth regions basal to the oral cone. The induced hydranth develops at an accelerated rate and spontaneous regeneration at other sites is inhibited. Beadle and Booth's report that oral cone grafts induce hydranth development in *Cordylophora* reconstitution masses is confirmed and extended.

The inducing properties of oral cone grafts are shared by grafts of other regions of the hydranth (tentacular ring, subtentacular region, hydranth neck, and even small fragments of tentacle) and by the rudiments of developing hydranths (tips of outgrowths from masses) but not by tissue lacking hydranth differentiation (stem coenosarc and stolon tips). Induction may be produced by differentiated tissue grafts when inverted or fragmentary, but not when macerated or killed, nor has induction occurred with thin agar or cigarette paper barriers inserted between the graft and host. There is no evidence that hydranth induction is mediated by a diffusing chemical; direct close contact with living differentiated tissue is necessary for induction to be produced in unspecialized tissue. J.M.

Autonomic Nervous Systems in Lower Chordates

By J. A. Colin Nicol

Biol. Rev., Vol. 27, 1952, pp. 1–48

This review presents a detailed survey of the visceral efferent systems of lower chordates from the protochordates to the Amphibia. The classical system of Langley's is used as a basis for discussion, a morphological description of the system in each of the major groups is presented, and this is followed by functional analyses, as far as the data permit. In these lower forms it is possible to trace an elaboration of complexity in the autonomic systems from the enteric nerve net of balanoglossids to the differentiated amphibian organization characteristic of tetrapods. The system is rudimentary in cyclostomes, but chromaffin tissue is present, and the vagus supplies the gut and heart. Sympathetic and parasympathetic systems show great diversity and specialization in fishes, from a rather primitive arrangement in elasmobranchs, to a high degree of differentiation in teleosts. The latter are characterized by a greater regularity in organization of the sympathetic trunks, and by augmentation of the fields of sympathetic innervation in the head and other peripheral effectors. In the Dipnoi the autonomic system appears to be on a lower level of morphological organization than in teleosts. In the Anura it is organized in the pattern found in mammals, and has cranial and sacral parasympathetic, and abdominal sympathetic components. A progressive elaboration of physiological complexity is traced along with morphological differentiation in the lower chordates, and the implications discussed. Analysis of evidence leads

to the conclusion that the autonomic nervous systems of vertebrates show two main independent lines of evolution from some simple level of organization such as that found in extant elasmobranchs. These two lines occur in actinopterygians leading to modern teleosts, and in choanichthyes leading to Dipnoi and tetrapods, and there has been a considerable degree of independent specialization and differentiation in these two groups. J.A.C.N.

Untersuchungen über die algenbewohnende Mikrofauna mariner Hartböden. I. Zur Oekologie und Systematik der Nematodenfauna von Plymouth

(On the Ecology and Taxonomy of the Free-Living Marine Nematodes of Plymouth)

By W. Wieser

Österr. Zool. Zeitschrift, Bd. 3, 1951, pp. 425–80

The free-living nematodes inhabiting the following seaweeds were studied: *Ceramium* sp., *Cladophora rupestris*, *Lomentaria articulata* between +3·25 and +0·8 m., *Gelidium corneum* between +2·75 and +1·10 m., *Fucus serratus* between +2·00 and +0·20 m., *Gigartina stellata* between +2·00 and +1·00 m., *Porphyra laciniata* between 1·95+ and +1·50 m. (above C.D.) and *Nitophyllum punctatum* between −0·70 and −3·00 m. (below C.D.). All samples were taken in the Tinside area of Plymouth Sound.

The population of the small and procumbent *Gelidium corneum* proved to be richer both in numbers and in species than that of the tuft-like *Ceramium* sp. The composition of the two faunas differs considerably, the former being dominated by relatively long and detritophilous species, the latter by small ones of the family Chromadoridae.

The composition of the nematode fauna of the two algae *Gigartina stellata* and *Fucus serratus* depends largely upon the extent to which epigrowth is developed on them. Apart from that, the fauna of *Gigartina stellata* proved to be much richer than that of *Fucus serratus*, which is due to the denser branching of the former weed. The habitats richest in species appear to be *Gigartina stellata* and *Nitophyllum punctatum*.

The distribution of length-classes in a given nematode population depends upon the shape of the seaweed inhabited. Two modes of distribution of length-classes were distinguished, viz. one with the smallest forms between 0·4 and 1 mm., amounting to more than 70 % of the total population, and a second one with these smallest forms comprising not more than 35 % of the population and being outnumbered by specimens over 1·5 mm. The vertical distribution of all species found is given. Typical species for the highest and

lowest zone, respectively, can be indicated with a high degree of probability. Altogether seventy species have been listed of which three genera, eleven species and one variety are new to science. These are described in detail. W.W.

THE INFLUENCE OF THE NATURE OF THE SUBSTRATUM ON THE METAMORPHOSIS OF THE LARVAE OF MARINE ANIMALS, ESPECIALLY THE LARVAE OF *OPHELIA BICORNIS* SAVIGNY

By D. P. Wilson

Ann. Inst. Océan., T. 27, 1952, pp. 49–156

A survey of the literature concerning larval settlement shows that the larvae of a number of species are able to postpone metamorphosis for a period of time during which they are able to select the substratum in or on which to metamorphose. This ability is most strongly developed in species confined to a single type of bottom deposit. Such a species is *Ophelia bicornis* Savigny whose larvae are unusually suitable material for experimentation. In a large number of experiments they have been used in an endeavour to determine the factors by which the larvae distinguish one sand from another. It is concluded that certain sands are repellent by virtue of organic matter, or living micro-organisms, on the surface of the grains, and that provided the sand be not unsuitable in grade the larvae favour relatively clean sands, the cleanest sands normally found in nature apparently containing sufficient nourishment for the adults. Organic materials present on such grains may be also of a different nature from those on grains which are repellent.

The paper contains discussions of various matters relative to the main theme. It is shown that *Ophelia bicornis* is found only in a few restricted localities from the Bay of Biscay to the entrance to the English Channel, and that all localities are bays or estuaries where strong tidal scour may occur and the sand clean, coarse and loose. Certain physical features of sands, particularly the readiness with which their grains sink or float when sprinkled dry on to water, are investigated. D.P.W.

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1951–52

The Council has to report with deep regret the death of the Librarian of the Plymouth laboratory, Miss M. A. F. Sexton, who had served the Association loyally and devotedly for many years.

The following have been elected Vice-Presidents of the Association during the year: Major E. G. Christie-Miller and Mr Morley H. Neale, C.B.E.

The Council and Officers

Four ordinary meetings of Council were held during the year, three in the rooms of the Royal Society, and one at the Plymouth laboratory. At these the average attendance was eighteen.

A special meeting of Council was held in the rooms of the Royal Society on 30 October 1951 to consider the pay of the crews of the Plymouth research ships.

During the year Dr C. F. A. Pantin, F.R.S., was appointed as Governor representing Cambridge University in place of Prof. J. E. Smith.

Dr Edward Hindle, F.R.S., attended a Royal Garden Party at Buckingham Palace as a representative of the Association in July 1951.

The Plymouth Laboratory

During the year the waterproof covering to the roof of the western half of the north building has been stripped and the roof has been relaid with asphalt. The covering to the roof of the bridge and passage connecting the north and south buildings has also been renewed with a roofing felt.

A small laboratory has been built, adjoining the constant temperature building, to be used for research with radioactive substances. The furnishing and fitting out of this laboratory has also been completed.

Permission has been obtained from H.M. Treasury to have detailed plans and specifications prepared for the extension of the library building.

The Aquarium

The aquarium has maintained its popularity with the general public and has continued to play a part in the education of large numbers of school children. Tanks have been well stocked, and among unusual exhibits may be mentioned the Red Bandfish (*Cepola rubescens*) and the very rare Stone Bass or Wreck-fish (*Polyprion americanus*), a specimen of which was caught by fishermen off Hope Cove, near Salcombe.

Some improvement to visibility in the tanks on the south side has been effected by fitting ground glass to the front windows, thus reducing afternoon sunbeam dazzle.

Research Ships

Apart from periods for annual refit the research vessels *Sabella*, *Sula* and *Gammarus* have worked regularly throughout the year. During the year the face-plate on the stern-post of the *Sabella* has been renewed, and a new rudder fitted to the *Gammarus*. Alterations have been made to the engine room of the *Sula* to give additional clearance above the engine.

New Research Ship

The Council has pleasure in reporting that during the year H.M. Treasury has sanctioned a grant to meet the cost of building a new research ship. This will be the first time that the Association has been able to build a ship specially designed for its research requirements.

The ship is to be steel-built, 115 ft. B.P., and powered by a main diesel engine, with an auxiliary for slow speeds. Messrs Graham & Woolnough of Liverpool are acting as naval architects to the Association, and are designing the ship to incorporate requirements and details which have been mainly drawn up by Mr G. A. Steven. The ship is to be built in the yard of Messrs Philip and Son Ltd. at Dartmouth.

The Staff

Dr Mary Parke and Mr P. G. Corbin have been promoted to the grade of Principal Scientific Officer.

Mr D. B. Carlisle and Mr G. R. Forster were appointed to the staff of the Plymouth laboratory in October 1951, in the grade of Scientific Officer.

Dr W. R. G. Atkins, O.B.E. (Mil.), F.R.S., was appointed a Commander of the Order of the British Empire in the King's Birthday Honours.

Dr D. P. Wilson has been awarded the Prix Georges Kohn 1951 of the Institut Océanographique, Paris.

Dr L. H. N. Cooper attended the Ninth General Assembly of the International Union of Geodesy and Geophysics in Brussels in August 1951, and the thirty-ninth meeting of the International Council for the Exploration of the Sea in Amsterdam in October 1951.

Occupation of Tables

The following one hundred and five workers have occupied tables at the Plymouth laboratory during the year:

E. ADAMS, Plymouth (Library).
Dr DAPHNE ATKINS, London (Biology of *Pinnotheres*).
Dr and Mrs G. BACCI, Naples (Sex reversal in *Ophryotrocha*).
R. BAINBRIDGE, Oxford (Plankton interrelationships).

Miss D. BALLANTINE, Development Commission (Taxonomy and culture of marine Flagellates).
A. C. G. BEST, London (General).
Dr ANNA M. BIDDER, Cambridge (Digestion in Cephalopods).
Prof. R. BIEBL, Vienna (Algal physiology).
L. BIRKETT, Lowestoft (Bottom sampling).
Dr H. BLASCHKO, Oxford (Amine oxidase in *Octopus* liver).
Dr B. P. BODEN, Cape Town (Phytoplankton and Euphausians).
B. B. BOYCOTT, Oxford (Brain and behaviour of *Octopus*).
L. R. BRIGHTWELL, Peacehaven (Experiments with *Eupagurus*).
Dr E. M. BROWN, London (Parasitic Dinoflagellates).
Dr EDITH BULBRING, Oxford (Amine oxidase in *Octopus* liver).
A. BURSA, Kenton (Dinoflagellates).
M. J. CANNY, Cambridge (Algae).
D. B. CARLISLE, Oxford (Endocrinology of Ascidians and *Leander*).
Dr G. S. CARTER, Cambridge (Library).
R. J. CHAPPELL, Penzance (Library).
Dr P. CHILDS, Plymouth (Gall bladders of fishes).
Dr P. N. J. CHIPPERFIELD, Brixham (Library).
I. G. CHRISTIE, London (General).
R. B. CLARK, Glasgow (Swimming in Polychaetes).
Dr G. L. CLARKE, Woods Hole (General).
Miss M. COLLIS, London (*Sabellaria*).
R. H. COOK, Cambridge (General).
H. COPLEY, Kenya (General).
C. A. COSWAY, Torquay (Library).
T. R. COWPER, Reading and C.S.I.R.O., Australia (Fisheries methods).
Dr D. J. CRISP, Brixham and Bangor (Library).
R. I. CURRIE, National Institute of Oceanography (Oceanography).
J. H. ELGOOD, Nigeria (Library).
D. ETHERINGTON, London (Sporozoa in marine annelids).
Dr MARIA FELINSKA, Cheltenham (Ciliates).
L. R. FISHER, Reading (Vitamin A in marine animals).
G. R. FORSTER, D.S.I.R. (Biology of prawns).
Cdr R. H. C. F. FRAMPTON, R.N. (Rtd.), Plymouth (Library).
Dr VERA FRETTER, London (Molluscs).
W. J. GODBEY, Cardiff (Architecture of Marine Stations).
P. HANSEN, Copenhagen (Library).
Dr T. J. HART, National Institute of Oceanography (Plankton).
G. A. HASWELL, London (Library).
Dr M. N. HILL, Cambridge (Geology of the English Channel).
Dr W. HOLMES, Oxford (Interrenal and adrenal bodies).
G. A. HORRIDGE, Cambridge (Annelid nervous systems).
Surg. Cdr (D) D. C. HOWE, R.N., Plymouth (Library).
G. HOYLE, London (Neuromotor activity of *Phallusia*).
O. D. HUNT, Newton Ferrers (Fouling organisms).
R. F. HUTTON, Miami (Fulbright Scholar) (Parasitology).
L. A. J. JACKMAN, Paignton (Library).
L. W. G. JONES, Brixham (Library).
W. C. JONES, Cambridge (*Leucosolenia*).
W. E. JONES, Aberystwyth (Ecology of *Gracilaria*).

Dr ELIZABETH M. KAMPA, Cambridge (Retinal pigment in fish).
R. S. KEIR, Development Commission (Development of Lamellibranchs).
G. KERKUT, Cambridge (Nervous systems of *Astropecten*).
Miss J. KERSLAKE, London (Ectocarpaceae).
Prof. W. B. R. KING, F.R.S., Cambridge (Geology of the English Channel).
Major B. G. KINLOCH, Uganda (General).
K. KOLSTAD, Oslo (Ecology of *Patella* species).
M. E. KORN, London (Cucumarians).
Miss P. KOTT, Australia (Biology of Tunicates).
Dr MARIE V. LEBOUR, Cawsand (Decapod Crustaceans).
Prof O. E. LOWENSTEIN, Glasgow (Electrophysiology of elasmobranch labyrinth).
Dr A. G. LOWNDES, Wells (Entomostraca).
M. F. MAHMOUD, Manchester (*Scalpellum* and *Balanus*).
Dr SHEINA M. MARSHALL, Millport (Egg laying in *Calanus* and use of isotopes).
A. J. MATTY, Nottingham (Elasmobranch endocrinology).
P. A. MAYES, London (Osmotic relations of *Littorina* species).
R. MAYNE, Plymouth (Library).
P. B. MCFARLANE, Cambridge (Geology of the English Channel).
Prof. N. MILLOTT, Jamaica (Melanin formation in invertebrates).
Miss M. MORRIS, Australia (Diurnal rhythms in luminescence).
J. E. MORTON, London (Marine Pulmonates).
B. S. NEWELL, Colonial Fisheries (Analysis of sea water and oceanographic methods).
Miss L. M. NEWTON, British Museum (Natural History) (Algae).
O. NORDLI, Florø, Norway (Phytoplankton).
Dr W. OHLE, Germany (Chemistry of sea water).
Dr A. P. ORR, Millport (Egg laying in *Calanus* and use of isotopes).
Prof. J. H. ORTON, F.R.S., Liverpool (*Patella*).
A. H. PAPWORTH, Northampton (General).
Miss G. D. PARRY, Cambridge (Ionic regulation in prawns).
Prof. E. PERCIVAL, New Zealand (General).
Prof. J. E. G. RAYMONT, Southampton (General).
Miss B. RICKARD, Plymouth (Library).
T. R. ROBERTS, Plymouth (Library).
G. A. ROBINSON, Development Commission (Phytoplankton).
D. J. ROCHFORD, Australia (General).
J. B. ROGERS, Admiralty (Oceanographic apparatus).
L. SÖMME, Oslo (Culturing of *Ulva*).
Dr A. J. SOUTHWARD, Port Erin (Intertidal ecology).
B. W. SPARROW, Newton Ferrers (Fouling organisms).
Dr C. P. SPENCER, Bangor (Physiology of diatoms).
Miss F. A. STANBURY, Plymouth (*Cladophora*).
Dr M. F. SUTTON, London (Regeneration in *Ciona*).
H. TEBBLE, British Museum (Natural History) (Polychaetes).
Miss M. TREHARNE, Plymouth (Library).
Miss B. C. UPTON, London (Methylene blue staining in Polychaetes).
B. WATTS, Watford (General).
Dr G. P. WELLS, London (*Arenicola*).
G. L. WILKINS, British Museum (Natural History) (Molluscs).
R. F. WRIGHTON, Birmingham (General).
H. V. WYATT, Plymouth (Littoral ecology).

During the year there have been a large number of short visits made by scientists to discuss problems with members of the staff, or see the work of the laboratory. Among these the following research workers from overseas have made visits: B. Ulrich, Düsseldorf; Dr and Mrs Gorbman, Columbia University; Dr C. S. Piggott, U.S. Embassy; Dr R. S. Dietz, U.S.N. Hydrographic Department; Dr Vera Koehring, New York; J. Lyman and T. S. Austin, U.S.N. Hydrographic Department; L. B. Mendel, Cape Town; V. Worthington, D. J. Owen, J. Hahn and C. Iselin, Jr., Woods Hole; Dr A. von Brandt, Hamburg; Prof. Hans Brattström, Bergen; Prof. K. Hidaka, Tokyo; Miss H. I. Jørgensen, Copenhagen; Dr L. R. Donaldson, Seattle.

The U.S. Research Ship *Albatross III* visited Plymouth during September 1951, working from Woods Hole under the scientific leadership of Mr V. Worthington.

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin, and were attended by 42 students from the following Universities and University Colleges: Oxford, Cambridge, London, Birmingham, Liverpool, Leeds, Sheffield, Belfast, Nottingham, Newcastle, Southampton, Aberystwyth, Bangor and Cardiff.

Also during the Easter Vacation Mr K. G. Messenger and Mr I. G. StC. Pringle brought seven boys from Uppingham School and Mrs M. E. Allen seven from the Bec School, London.

Scientific Work of the Plymouth Laboratory Staff

Physics and Chemistry of Sea Water

A survey has been made of the surface temperatures and the mean temperature of the water column at Station E 1 for each year since 1921 to 1949, both included, but with a war gap. The maximum column-temperature 15·97° C. was in 1949, followed by 15·43° C. in 1921, and the maximum sunshine was also in 1949, but there was no obvious relation between hours of sunshine, or vertical illumination, and water temperature in the other years. Wind force and evaporation are important factors difficult to assess, but Dr W. R. G. Atkins and Miss P. G. Jenkins have, as a first step, tabulated the difference between the mean monthly vapour pressure of the air, as given by the Meteorological Office and the vapour pressure of the surface water of the sea. The excess pressure of the sea is extremely irregular, but is usually least in summer, which suggests that cooling by evaporation is then at a minimum.

The daylight records for 1947–9 are being published by the Royal Meteorological Society, who have also recently published measurements of the apparent transmission of light through clouds, made by Dr Atkins during the war, using observations on cloud thickness and height obtained by the Officers of the Meteorological Flight of the Royal Air Force at Bircham Newton in Norfolk. The relevant daylight charts were got using a sodium cell

no longer on the market; tests are accordingly being made on the stability of another emission cell as probably preferable to the selenium rectifier cell which has, even in England, only a quite limited period of stability.

The work on the scattering of light in natural waters and its variation with angle of incidence has now been prepared for publication by Dr H. H. Poole and Dr Atkins; equipment has been assembled for following this variation through the spectrum.

Dr L. H. N. Cooper has continued his examination of hydrographical records from the Celtic Sea collected during the last 40 years and has published three papers in Volume xxx, No. 3 of the *Journal*.

In one he has described the physical and chemical oceanography of the water bathing the continental slope of the Celtic Sea. The extension of the Gulf of Gibraltar water into the Eastern North Atlantic is very variable both in space and time and, at a given position, very large changes in temperature and salinity may occur in a few months. South-west of Ireland at around 800–1000 m. there is a fluctuating conflict between this Gulf of Gibraltar water deficient in oxygen (65–68% saturated) and well oxygenated (>85%) cascaded water from the north, probably from the Rockall Table Mount. Between 1000 and 2000 m. depth south of the Celtic Sea a decrease in phosphate content of at least 0·2 μg.-atom/l. seems to have occurred between 1930 and 1950.

The properties have been outlined of a number of recognizably different water masses in the ocean near the continental slope. The vertical structure of these waters in June 1914 has been derived from observations by the Norwegian vessel *Armauer Hansen*. The deep water observations made by R.R.S. *William Scoresby* and R.R.S. *Discovery II* on behalf of the Plymouth laboratory have been worked up.

In the second paper Dr Cooper has described his hypothesis of 'capsizing' of water masses over a continental slope in high on-slope winds. Such a process would be powerful enough to produce the observed distribution of properties in the ocean abreast of the slope. Although it is compatible with the observations available here, much more work is needed to prove it. Attention has been focused on the importance of the topography of the continental slope in studies of the exchange of water masses and their nutrient resources between the deep ocean and the continental shelf. On the basis of the distribution of temperature and salinity, the existence of a submarine canyon in the continental slope was predicted at 50° 30′ N., 11° 00′ W. This canyon has been sought by H.M. Survey Ship *Cook* and found at the position forecast. The success of this prediction will now allow the publication of other work on water movements over the slope, which has had to be held up for confirmation of certain debatable points.

The silicate analyses obtained in 1950 have allowed the preparation of a paper in which the chemistry of silicate in sea water has been re-examined.

In December 1950 a hydrographical investigation was made of water movements along the South Devon coast in connexion with the occurrence of herring off Plymouth.

The monthly cruises to Station E 1 and routine determinations of phosphate, total phosphorus and silicate have been continued by Mr F. A. J. Armstrong. Samples taken by Dr Cooper on two short cruises in December 1950 have also been analysed. In June and July 1951, samples were taken in the Teign estuary and analysed to assist Prof. J. H. Orton in his studies on *Patella*.

Methods of determining and analysing the suspended matter in smaller samples have been developed, and it has been found practicable to use samples of about 2 litres, which may be collected with a Nansen-Pettersen bottle. Seasonal changes at Station E 1 are being studied by these methods.

Plankton

Estimations of the chlorophyll content of water at Station E 1 have been resumed by Dr Atkins. Using the Unicam spectrophotometer it is possible to get a good spectral absorption curve from as little as one litre of surface or deep water even in late autumn.

Dr H. W. Harvey, in collaboration with Dr C. P. Spencer of the Bangor Marine Biological Laboratory, has continued investigating the uptake of nitrogen compounds by *Nitzschia closterium*, the formation of plant pigments, and the rate of growth.

Ammonia nitrogen is utilized and built up into organic nitrogen by nitrogen deficient cells as rapidly in darkness as in the light, nitrate nitrogen less rapidly, and nitrite nitrogen very slowly or not at all, whereas it is utilized as rapidly as ammonia or nitrate nitrogen in the light. This suggests that nitrate is not reduced via nitrite in the plant in darkness, the nitrite stage in the reduction of nitrate to ammonia being by-passed. An account of a rapid method of determining microgram quantities of organic nitrogen in plant and animal tissue has been published in the *Analyst*.

The synthesis of chlorophyll *a* and other pigments by *Nitzschia* stops during the growth of a culture where the available nitrogen in the medium is exhausted or nearly exhausted, while cell division continues with the formation of nitrogen and chlorophyll deficient cells. When available nitrogen is supplied to these deficient cells, synthesis of chlorophyll can take place in darkness. The quantity of chlorophyll and other pigments per cell is greater in diatoms grown in dim light than in bright light, that is, at light intensities comparable to those at depths of 30 m. and of 10 m. respectively in the open sea on a bright day with the sun obscured by cloud. Preliminary experiments show that the effect of changing the light intensity during the exponential growth of the diatom is complex.

Much time has been devoted to improving technique for estimating the increase in number of diatoms (mean time per division) during growth in

bacteria-free culture under conditions of constant light, temperature and aeration. Dr Spencer's observations, some of a preliminary nature, are showing the following trends. Provided the diatom has become adapted to the environment, growth proceeds at an exponential rate, which is remarkably constant from experiment to experiment, until the limiting nutrient in the medium is exhausted; then the rate gradually decreases until a stationary stage is reached. This exponential rate is the same whether the diatoms are supplied with ammonium, nitrite or nitrate, and is the same over a wide range of hydrogen ion and bicarbonate concentrations, and is similar over a wide range of light intensities.

When the diatoms have not become adapted to the environment, the exponential rate tends either to be irregular, or, as in many experiments, to change suddenly to a lesser exponential rate which remains constant until one or other of the inorganic requirements are exhausted in the medium.

Preliminary experiments show that periods of darkness during the growth of the culture have no effect on the rate of cell division during the illuminated periods, provided the supply of carbon dioxide is not limiting.

When a medium is inoculated with the diatoms there is a lag before cell division starts. This lag period is constant from experiment to experiment, when the inoculum has been growing exponentially in a medium which is not deficient in a nutrient. The period is less when the diatoms are subcultured into a medium containing ammonia, than when they are subcultured into one containing nitrate or nitrite as nitrogen source. When the inoculum is taken from a culture in which the nitrogen source has become exhausted, that is, consisting of cells which are nitrogen deficient, the lag period is lengthened progressively with the nitrogen deficiency of the cells. The length of the lag period rises until the cells of the inoculum have reached the point of maximum deficiency and thereafter remains constant for a period of some days. Further increase in the length of the lag period occurs only after storage of the inoculum cells for considerable periods. During the lag period the cells synthesize both organic nitrogen and chlorophyll.

It is the final aim of this investigation to relate culture experiments to the growth of phytoplankton in the sea; their adaptation to varying light intensity and temperature, and the effect upon them of those traces of unknown substances which render waters from different localities fertile or infertile to the growth of particular species.

Over 100 different plant organisms, mainly flagellate forms, are now being maintained by Dr Mary Parke in species-pure cultures in addition to many mixed cultures containing organisms of interest awaiting isolation. A study of some new members of the Chrysophyceae with three flagella is in progress. During the year cultures for research purposes have been sent successfully by air to U.S.A., Norway, Italy and France. A large number of cultures have also been sent to institutions in this country.

Miss D. Ballantine, on a Development Commission Fisheries Research Training Grant, has been studying the effects of different salinities and of artificial sea water on cultures from the stocks maintained by Dr Parke. Over eighty-five different forms have been used, and although these have been maintained for over six months very little difference beyond the normal variation within a species has been found. The density of the organisms in the cultures did, however, vary considerably.

Miss Ballantine is also making a comparative study of the methods of estimation of numbers of flagellates in a unit volume of water, and preparing descriptions of three new species of dinoflagellates.

Mr F. S. Russell has re-examined a number of samples of the copepod *Calanus* from the collections on which his earlier observations on the vertical distribution and biology of the species have been based. It can be stated that the published results refer to the form *helgolandicus*, the more northerly form *finmarchicus* having occurred only in small numbers in the catches. A short account of this revision has been published in Volume XXX, No. 2 of the *Journal*.

Mr Russell has also succeeded in rearing to maturity some specimens of the rare medusa *Gonionemus*. These were kindly sent, while being budded off from the hydroid, by Dr H. O. Bull, who found them in the tanks of the Dove Marine Laboratory, Cullercoats.

Mr P. G. Corbin's inspection of the 1951 weekly half-hour oblique hauls with the 2 m. stramin ring-trawl shows no major change in the macroplankton production of this area from the low level prevailing during recent years. The report for 1949 was published in Volume XXX, No. 2 of the *Journal*.

Fauna and Flora of the Sea Floor

Having been invited by the Comité de Perfectionnement, Institut Océanographique, Paris, to submit for the Prix Georges Kohn 1951 a paper on the influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, Dr D. P. Wilson has written a memoir in which is included an historical survey of the literature relating to this subject. Much of the memoir is, however, based on his work with the larvae of *Ophelia bicornis* and contains a long and detailed account of three seasons' experimental work with this species. The geographical distribution of *Ophelia bicornis* and its local distribution in the Exe estuary is considered in relation to the factors, so far as they are known, which influence settlement. Observations on the wettability of some sands are also included. The memoir has been published in the *Annales de l'Institut Océanographique*.

Since this memoir was completed a further series of experiments with the larvae of *Ophelia bicornis* have been made. These have yielded results which are expected to throw further light on the main problem when they have been critically studied.

Mr G. M. Spooner has continued his studies on amphipod crustaceans.

During a visit to the British Museum the greater part of the *Gammarus* material from British, N. European, and Arctic waters was examined and much of it re-identified. Following the publishing of a paper on *G. zaddachi oceanicus*, another dealing with the two other arctic forms, *G. setosus* Dementiera and *G. wilkitzkii* Birula, is in preparation. Both of these are valid species. Overlooked characters have to be pointed out. The latter species is more different from the temperate *G. zaddachi* than has been supposed.

An identification key for British species of *Gammarus* has been prepared.

The amphipod faunas of the trawling grounds, where these animals form an important element in the diet of bottom-feeding fish, are receiving attention. In addition to the detailed recording of amphipods in quantitative bottom samples and in the stomachs of young rays, a regular examination has been made of the fauna lodging amongst coils of *Chaetopterus* tubes and on the carapaces of spider crabs.

A watch has been kept by Mr Spooner on the westward spread of the mollusc *Crepidula fornicata* (American slipper limpet) into the Plymouth area, and of the grass *Spartina townsendii*, which is now well established in the estuaries of the Avon, Erme, Tavy, Tamar, and Lynher rivers.

A re-examination of the species of sessile Scyphomedusae (Lucernariidae) in the Plymouth area has been started by Mr P. G. Corbin. From preliminary work it appears that the existing list is in need of revision.

Dr Mary Parke's revision of the late Mr G. F. Tregelles's manuscript on the marine algae of Devon has now been completed and is in the press (being published as an appendix to the *Transactions of the Devonshire Association*).

In addition Dr Parke has compiled a preliminary Check List of the British marine algae which includes the plant divisions Cyanophyta, Chlorophyta (Chlorophyceae), Chrysophyta (Xanthophyceae), Phaeophyta and Rhodophyta. Miss D. Ballantine has assisted Dr Parke with some of the work involved in the production of the Check List.

Dr H. G. Vevers has continued to use his underwater photographic apparatus in a quantitative survey of the epifauna on the trawling and dredging grounds in the Plymouth area. He has published a paper in Volume xxx, No. 1 of the *Journal*, which describes the apparatus and its mode of operation, and gives the first results obtained. It has been found that the dense aggregations of *Ophiothrix fragilis* photographed on some grounds are not of seasonal occurrence, but represent constant populations, which can be found at any time of the year. Further work is being done on the biology of these populations, in which the average density of the brittle-stars may be more than 100 individuals per square metre in certain places. A start has also been made on a photographic survey of the rich rocky bottom area near the Mewstone. Further improvements are being made in the design of the photographic apparatus.

In his work on the pigmentation of marine animals Dr Vevers has completed

a preliminary study of the carotenoids in the integument of dark brown specimens of *Asterias rubens*, published in Volume xxx, No. 3 of the *Journal*, and is now working on the pigmentation of other colour phases of this species. In the dark brown specimens the main pigment is esterified astaxanthin, most of which is present in the form of a carotenoid-protein complex.

Mr N. A. Holme has been continuing work on the 'biomass' of the bottom fauna in the Plymouth area. Material collected at twenty stations during 1950 has been examined, particular attention being paid to possible sources of error in the collection and subsequent treatment of samples. A sample covering $\frac{1}{2}$ m.^{2} is sufficient for a qualitative evaluation of the fauna, but few species are sufficiently dense for an adequate estimation of their numbers in a sample of this size. The total figures for the quantity of living matter are of the same order (*c.* 50 g. fresh weight per m.^{2}) at each station, so that the results will enable long-term changes in density to be followed. Several species, previously common, are now absent or rare; this may be correlated with the hydrographic changes which occurred in the early thirties. A new record for the area is of a species of *Glossobalanus* (Enteropneusta), three specimens being taken by the bottom-sampler in the neighbourhood of the Eddystone. This species probably produces the tornaria larvae which are found in the Plymouth plankton from time to time.

Collections of *Ensis*, together with the sand they inhabit, have now been made on most of the suitable beaches of south Devon and Cornwall; other samples have been obtained from the Scilly Isles, Jersey, and Milford Haven. The soils have been mechanically graded by sieving and rates of sedimentation and some correlation was found between the type of soil and the distribution of the three species. The species inhabit a fairly wide range of sands, *E. arcuatus* showing a marked preference for coarser soils. *E. siliqua* and *E. ensis* inhabit similar grades of sand, but the former is typically a shore or shallow water species, while the latter is typically an offshore species. Clearly there are many other factors besides soil grade affecting distribution, one of the most puzzling being that of depth; differences in soils at varying depths are insufficient to explain this.

Mr G. R. Forster has completed his paper on the breeding and growth of *Leander serratus*, which was published in Volume xxx, No. 2 of the *Journal*, together with a note on the biology of *Leander squilla*.

Observations on the behaviour of *Leander* spp. have been continued in the laboratory and in the field, the chief problem being to ascertain the nature of the orientation which these animals use during their tidal and diurnal migrations. Both vision and current perception appear to be employed, possibly linked with an internal rhythm in activity.

The Admiralty has been kind enough to allow Mr Forster to take a course in shallow water diving with the Royal Navy. With the co-operation of the Diving School, H.M.S. *Defiance*, preliminary underwater observations have

been made. These showed that several animals, notably *Cerianthus lloydii* and *Myxicola infundibulus* are very abundant beyond the *Laminaria* zone in the Sound, although they have very rarely been taken by dredging. It is hoped to make a survey of shallow water sublittoral communities by direct observation when diving apparatus is available.

Physiology of Marine Animals

Dr J. S. Alexandrowicz has investigated tumours noticed by Mr G. A. Steven in a specimen of the red mullet (*Mullus surmuletus*). These tumours proved to be a manifestation of the Lymphocystis disease regarded as resulting from infection by a virus agent. Special attention has been given to the inclusion bodies in the growing tumour cells which have been considered to represent the agglomeration of the virus substance. The transformations of these inclusion bodies observed in certain cells are interpreted as stages in the life cycle of the virus agent during which it presumably acquires the ability to transmit the infection. The results have been published in Volume xxx, No. 2 of the *Journal*.

In continuation of his investigation on the muscle receptor organs in crustaceans, Dr Alexandrowicz has examined these organs in the thoracic region of *Homarus vulgaris* and *Palinurus vulgaris*. It has been found that, apart from elements belonging to the same category as those previously reported from the abdomen, there are in the thorax nerve cells of a different kind which are also connected with certain muscles. The results are nearly ready for publication.

The first part of the observations on the nervous system in stomatopods has been prepared for publication. It deals with the system of median connectives homologous to the so-called unpaired nerve in insects. It has been shown that in *Squilla mantis* it is in relation with the large blood sinuses and contains two sorts of nerve fibres: one of these comprises motor elements; it is suggested that the other may have a neurosecretory function. An account of this work is being published in the *Pubblicazioni della Stazione Zoologica di Napoli*.

In a series of investigations Dr J. A. C. Nicol has been able to trace the neuronal organization and pathways of certain giant nerve fibres in various polychaete worms. These histological studies have laid a firm foundation for carrying out physiological experiments and interpreting the results. In *Branchiomma vesiculosum* the giant axon system has been utilized to investigate the action of various pharmacological agents in the neuromuscular junction. Although essentially cholinergic it has been found that this junction is not blocked by atropine and D-tubocurarine. It thus stands in marked contrast to the conditions encountered in hirudineans and vertebrates, in which curare has a paralyzing effect on locomotory muscles, and points to the existence of some diversity in receptor surfaces concerned with neuro-

muscular transmission in the annelid phylum. This work has been accepted for publication in *Physiologia Comparata et Oecologia.*

Dr Nicol has also begun a series of investigations on the physiology of luminescence in marine animals, and attention has first been focused on the polychaete *Chaetopterus variopedatus*. In this animal the production of light is due to the secretion of a luminescent material from certain restricted regions of the body, especially from glands on the aliform notopodia and in notopodia of the posterior regions. The glandular elements responsible have been identified as densely staining eosinophilic epithelial cells. By the use of recording apparatus consisting of a multiplier photocell and string galvanometer or oscilloscope it has been possible to obtain photographic records of the luminescent response, although the absolute intensity of the light is very low. These studies have shown that the luminescent response is under nervous control, and light is produced only as the result of external stimulation. The light glands, under electrical stimulation, display some of the characteristics of muscular effector organs, in that fatigue, summation, and a sustained response can be obtained. Additional studies have involved the action of unbalanced ionic solutions and pharmacological agents on the light glands. Two accounts of this work have been published in Volume xxx, No. 3 of the *Journal.*

Dr J. Lowy has made a detailed investigation of the mechanism of tonic contraction in lamellibranch muscle. The spontaneous electrical and mechanical activity in the intact posterior adductor muscle of *Mytilus edulis* is recorded continuously with the animal in water or exposed to air. Records of phasic contraction of the muscle when the animal is in water show that the speed of relaxation can be 'accelerated' and evidence from experiments with adductor muscle preparations suggests that this may be due to the action of inhibitory nerves. Both phasic and tonic contraction of the muscle is accompanied by electrical activity and when the load supported by the muscle is increased the frequency of electrical activity also increases. The results obtained in these experiments lead to the conclusion that the *Mytilus* muscle cannot maintain a steady state of contraction without expenditure of energy.

It was also found that during the course of normal tonic contraction the frequency of electrical activity decreases progressively with time whereas the speed of relaxation after a period of tonus does not decrease. These observations point to the possibility that the 'viscosity' of this type of muscle may be increased by motor and decreased by inhibitory nerve impulses. This hypothesis is now being tested by Dr Lowy in experiments with preparations of the retractor muscles of *Mytilus*, the adductor muscles of *Mya arenaria* and the two portions of the adductor muscle of *Pecten*. It is hoped to publish a complete account of the results in the near future.

Mr D. B. Carlisle has continued work started in Oxford and Naples concerning the endocrinology of the pituitary of ascidians and that of the

eyestalks of crustaceans, especially with regard to the physiology of moulting and of sex.

Fish and Fisheries

A third paper—on age and growth rate—has been completed by Mr G. A. Steven in continuation of his work on mackerel biology. Owing to difficulty of age determination in this fish the age and growth had not previously been satisfactorily determined. Two schools of thought arose, one attributing a length of little over 10 cm. at the end of the first year of life while the other ascribed lengths of up to 25 cm. to 1-year-old fish. Mr Steven's results provide firm support for the second school. Direct age readings from scales and otoliths have been made of fish up to 6 years of age, and the probable sizes at greater ages have been calculated. It would seem that mackerel have a normal life span of 20 years or more.

The possibility of forecasting fishing prospects in the Cornish deep sea fishery is now being investigated, with promising initial results. Purely tentative assessments indicate that the prospects for good fishing in 1952 are in the order of 14 as against 1 for 1950 and 21 for 1949. No suitable data upon which to assess the 1951 prospects were obtained. Unfortunately this fishery is so greatly influenced by marketing conditions that actual yields may have little relation to natural stocks.

A beginning has also been made with a trawling survey of grounds in the vicinity of Plymouth for comparison with exactly comparable surveys made in 1913–14 and in the early 1920's. It is too early yet to draw firm conclusions from this work; but preliminary trends suggest present catches to be poorer than those of the 1920's but better than those of the 1913–14 period.

Mr P. G. Corbin has continued the collection of sand-eels with a trawl fitted with a fine mesh cover on the cod-end. Good samples of two off-shore species, *Ammodytes immaculatus* and *Gymnammodytes semisquamatus*, have now been accumulated and from this material it is hoped to be able to work out something of their life histories.

Mr P. G. Corbin, in collaboration with Mr G. A. Steven, has continued the development and trials of the new type of ringless conical net referred to in last year's Report of the Council. A full scale model 30 ft. (*c.* 9·1 m.) in diameter and 90 ft. (*c.* 27·5 m.) long, has now been delivered from the makers. Trials will be started as soon as the rigging of the net is finished.

In addition to an attempt to fill a gap in our knowledge of the life histories of food fishes by capturing the small fast-swimming stages, one of the original objectives has been to design a large pelagic net to fish in oceanic depths for some of the larger organisms known to be present, but which have hitherto escaped capture in any numbers. For this, a large net is required which is at the same time convenient to handle: it will also be necessary to fish the net at some speed. There will be a high frictional drag on a large conical net and

a strong lifting effect which will increase rapidly with increasing towing speeds. It seems improbable then that strictly horizontal hauls with a 30 ft. diameter conical net will be able to be made in deep water owing to the lift of a net of this size, although vertical and oblique hauls will be possible. Neither does the use of a depressor, or a series of depressors, seem to offer a practicable means of keeping down so large a net. A solution of the depth-keeping problem appears, however, to be within sight as a result of work by Mr Corbin on the design and development of a self-depressing version of the ringless net. An 8 ft. diameter (*c.* 2·4 m.) model has been used in performance trials and gave very efficient depression of a $1\frac{3}{4}$ in. circumference steel trawl warp when fishing at speeds up to 6 knots. The stability of the net and warp was not affected by towing in tight S-bends and turns. It is hoped to make further trials with a considerably larger model of this self-depressing net.

Further tests on preservatives for nets, trawl twines and ropes are being carried out by Dr Atkins and Mr F. J. Warren at Pier Cellars. Two of the newer preservatives have given good results on duplicate series of nets. None of the twines or ropes has failed as yet.

Library

The thanks of the Association are again due to many foreign Government Departments, to Universities and to other Institutions at home and abroad for copies of books and current numbers of periodicals either presented to the Library or received in exchange for the *Journal* of the Association.

Thanks are also due to those who have sent books or reprints of their papers, which are much appreciated.

Dr M. V. Lebour has most generously presented to the Library a valuable collection of reprints and books, including many works on parasitology, crustacea, mollusca and plankton, which will prove of great use to workers at the laboratory. Professor L. F. de Beaufort has been kind enough to arrange for the Library to receive all future Reports of the Siboga Expedition, to complete the set bequeathed to us by the late Sir Sidney Harmer.

The Library has again been much used by visiting members of the Association.

Published Memoirs

Volume XXX, No. 1, of the *Journal* was published in June 1951, No. 2 in October 1951 and No. 3 in February 1952.

The following papers, the outcome of work done at the laboratory, have been published elsewhere than in the *Journal* of the Association:

ABBOTT, B. C. & RITCHIE, J. M., 1951. The onset of shortening in striated muscle. *Journ. Physiol.*, Vol. 113, pp. 336–45.

ALEXANDROWICZ, J. S., 1951. Muscle receptor organs in the abdomen of *Homarus vulgaris* and *Palinurus vulgaris*. *Quart. Journ. Micro. Sci.*, Vol. 92, pp. 163–99 and 3 plates.

ATKINS, W. R. G., 1951. The relation between thickness of cloud layers and their transmission of light. *Quart. Journ. Roy. Met. Soc.*, Vol. 77, pp. 659–62.

ATKINS, W. R. G., 1951. Vitamin C reserves of British troops in England and Scotland during the winter and spring, 1941–42. *Brit. Journ. Nutrition*, Vol. 5, pp. 275–86.

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BACCI, GUIDO, 1949. Ricerche su *Asterina gibbosa* (Penn.). I. La migrazione delle gonadi. *Archivio Zool. Ital.*, Vol. 34, pp. 25–9.

BACCI, GUIDO, 1949. Ricerche su *Asterina gibbosa* (Penn.). II. L' ermafroditismo in una popolazione di Plymouth. *Archivio Zool. Ital.*, Vol. 34, pp. 49–73.

BATHAM, E. J. & PANTIN, C. F. A., 1951. The organization of the muscular system of *Metridium senile*. *Quart. Journ. Micro. Sci.*, Vol. 92, pp. 27–54 and plate.

BODEN, BRIAN P., 1951. The egg and larval stages of *Nyctiphanes simplex*, a euphausiid crustacean from California. *Proc. Zool. Soc. Lond.*, Vol. 121, pp. 515–27.

BRIGHTWELL, L. R., 1951. Some experiments with the common hermit crab (*Eupagurus bernhardus* Linn.), and transparent univalve shells. *Proc. Zool. Soc.*, Vol. 121, pp. 279–83.

CATTON, W. T., 1951. Blood cell formation in certain teleost fishes. *Blood, Journ. Hematology*, Vol. VI, pp. 39–60.

DULY, S. J., 1950. The corrosion of steel by sea salt of given moisture content. *Journ. Soc. Chemical Industry*, Vol. 69, pp. 304–6.

HANSON, JEAN, 1951. The blood-system in the Serpulimorpha (Annelida, Polychaeta). III. Histology. *Quart. Journ. Micr. Sci.*, Vol. 92, pp. 255–74.

HART, T. J. & MARSHALL, N. B., 1951. Breeding ground of pilchards off the coast of South-West Africa. *Nature*, Vol. 168, pp. 272–3.

HARVEY, H. W., 1951. Micro-determination of nitrogen in organic matter without distillation. *The Analyst*, Vol. 76, pp. 657–60.

HORRIDGE, G. A., 1951. Occurrence of *Asparagopsis armata* Harv. on the Scilly Isles. *Nature*, Vol. 167, pp. 732–3.

LOWENSTEIN, O. & ROBERTS, T. D. M., 1951. The localization and analysis of the responses to vibration from the isolated elasmobranch labyrinth. A contribution to the problem of the evolution of hearing in vertebrates. *Journ. Physiol.*, Vol. 114, pp. 471–89.

NICOL, J. A. COLIN, 1951. Giant axons and synergic contractions in *Branchiomma vesiculosum*. *Journ. Exp. Biol.*, Vol. 28, pp. 22–31.

NICOL, J. A. COLIN, 1952. Autonomic nervous systems in lower chordates. *Biol. Rev.*, Vol. 27, pp. 1–49.

NICOL, J. A. COLIN, 1952. Colours of marine animals. *School Sci. Rev.*, Vol. 33, pp. 208–18.

ORTON, J. H., 1952. Protandry with self-fertilization in the American slipper limpet, *Crepidula fornicata*. *Nature*, Vol. 169, pp. 279–80.

RUSSELL, F. S., 1951. The work of the Plymouth Laboratory of the Marine Biological Association of the United Kingdom. (Summary of Lecture.) *Annl. Repts. & Trans. Plymouth Inst.*, Vol. XXI, pp. 164–6.

RUSSELL, F. S., 1951. Hydromedusae: Families: Zancleidae, Cladonemidae and Eleutheriidae. *Cons. Int. Explor. Mer., Zooplankton*, Sheet 30.

RUSSELL, F. S., 1951. Hydromedusae: Families: Clavidae and Hydractiniidae. *Cons. Int. Explor. Mer., Zooplankton*, Sheet 31.

SEXTON, E. W. & REID, D. M., 1951. The life-history of the multiform species *Jassa falcata* (Montagu) (Crustacea amphipoda) with a review of the bibliography of the species. *Journ. Linnean Soc. London.*, Zool., Vol. XLII, pp. 29–91.

SPOONER, G. M., 1951. Distribution of British freshwater Amphipoda. *Nature*, Vol. 167, p. 530.

VEVERS, H. G., 1951. Sexual dimorphic colour characters in animals. *Endeavour*, Vol. X, pp. 183–7.

WELLS, G. P., 1951. On the behaviour of *Sabella*. *Proc. Roy. Soc.*, Ser. B, Vol. 138, pp. 278–99.

WELLS, G. P. & ALBRECHT, ELINOR B., 1951. The integration of activity cycles in the behaviour of *Arenicola marina* L. *Journ. Exp. Biol.*, Vol. 28, pp. 41–50.

WELLS, G. P. & ALBRECHT, ELINOR B., 1951. The role of oesophageal rhythms in the behaviour of *Arenicola ecaudata* Johnston. *Journ. Exp. Biol.*, Vol. 28, pp. 51–6.

WIESER, WOLFGANG, 1951. Untersuchungen über die algenbewohnende Mikrofauna mariner Hartböden. I. Zur Oekologie und Systematik der Nematodenfauna von Plymouth. *Österr. Zool. Zeit.*, Vol. 3, pp. 425–80.

WILSON, D. P., 1951. *Life of the Shore and Shallow Sea.* (2nd edition, revised.) London, Nicholson and Watson, 213 pp.

WILSON, D. P., 1951. Larval metamorphosis and the substratum. *Ann. Biol.*, T. 27, pp. 259–69.

WILSON, D. P., 1952. The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of *Ophelia bicornis* Savigny. *Ann. Inst. océanogr.*, Vol. 27, pp. 49–156.

Membership of the Association

The total number of members on 31 March 1952 was 659, being 47 more than on 31 March 1951; of these the number of life members was 84 and of annual members 575. The number of Associate members is six.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Capital Grant. The Council wish to record their thanks to the Development Commissioners for a capital grant to meet the cost of building the special laboratory for research with radioactive substances.

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

From the Fishmongers' Company (£425), the Royal Society (£50), British Association (£50), Physiological Society (£30), the Cornwall Sea Fisheries Committee (£10), the Universities of London (£210), Cambridge (£125), Oxford (£100), Bristol (£50), Birmingham (£31. 10*s.*), Leeds (£20), Durham (£10. 10*s.*), Manchester (£10. 10*s.*), Sheffield (£10. 10*s.*), Nottingham (£10. 10*s.*), Exeter (£10. 10*s.*), Leicester (£10. 10*s.*), Hull (£10. 10*s.*), Southampton (£10. 10*s.*), and the Imperial College of Science and Technology (£10).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1952–53

President

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

Vice-Presidents

The Earl of IVEAGH, C.B., C.M.G.
Viscount ASTOR
Sir NICHOLAS E. WATERHOUSE, K.B.E.
Col. Sir EDWARD T. PEEL, K.B.E., D.S.O., M.C.
G. P. BIDDER, Sc.D.
W. T. CALMAN, C.B., D.Sc., F.R.S.
Vice-Admiral Sir JOHN A. EDGELL, K.B.E., C.B., F.R.S.
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S.
E. S. RUSSELL, O.B.E., D.Sc.
Sir EDWARD J. SALISBURY, Kt., C.B.E., D.Sc., Sec.R.S.
Admiral Sir AUBREY C. H. SMITH, K.B.E., C.B., M.V.O.
A. T. A. DOBSON, C.B., C.V.O., C.B.E.
Major E. G. CHRISTIE-MILLER
MORLEY H. NEALE, C.B.E.
The Rt. Hon. Major Sir THOMAS L. DUGDALE, Bt., M.P.

COUNCIL

To retire in 1953

G. E. R. DEACON, D.Sc., F.R.S.
E. FORD
F. C. FRASER, D.Sc.
Prof. J. E. HARRIS, Ph.D.
Prof. C. M. YONGE, D.Sc., F.R.S.

To retire in 1954

J. S. COLMAN
H. CARY GILSON
Prof. ALASTAIR GRAHAM, D.Sc.
N. A. MACKINTOSH, C.B.E., D.Sc.
Prof. J. Z. YOUNG, F.R.S.

To retire in 1955

Prof. H. GRAHAM CANNON, Sc.D., F.R.S.
O. D. HUNT
Prof. O. E. LOWENSTEIN, Ph.D.
G. P. WELLS, Sc.D.
R. S. WIMPENNY

Hon. Treasurer

Major E. G. CHRISTIE-MILLER, 38 Hyde Park Street, London, W. 2

Secretary

F. S. RUSSELL, D.S.C., D.F.C., F.R.S., The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

G. P. BIDDER, Sc.D.
H. J. JOHNS, C.B., M.B.E. (Ministry of Agriculture and Fisheries)
The Worshipful Company of Fishmongers:
The Prime Warden
Major E. G. CHRISTIE-MILLER
HARRISON S. EDWARDS
Prof. A. C. HARDY, D.Sc., F.R.S. (Oxford University)
C. F. A. PANTIN, Sc.D., F.R.S. (Cambridge University)
EDWARD HINDLE, Sc.D., F.R.S. (British Association)
H. W. PARKER, D.Sc. (Zoological Society)
Prof. A. V. HILL, C.H., O.B.E., Sc.D., F.R.S. (Royal Society)

BALANCE SHEET 1951–52

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET 31ST MARCH 1952

31st March 1951		£	£
	CAPITAL RESERVE ACCOUNT:		
	As at 31st March 1951	32,688	
	Add: Grants received and receivable from the Development Fund in respect of cost to date of new Research Vessel	6,216	
32,688			38,904
	SURPLUS ACCOUNT:		
	As at 31st March 1951	6,903	
	Add: Excess of Income over Expenditure for the year	1,331	
6,903			8,234
39,591			47,138
	AQUARIUM SINKING FUND:		
	As at 31st March 1951	224	
	Add: Donations for rebuilding Aquarium Tanks ...	28	
224			252
		£	
	E. T. BROWNE BEQUEST FUNDS:		
	Library Fund, as at 31st March 1951	1,189	
	Add: Interest on Investment	36	
		1,225	
	Special Apparatus Fund, as at 31st March 1951	2,586	
	Add: Interest on Investment	81	
		2,667	
	Less: Expenditure during the year	34	
		2,633	
	Scientific Publications Fund, as at 31st March 1951	2,169	
	Add: Interest on Investment	61	
		2,230	
5,945			6,088
	ROYAL SOCIETY GRANT—PUBLICATION OF MONOGRAPH ON MEDUSAE OF BRITISH ISLES ...	750	
—	*Add:* Bank Deposit Interest credited during year	3	
			753
	COMPOSITION FEES FUND:		
	As at 31st March 1951	857	
	Add: Fees received during year	63	
857			920
	BUILDINGS RECONSTRUCTION FUND:		
	As at 31st March 1951	176	
	Add: War Damage Compensation receivable during year	792	
		968	
	Less: Expenditure during year	160	
176			808
	CURRENT LIABILITIES:		
890	Accrued Expenses, etc.	1,228	
180	Subscriptions and Grant received in advance	154	
—	First Instalment under Contract for Construction of new Research Vessel	5,894	
			7,276
£47,863			£63,235

31st March 1951		£	£
	FIXED ASSETS, at valuations as estimated by the Director at 31st March 1952:		
	Boats and Equipment:		
11,000	F.V. 'Sula'	11,000	
200	Motor Boat 'Gammarus'	200	
100	Nets, Gear and General Equipment	100	
11,300		11,300	
8,851	Laboratory Apparatus, Equipment and Machinery	9,315	
17,887	Library at valuation of Mr Ridgill Trout in January 1941, plus additions at cost	18,687	
38,038		39,302	
—	New Research Vessel (in course of construction). Cost to 31st March 1952	6,216	
38,038			45,518
232	**GENERAL FUND INVESTMENT** at Book Value £352. 2s. 3d. 2½ % Treasury Stock ... ... (Market Value £204. Last year £238)		232
5,795	**E. T. BROWNE BEQUEST FUND INVESTMENTS**, at cost £5901. 8s. 7d. British Transport 3 % Guaranteed Stock 1978/88 ... ... (Market Value £4544. Last year £5223)		5,795
	COMPOSITION FEES FUND INVESTMENTS, at cost:		
	£18. 8s. 6d. 2½ % Treasury Stock	16	
	£932. 15s. 9d. British Transport 3 % Guaranteed Stock 1978/88	888	
857	(Market Value £729. Last year £784)		904
	CURRENT ASSETS:		
	STOCKS ON HAND as valued by the Director:		
	Specimens 600		
	Chemicals 250		
	Journals 400		
1,250		1,250	
	SUNDRY DEBTORS:		
	Sale of Specimens, Journals, Nets and Hydrographical Gear 1,015		
	Recoverable Expenditure 70		
	War Damage Compensation receivable ... 140		
1,785		1,225	
89	**PREPAYMENTS**	65	
	BALANCE AT BANK AND CASH IN HAND:		
	Coutts & Co., London		
	Current Account 6,590		
	Deposit Account 753		
	7,343		
	Lloyds Bank Ltd., Plymouth 845		
	Cash in Hand 58		
(−183)		8,246	
			10,786

Notes:

1. The Association had a capital commitment at 31st March 1952 in respect of a new Research Vessel amounting to £112,000 which will be recoverable under a Development Fund Grant.
2. A grant of £1,620 from the Development Fund has been wholly expended on the construction of a laboratory for research with radio-active tracers.

£47,863

JOHN E. HARRIS
L. HARRISON MATTHEWS } *Members of the Council*

£63,235

REPORT OF THE AUDITORS TO THE MEMBERS OF THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM:

Capital expenditure on the erection of buildings on land held on lease from the War Department is excluded. Subject to the foregoing, in our opinion and to the best of our information and according to the explanations given to us, the above balance sheet and annexed income and expenditure account give a true and fair view of the state of the Association's affairs as at 31st March 1952, and of the excess of income over expenditure for the year ended on that date.

We have obtained all the information and explanations which to the best of our knowledge and belief were necessary for our audit. In our opinion the Association has kept proper books of account and the above mentioned accounts, which are in agreement therewith, give in the prescribed manner the information required by the Companies Act, 1948.

Norwich Union House
2, St Andrew's Cross
Plymouth
13th May 1952.

PRICE WATERHOUSE & Co.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT FOR THE YEAR ENDED 31ST MARCH 1952

Year ended 31st March 1951		£	£
17,275	SALARIES, including Association's contributions to Superannuation Scheme and National Insurance		20,321
12,828	LABORATORY AND BOATS' CREWS' WAGES, including National Insurance, contributions to Superannuation Scheme, War Bonus and Employer's Liability Insurance		15,716
765	UPKEEP OF LIBRARY		677
1,706	SCIENTIFIC PUBLICATIONS, *less* sales		1,692
	UPKEEP OF LABORATORIES AND AQUARIUM:		
479	Buildings and Machinery	734	
651	Electricity, Gas, Coal and Water	914	
1,159	Chemicals and Apparatus	1,148	
136	Insurances, Tithe, Ground Rent and Rent of Store ...	159	
587	Travelling Expenses	572	
74	Audit Fee	63	
764	Stationery, Postages, Telephone, Carriage and Sundries	867	
207	Specimens	247	
			4,704
	MAINTENANCE AND HIRE OF BOATS:		
633	Petrol, Oil, Paraffin, etc.	741	
1,486	Maintenance and Repairs to Nets, Gear and Apparatus	1,762	
224	Boat Hire, Collecting Expenses and Upkeep of Truck	176	
690	Insurances	659	
1,380	Hire of R.V. 'Sabella'	1,380	
			4,718
40	ENTERTAINMENT EXPENSES		47
35	BANK CHARGES		31
2,223	BALANCE, being Excess of Income over Expenditure for the year		1,331
£43,342			£49,237

Note: No provision is made for replacement of Fixed Assets.

Year ended 31st March 1951		£	£
	GRANTS AND TABLE RENTS:		
36,350	Ministry of Agriculture and Fisheries grant from Development Fund	42,000	
500	Fishmongers' Company	450	
1,273	Miscellaneous (including British Association £50, Royal Society £50, Physiological Society £30, Cornwall Sea Fisheries Committee £10, Universities of: London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s.* 0*d.*, Leeds £20, Durham £10. 10*s.* 0*d.*, Exeter £10. 10*s.* 0*d.*, Leicester £10. 10*s.* 0*d.*, Manchester £10. 10*s.* 0*d.*, Nottingham £10. 10*s.* 0*d.*, Southampton £10. 10*s.* 0*d.*, Hull £10. 10*s.* 0*d.*, Sheffield £10. 10*s.* 0*d.*, Imperial College £10, and Ministry of Works £104) ...	1,125	
			43,575
514	SUBSCRIPTIONS (excluding subscriptions received in advance)		540
65	FEES FOR TESTS OF MATERIALS		46
	SALES:		
2,350	Specimens	2,633	
410	Fish	680	
	Nets, Gear and Hydrographical Apparatus ...	1,168	
428	*Less:* Cost of Materials	730	
		438	
			3,751
31	INTEREST ON INVESTMENTS		36
6	SALE OF DR M. V. LEBOUR'S BOOK		5
7	SALE OF 'PLYMOUTH MARINE FAUNA'		2
	AQUARIUM:		
	Admission Fees	1,575	
	Sales of Guides and Postcards	114	
		1,689	
	Less: Maintenance of Building	17	
	Printing Guides and Tickets	130	
	Advertising	58	
	Food	107	
	Wages	95	
		407	
1,408			1,282
£43,342			£49,237

LIST OF GOVERNORS, FOUNDERS, MEMBERS, HONORARY AND ASSOCIATE MEMBERS

1952

GOVERNORS

The British Association for the Advancement of Science, *Burlington House, W.* 1
The University of Oxford
The University of Cambridge
The Worshipful Company of Clothworkers, 48 *Fenchurch Street, E.C.* 3
The Worshipful Company of Fishmongers, *London Bridge, E.C.* 4
The Prime Warden. (**Council,** 1886→)
Edwards, Harrison S., *Westhumble Lacey, nr Dorking, Surrey.* (**Council,** 1950→)
Christie-Miller, Major E. G., 38 *Hyde Park Street, W.* 2. (**Council,** 1941→; **Hon. Treasurer,** 1941→; **Vice-President,** 1951→)
The Zoological Society of London, *Regent's Park, N.W.* 8
The Royal Society, *Burlington House, Piccadilly, W.* 1
Ministry of Agriculture and Fisheries, 3 *Whitehall Place, S.W.* 1
Bayly, Robert (the late). (**Council,** 1896–1901)
Bayly, John (the late)
Browne, E. T. (the late). (**Council,** 1913–19; 1920–37)
Thomasson, J. P. (the late). (**Council,** 1896–1903)
Bidder, G. P., Sc.D., *Cavendish Corner,* 221 *Hills Road, Cambridge.* (**Council,** 1899→; **President,** 1939–45; **Vice-President,** 1948→)
The Lord Moyne, P.C., D.S.O. (the late). (**Vice-President,** 1929; 1939–45; **President,** 1930–39)
Allen, E. J., C.B.E., D.Sc., LL.D., F.R.S. (the late) (Honorary.) (**Council,** 1895–1942; **Secretary,** 1895–1936; **Hon. Governor,** 1937–42)

FOUNDERS

1884 The Corporation of the City of London, *The Guildhall, E.C.* 3
1884 The Worshipful Company of Mercers, *Mercers' Hall,* 4 *Ironmonger Lane, E.C.* 2
1884 The Worshipful Company of Goldsmiths, *Goldsmiths' Hall, Foster Lane, E.C.*2
1884 The Royal Microscopical Society, *B.M.A. House, Tavistock Square, W.C.* 1
1884 Bulteel, Thos. (the late)
1884 Burdett-Coutts, W. L. A. Bartlett (the late)
1884 Crisp, Sir Frank, Bart. (the late). (**Council,** 1884–92; **Hon. Treasurer,** 1884–88)
1884 Daubeny, Captain Giles A. (the late)
1884 Eddy, J. Ray (the late)
1884 Gassiott, John P. (the late)
1884 Lankester, Sir E. Ray, K.C.B., F.R.S. (the late). (**Hon. Secretary,** 1884–90; **President,** 1891–1929)
1884 Lord Masham (the late)

1884 Moseley, Prof. H. N., F.R.S. (the late). (**Chairman of Council**, 1884–88)
1884 Lord Avebury, F.R.S. (the late). (**Vice-President**, 1884–1913)
1884 Poulton, Prof. Sir Edward B., F.R.S. (the late). (**Council**, 1888–94)
1884 Romanes, Prof. G. J., LL.D., F.R.S. (the late). (**Council**, 1884–91)
1884 Worthington, James (the late)
1885 The 15th Earl of Derby (the late)
1887 Weldon, Prof. W. F. R., F.R.S. (the late). (**Council**, 1890–1901; representing British Association, 1901–5)
1888 Bury, Henry, *The Gate House*, 17 *Alumdale Road, Bournemouth West*
1888 The Worshipful Company of Drapers, *Draper's Hall, E.C.* 2
1889 The Worshipful Company of Grocers, *Grocers' Hall, Princes Street, E.C.* 2
1889 Thompson, Sir Henry, Bart. (the late). (**Vice-President**, 1890–1903)
1889 Lord Revelstoke (the late)
1890 Riches, T. H. (the late). (**Council**, 1920–25)
1892 Browne, Mrs E. T. (the late)
1898 Worth, R. H., M.Inst.C.E., (the late)
1899 The Earl of Iveagh, C.B., C.M.G., 11 *St James's Square, S.W.* 1. (**Vice-President**, 1929→)
1902 Gurney, Robert, D.Sc. (the late). (**Council**, 1932–5)
1904 Shaw, Joseph, K.C. (the late)
1909 Harding, Colonel W. (the late)
1910 Murray, Sir John, K.C.B., F.R.S. (the late). (**Council**, 1896–99; **Vice-President**, 1900–13)
1912 Swithinbank, H. (the late)
1913 Shearer, Dr Cresswell, F.R.S. (the late)
1913 Heron-Allen, E., F.R.S. (the late)
1918 Evans, George (the late). (**Hon. Treasurer**, 1915–31; **Vice-President**, 1925–33)
1920 McClean, Capt. W. N., 39 *Phillimore Gardens, W.* 8
1920 Lord Buckland of Bwlch (the late)
1920 Llewellyn, Sir D. R. (the late)
1921 Harmer, F. W. (the late)
1924 The MacFisheries, Ltd., *Ocean House, Pudding Lane, E.C.* 3
1924 Lady Murray (the late)
1925 The Institution of Civil Engineers, *Great George Street, Westminster, S.W.* 1
1925 Discovery Committee
1927 Bidder, Miss Anna M., Ph.D., *Cavendish Corner*, 221 *Hills Road, Cambridge*. (**Council**, 1948–51)
1933 Peel, Col. Sir Edward T., K.B.E., D.S.O., M.C., *c/o Messrs Peel and Co., Ltd. P.O. Box* 331, *Alexandria, Egypt*. (**Vice-President**, 1936→)
1938 Buchanan, Dr Florence (the late)
1945 Brown, Arthur W. W. (the late)

MEMBERS

* Life Members

1949 Abbott, B. C., *Biophysics Department, University College, Gower Street, London, W.C.* 1
1945 Aberdeen University Library, *The University, Aberdeen*
1934 Adam, Mrs K. M. G., 84 *Lasswade Road, Edinburgh* 9
1951 Adams, E., 2 *Woodford Crescent, Marsh Mills, Plympton, Devon*

1940 Adrian, Prof. E. D., O.M., M.D., D.Sc., LL.D., P.R.S., *St Chad's*, 48 *Grange Road, Cambridge*
1947 Affleck, R. J., *Snob's Creek Fish Hatchery, Private Mail Bag, via Alexandra, Victoria, Australia*
1949 Aleem, A. A., Ph.D., *Faculty of Science, Farouk I University, Moharram Bey, Alexandria, Egypt*
1950 Alexandrowicz, J. S., Ph.D., M.D., *The Laboratory, Citadel Hill, Plymouth, Devon*
1951 Allen, J. A., *Department of Zoology, The University, Glasgow, W.* 2
1952 Allen, Miss J. M., *Tenements Farm, Chipperfield, Herts.*
1949 Allen, Mrs M. E., 82 *Oaks Avenue, Worcester Park, Surrey*
*1927 Amirthalingam, C., Ph.D., 2 *Dickmans Path, Colombo, Ceylon*
1950 Arnold, D. C., *Fair Acre, Abbotskerswell, Newton Abbot, Devon*
1944 Ashby, D. G., 195 *Chesterton Road, Cambridge*
*1911 Viscount Astor, 3 *Elliot Terrace, Plymouth, Devon.* (**Vice-President**, 1911→)
*1929 Atkins, Miss D., D.Sc., *The Laboratory, Citadel Hill, Plymouth, Devon*
*1939 Atkins, W. R. G., C.B.E., Sc.D., F.R.I.C., F.Inst.P., F.R.S., *The Old Vicarage, Antony, Torpoint, Cornwall*
*1910 Atkinson, G. T., *Gresham House, Esplanade, Lowestoft, Suffolk*
1951 Atlantic Biological Station, *St Andrews, N.B., Canada*
1950 Attridge, J., 44 *Windermere Road, Muswell Hill, London, N.* 10

1948 Baal, H. J., 3 *Bel Royal Villas, Jersey, C.I.*
1950 Baerends, Prof. G. P., *Zoological Laboratory, Reitemakersrijge* 14, *Groningen, Holland*
1949 Bagenal, T., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Bahl, Prof. K. N., D.Sc., *Department of Zoology, The University, Lucknow, India*
*1952 Baily, Joshua L. Jr., 4435 *Ampudia Street, San Diego* 3, *Calif., U.S.A.*
1950 Bainbridge, R., 43 *Strathmore Avenue, Hull*
*1920 Baker, J. R., D.Sc., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1936 Baldwin, Prof. E., Ph.D. *Department of Biochemistry, University College, Gower Street, London, W.C.* 1. (**Council**, 1946–48)
1950 Ballantine, Miss D., *Priors Close, Cambo Place, Cullercoats, Northumberland*
1951 Bangor, Marine Biological Station, *University College of North Wales, Bangor, Caern*
1949 Barnard, E. E. P., 7 *Webster Gardens, Ealing, London, W.* 5
1939 Barnes, H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1939 Barrington, Prof. E. J. W., D.Sc., *Department of Zoology, The University, Nottingham*
1951 Barron, H., 65 *Sumerton Road, Belfast, N. Ireland*
1946 Barter, W. Y., 29 *Sea View Avenue, Plymouth, Devon*
1939 Bassindale, R., *Department of Zoology, The University, Bristol*
1946 Batham, Miss E. J., Ph.D., *Portobello Marine Biological Station, via Port Chalmers, Otago, New Zealand*
1950 Baughman, J. L., *Texas Game, Fish and Oyster Commission, Rockport, Texas, U.S.A.*
1939 Baxter, E. W., *Biology Department, Medical School, Guy's Hospital, London, S.E.* 1
*1929 Baylis, L. E., Ph.D., *Department of Physiology, University College, Gower Street, London, W.C.* 1

1934 Beadle, L. C., *Department of Biology, University College of East Africa, P.O. Box* 262, *Kampala, Uganda*
1928 Beer, G. R. de, D.Sc., F.R.S., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1950 Bell, Mrs E. B., *Solva, Glanford Road, Brigg, Lincs*
1947 Berrill, Prof. N. J., F.R.S. *Department of Zoology, McGill University, Montreal, Canada*
1947 Best, A. C. G., 6 *Station Road, Loudwater, High Wycombe, Bucks*
1948 Betts, Slade, 100 *Avondale Road, Bromley, Kent*
1903 Bidder, Col. H. F., *The Malting House, Nettlebed, near Henley-on-Thames, Oxon*
*1945 Bingley, F. J., *Flatford Mill Field Centre, East Bergholt, near Colchester, Essex*
1925 Birkbeck College, *Malet Street, London, W.C.* 1
1951 Birkett, L., *Fisheries Laboratory, Lowestoft, Suffolk*
1931 Birtwistle, W., 73 *North Street, Skibbereen, Co. Cork, Eire*
1947 Bishop, M. W. H., *Meadow Farm, Waterbeach, Cambs*
1945 Black, J. A., *Ash House, Caton, near Lancaster, Lancashire*
1947 Black, Miss M. K., *c/o F. Band, High Street, Benwick, March, Cambs*
1951 Blackburn, M., *C.S.I.R.O. Fisheries Division, Cronulla, N.S.W., Australia*
1930 Blaschko, Dr H., *Department of Pharmacology, South Parks Road, Oxford*
1952 Blaxter, J. H. S., *Pathside, Frithesden Copse, Berkhamsted, Herts*
1910 Bloomer, H. H., *Longdown, Sunnydale Road, Swanage, Dorset*
1951 Boden, B. P., Ph.D., *Bermuda Biological Station, St George's West, Bermuda*
1936 Bogue, Prof. J. Yule, D.Sc., *Heyscroft, Hartley Road, Altrincham, Cheshire*
1932 Bolitho, Capt. R. J. B., *Gorey, Jersey, C.I.*
1945 Boney, A. D., 1 *Whiteford Road, Mannamead, Plymouth, Devon*
*1933 Boschma, Prof. Dr H., *Rijksmuseum van Natuurlijke Historie, Leiden, Holland*
1947 Bossanyi, J., *Dove Marine Laboratory, Cullercoats, Northumberland*
1949 Braithwaite, E. R., *Research Department, Acheson Colloids Ltd., Prince Rock, Plymouth, Devon*
1940 Brambell, Prof. F. W. Rogers, D.Sc., F.R.S., *Department of Zoology, University College of North Wales, Bangor, Caern.* (**Council**, 1944–47, 1948–51)
1924 Brightwell, L. R., 1 *Edith Avenue, Peacehaven, Sussex*
1933 Bristol University, *Department of Zoology, Bristol*
1941 British Celanese Ltd., *Celanese House, Hanover Square, London, W.* 1
1948 British Cod Liver Oils (Hull and Grimsby) Ltd., *P.O. Box No.* 18, *Hull*
1939 British Ropes Ltd., *Western Avenue, Cardiff*
*1946 Brock, Mrs C. H., Ph.D., *Dept. of Agriculture, Downing Street, Cambridge*
1946 Brough, Prof. James, D.Sc., *Department of Zoology and Comparative Anatomy, University College, Newport Road, Cardiff*
1928 Brown, Miss E. M., Ph.D., 6 *Effingham Lodge, Surbiton Crescent, Kingston-on-Thames, Surrey*
1936 Brown, Herbert H., O.B.E., Ph.D., *Fisheries Division, F.A.O. of U.N., Viale delle Terme di Caracalla, Rome, Italy*
*1925 Bull, Herbert O., D.Sc., *Dove Marine Laboratory, Cullercoats, Northumberland*
1951 Burgess, G. H. O., *Department of Zoology, University College, Hull*
1920 Burne, R. H., F.R.S., *c/o Westminster Bank*, 329 *High Holborn, London, W.C.* 1
1948 Burrows, Mrs E. M., Ph.D., *Hartley Botanical Laboratories, The University, Liverpool* 3
1950 Bursa, A., *Oceanographic Institution, Woods Hole, Mass., U.S.A.*

1947 Burton, Miss J. M., 55 *Popes Grove, Twickenham, Middlesex*
1930 Burton, M., D.Sc., *British Museum (Natural History), Cromwell Road, London, S. W.* 7. (**Council**, 1936–39)
1947 Burton, R. F., 55 *Popes Grove, Twickenham, Middlesex*
*1949 Bush, Prof. S. F., D.Phil., *Department of Zoology, University of Natal, Pietermaritzburg, S. Africa*
1949 Butcher, A. W., *Three Salmons Hotel, Usk, Monmouthshire*

1949 Cameron, H. D., 5 *Compton Park Road, Mannamead, Plymouth, Devon*
*1950 Cameron, Prof. W. M., *Institute of Oceanography, University of British Columbia, Vancouver, Canada*
1949 Campbell, L. E., Ph.D., F.R.I.C., *British Food Manufacturing Industries Research Association*, 2 *Dalmeny Avenue, London, N.* 7
1920 Cannon, Prof. H. Graham, Sc.D., F.R.S., *Department of Zoology, Victoria University, Manchester*. (**Council**, 1927–30, 1932–34, 1937–41, 1942–45, 1952→)
1950 Cant, Miss M. A., 8 *Clyde Road, Sutton, Surrey*
1950 Capstick, C. K., 24 *Kennersdene, Tynemouth, Northumberland*
1927 Carruthers, J. N., D.Sc., F.Inst.P., *Hydrographic Department, Admiralty, Cricklewood, London, N.W.* 2. (**Council**, 1948–51)
1923 Carter, G. S., Ph.D., *Department of Zoology, Downing Street, Cambridge*
1948 Carthy, J. D., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
*1931 Cattell, Dr McKeen, *Cornell University Medical College*, 477 *First Avenue, New York City, U.S.A.*
1948 Cattley, J. G., *Fisheries Laboratory, Lowestoft, Suffolk*
1949 Centre de Recherches et d'Etudes Océanographiques, 1 *rue Victor Cousin, Paris (Ve), France*
*1949 Chang, H. W., *Zoological Institute, Academia Sinica*, 320 *Yo Yang Road, Shanghai, China*
*1949 Chapman, Garth, Ph.D., *Dytchleys, Coxtie Green, Brentwood, Essex*
1951 Chappell, R. J., *Kenilworth, Paul Hill, Newlyn, Penzance, Cornwall*
1936 Charterhouse School, *Biological Department, Godalming, Surrey*
1947 Cheng, Prof. Chung, Ph.D., *Department of Oceanography, National Amoy University, Amoy, China*
*1947 Chidambaram, K., *Fisheries Biological Station, West Hill Post, South Malabar, India*
1952 Childs, P., F.R.C.S., 8 *The Crescent, Plymouth, Devon*
1946 Chipperfield, Philip N. J., Ph.D., *Hillside, Manor Road, Brixham, Devon*
1951 Christie, I. G., 7 *Quarry Park Road, Cheam, Surrey*
1942 Christie-Miller, Major E. G., 38 *Hyde Park Street, London, W.* 2. (**Council**, 1941→; **Hon. Treasurer**, 1941→; **Vice-President** 1951→)
1950 Clair, C. le, *Glebe Cottage, Cornwood, Ivybridge, Devon*
1952 Clark, J. T., 12 *Hazel Avenue, Torquay, Devon*
1947 Clarke, Miss D. H., *Gowdhurst, Chart Lane, Dorking, Surrey*
1951 Clarke, Mrs J., 32 *Boolarong Road, Pymble, Sydney, N.S.W., Australia*
1949 Clarke, K. U., *Department of Zoology, The University, Nottingham*
1944 Clarke, Robert H., '*Discovery*' *Investigations, Queen Anne's Chambers*, 41 *Tothill Street, London, S.W.* 1
1951 Claxton, A. J., 26 *Broad Street, King's Lynn, Norfolk*
1951 Clay, Miss E., *Green Hollow, Gattery Lane, Brixham, Devon*
1936 Clothier, Peter, *Hill Close, Street, Somerset*

1939 Clowes, A. J., *Division of Fisheries, Beach Road, Sea Point, Cape Town, S. Africa*
*1886 Coates and Co. (Plymouth), Ltd., *Black Friars Distillery, Southside Street, Plymouth, Devon*
*1945 Cobham, Lt.-Cdr. A. J., R.N., *Noel Cottage, Castle Street, Portchester, Hants*
*1925 Cockshott, Lt.-Col. A. M., R.A.S.C., *Cotteswold Naturalists' Field Club, City Library, Gloucester*
1933 Cole, H. A., D.Sc., *Fisheries Experiment Station, Castle Bank, Conway, Caern*
*1948 Collier, Albert, *c/o Fish and Wildlife Service, Ft Crockett, Galveston, Texas, U.S.A.*
*1885 Collier and Co., 53 *Southside Street, Plymouth, Devon*
1950 Collins, William N., 603 *Thatcher Avenue, River Forest, Illinois, U.S.A.*
1947 Collis, Miss M. M., 27 *Mowbray Road, Cambridge*
1930 Colman, J. S., *Marine Biological Station, Port Erin, Isle of Man.* (**Council**, 1951→)
1947 Cook, Miss P. M., 51 *Runnymeade Crescent, Streatham, London, S.W.* 16
1940 Cook, R. H., *Moor Close, Melbourn, Cambridge*
*1933 Cooper, L. H. N., D.Sc., F.R.I.C., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, P. G., *The Laboratory, Citadel Hill, Plymouth, Devon*
1937 Corbin, Mrs P. G., Ph.D., *Dostabrook, Horrabridge, Devon*
1946 Corlett, John, M.Sc., *Fisheries Laboratory, Lowestoft, Suffolk*
1937 Cosway, C. A., *South Devon Technical College, Teignmouth Road, Torquay, Devon*
1941 Cott, H. B., D.Sc., *University Museum of Zoology, Cambridge*
1948 Council for Promotion of Field Studies, *Dale Fort Field Centre, Haverfordwest, Pembs*
1952 Cowper, T. R., *C.S.I.R.O. Fisheries Division, Cronulla, N.S.W., Australia*
1936 Crawford, G. I., 18 *East Drive, Carshalton Beeches, Surrey*
1952 Crawshaw, K. Ridgway, *Heron Cottage, White Notley, Witham, Essex*
*1928 Crew, Prof. F. A. E., M.D., D.Sc., F.R.S., *Usher Institute, Warrenden Park Road, Edinburgh* 9
*1952 Crisp, D. J., Ph.D., *Bryn Hydd, Holyhead Road, Bangor, Caern*
1929 Crofts, Miss D. R., D.Sc., *Deerbank, Noisey Wood, Billericay, Essex*
1951 Currie, R. I., '*Discovery*' *Investigations, British Museum* (*Natural History*), *Cromwell Road, London, S.W.* 7
1950 Cushing, D. H., D.Phil., *Fisheries Laboratory, Lowestoft, Suffolk*
*1930 Cuthbertson, Norman, 101 *Johnstone Avenue, Dartmouth, Nova Scotia, Canada*

1952 Dale, E., 13 *North Street, Royton, Oldham, Lancs*
1922 Dale, Sir Henry H., O.M., G.B.E., F.R.C.P., LL.D., F.R.S., *The Wellcome Trust*, 28 *Portman Square, London, W.* 1. (**Council**, 1922–28)
1948 Dales, R. Phillips, Ph.D., 67 *Westmoreland Avenue, Squirrels Heath, Essex*
1947 Dall, William, *Grace Street, Corinda, S.W.* 4, *Brisbane, Queensland, Australia*
*1919 Damant Capt. G. C. C., C.B.E., R.N., *Thursford, Cambridge Road, East Cowes, I. of W.* (**Council**, 1928–31, 1937–40)
1939 Danielli, Prof. J. F., D.Sc., *Department of Zoology, King's College, Strand, London, W.C.* 2. (**Council**, 1944–45)
1947 Danmarks Akvarium, *Charlottenlund, Denmark*
1929 Darby, Dr H. H., *Carnegie Institution of Washington*, 5241 *Broad Branch Road, N.W., Washington* 15, *D.C., U.S.A.*

1948 Dartmouth: The Royal Naval College, *Dartmouth, Devon*
1946 Das, S. M., D.Sc., *Department of Zoology, The University, Lucknow, India*
1920 Davidson, Dr W. Cameron, *Avonleigh, Acadia Road, Torquay, Devon*
1931 Dawes, B., D.Sc., *Department of Zoology, University of London, King's College, Strand, London, W.C. 2*
1944 Day, Prof. J. H., D.F.C., *Department of Zoology, University, Rondebosch, Cape Town, S. Africa*
1948 Day, Lionel E., 24 *Inverness Avenue, Westcliff-on-Sea, Essex*
1938 Deacon, G. E. R., D.Sc., F.R.S., 55 *Broadhurst, Ashtead, Surrey*. (**Council,** 1946–49, 1950→)
1952 Deevey, Georgiana B., Ph.D., *The Bingham Oceanographic Laboratory, Yale University, New Haven, Conn., U.S.A.*
1952 Delaware: Department of Biological Sciences, University of Delaware, *Newark, Delaware, U.S.A.*
1939 Dennell, Ralph, D.Sc., *Department of Zoology, The University, Manchester* 13
*1915 Dick, G. W., J.P., 500 *Manning Road, Durban, Natal, S. Africa*
1944 Digby, P. S. B., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1948 Dodd, J. M., *Gatty Marine Laboratory, The University, St Andrews, Fife*
1942 Dollner, H., 3516 *Northcliffe, Montreal, N.D.G., Canada*
1949 Doochin, Herman D., *School of Biological Science, Stanford University, Stanford, California, U.S.A.*
1946 Douglas, Leslie, 11 *Harbour View, Seahouses, Northumberland*
1940 Dowson, Capt. W. B., *Roskellan, Mawnan, near Falmouth, Cornwall*
1952 Dugdale, Rt. Hon. Major Sir Thomas L., Bt., M.P., *Ministry of Agriculture and Fisheries, 55 Whitehall, London, S.W. 1*. (**Vice-President,** 1952→)
1946 Duly, S. J., 68 *Richmond Hill Court, Richmond, Surrey*
1950 Duncan, Miss N., *Marine Biological Station, Port Erin, Isle of Man*
1939 Dundee University College Library, *Dundee, Forfar*
1949 Dussart, B. H., 13 *Quai de Rives, Thonon (Haute-Savoie), France*

*1934 Eales, Miss N. B., D.Sc., *Zoology Department, The University, Reading*
1945 Edgell, Vice-Admiral Sir John A., K.B.E., C.B., F.R.S., 4 *Royal Avenue, Worcester Park, Surrey*. (**Council,** 1945–48, **Vice-President,** 1948→)
1951 Edwards, C., 45 *Queensberry Park, Rosetta, Belfast, N. Ireland*
1927 Eggleton, P., D.Sc., *Department of Physiology, The University, Edinburgh*
1928 Egypt: Coastguard and Fisheries Service, *Alexandria, Egypt*
1948 Elgood, J. H., 27 *Knightscroft Avenue, Rustington, Sussex*
1950 Elliott, Mrs J. H., 39 *Woodhaw, Egham, Surrey*
*1929 Elmhirst, L. K., *Dartington Hall, Dartington, near Totnes, Devon*
1931 Enoch, C. E. D., *Rayman Lodge, Sherborne Road, Parktown, Johannesburg, S. Africa*
1951 Etherington, D., 1 *St John's Gardens, London, W. 11*
*1947 Evans, Miss G. C., *Gerrans, Portscatho, near Truro, Cornwall*
*1923 Evans, W. Edgar, 38 *Morningside Park, Edinburgh*
1942 Ewer, D. W., *Department of Zoology, Natal University College, P.O. Box* 375, *Pietermaritzburg, Natal, S. Africa*

*1929 Faouzi, Dr Hussein, *Faculty of Science (Department of Zoology), Farouk I University, Moharram Bey, Alexandria, Egypt*
1948 Faulkner, I. J., Ph.D., *I.C.I. Billingham Division, Billingham, E. Durham*

1950 Featherstone, Miss M. J., 3 *Clarence Road, Bickley, Kent*
1950 Felinska, Mrs Maria, Dr Phil., *Stowell Park, near Cheltenham, Glos*
*1933 Fellowes, Miss Rosalind, 23 *The Cloisters, Windsor Castle, Berks*
1950 Fisher, L. R., 23 *Langton Avenue, Chelmsford, Essex*
1940 Foote, Miss V. V. J., *Newent Court, Newent, Glos*
1928 Ford, E., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae.* (**Council**, 1950→)
1935 Ford, E. B., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1952 Ford, Miss V. E., 60 *Dudley Road, Hollingbury, Brighton, Sussex*
1939 Forrest, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1950 Forster, G. R., *The Laboratory, Citadel Hill, Plymouth, Devon*
1949 Fountain, H. C., *The Store Cottage, Polbathic, Torpoint, Cornwall*
1912 Fox, Prof. H. M., F.R.S., *Bedford College for Women, Sussex Lodge, Regent's Park, London, N.W.* 1. (**Council**, 1928–30, 1931–34, 1944–47)
1942 Foxon, G. E. H., *Department of Biology, Guy's Hospital Medical School, London Bridge, London, S.E.* 1
1950 Frampton, Cdr R. H. C. F., R.N. (Rtd), *Ministry of Agriculture and Fisheries, Citadel Hill, Plymouth, Devon*
1924 Fraser, Miss E. A., D.Sc., *Orchard Cottage, Abinger Common, Dorking, Surrey*
1935 Fraser, F. C., D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7. (**Council**, 1950→)
*1935 Fraser, James H., Ph.D., *Marine Laboratory, Wood Street, Torry, Aberdeen*
*1939 Fretter, Miss Vera, D.Sc., *Department of Zoology, Birkbeck College, Malet Street, London, W.C.* 1
*1930 Fritsch, Prof. F. E., D.Sc., F.R.S., 34 *Causewayside, Cambridge.* (**Council**, 1931–34, 1937–40, 1943–46)
1949 Fuller, A. S., 30 *Staines Avenue, Cheam, Surrey*
1948 Furness, W. J., *Inglewood, Abbey Park Road, Grimsby, Lincs*

1941 Gardiner, Mrs A. C., 6 *Klementinenstrasse, Munich*, 23, *Germany*
1949 Gates, J. T., 19 *Fircroft Road, Hook Rise, Surbiton, Surrey*
*1928 Gates, Prof. R. R., D.Sc., LL.D., F.R.S., *Biological Laboratories, Harvard University, Cambridge* 38, *Mass., U.S.A.*
1948 Gatty Marine Laboratory, (The Principal), *The University, St Andrews, Fife*
1950 Gauld, D. T., Ph.D., *Marine Station, Millport, Isle of Cumbrae*
1935 Gilson, H. Cary, *Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Westmorland.* (**Council**, 1940–43, 1947–50, 1951→)
1951 Glaister, Mrs K., 12 *Grey Close, London, N.W.* 11
1945 Glasgow University, Zoology Department, *Glasgow, W.* 2
1951 Glasson, D. R., Ph.D., 34 *Craven Avenue, St Judes, Plymouth, Devon*
1946 Glover, R. S., *Oceanographical Laboratory*, 78 *Craighall Road, Edinburgh*, 5
1951 Gokhale, S. V., 1 *Church Road, Port Erin, Isle of Man*
1951 Gold Coast, University College of, *P.O. Box* 4, *Achimota, Gold Coast*
1951 Goodbody, I. M., *Natural History Department, Marischal College, Aberdeen*
1950 Goodley, E. F. W., 2 *Thickthorn Lane, Laleham, Staines, Middlesex*
1939 Goodrich, Dr Helen Pixell, 12 *Park Town, Oxford*
1939 Gordon, Miss Isabella, D.Sc., *British Museum (Natural History), Cromwell Road, London, S.W.* 7
1943 Gourock Ropework Co., Ltd., 92 *Bay Street, Port Glasgow, Renfrew*

1931 Graham, Prof. Alastair, D.Sc., *Department of Zoology, Birkbeck College, Malet Street, London, W.C.* 1. (**Council**, 1951→)
1949 Graham, F. G., *Trethake, Plymstock Road, Oreston, near Plymouth, Devon*
1931 Graham, Michael, O.B.E., *Fisheries Laboratory, Lowestoft, Suffolk.* (**Council**, 1931–32, 1933–36, 1943–46, 1949–52)
1930 Gray, Sir Archibald M. H., C.B.E., M.D., F.R.C.P., F.R.C.S., 39 *Devonshire Place, London, W.* 1
1912 Gray, Prof. J., C.B.E., M.C., Sc.D., LL.D., F.R.S., *Department of Zoology, Downing Street, Cambridge.* (**Council**, 1920–24, 1928→; representing Cambridge University, 1928–45; **President**, 1945→)
1943 Great Grimsby Coal, Salt and Tanning Co., *Fish Dock Road, Grimsby, Lincs*
1949 Green, J., 61 *Ruskin Road, Crewe, Cheshire*
1950 Greene, Miss S. M., *Dalegarth, Milner Road, Ansdell, Lytham-St-Annes, Lancs*
1950 Greenfield, Leonard, J., *Marine Laboratory, University of Miami, Coral Gables* 34, *Florida, U.S.A.*
1948 Grigg, Miss Ursula M., *Dove Marine Laboratory, Cullercoats, Northumberland*
1948 Grove, A. V., 86 *Gowar Road, Sketty, Swansea, Glam*
1947 Guiler, E. R., *Department of Zoology, University of Tasmania, Hobart, Tasmania*
1947 Gundry, Joseph, and Co., *Bridport, Dorset*

1951 Hague, Miss K. M., 20 *Fairview Road, Dartmouth, Devon*
1946 Haifa: Sea Fisheries Research Station, *P.O. Box* 50, *Haifa, Palestine*
1950 Haines, Surg.-Lieut. D. O., R.N., 217 *Cliffe Road, Strood, Rochester, Kent*
1952 Hall, D. N. F., 12 *Cliff Road, Carlton, Nottingham*
1950 Hall, Major H. W., O.B.E., M.C., *Downton Fields, Hordle, Lymington, Hants*
1949 Hall, Miss N. F., *Tyne Brand Products Ltd., North Shields, Northumberland*
*1946 Hamond, Richard, *Morston, Holt, Norfolk*
1947 Harbott, A. J., *Wensleydale,* 7 *Manorcrofts Road, Egham, Surrey*
1923 Hardy, Prof. A. C., D.Sc., F.R.S., *Department of Zoology and Comparative Anatomy, University Museum, Oxford.* (**Council**, 1938–41, 1942→; representing Oxford University, 1946→)
1929 Harington, Sir Charles R., Ph.D., F.R.S., *National Institute of Medical Research, The Ridgeway, Mill Hill, London, N.W.* 7
1950 Harley, Miss M. B., *Department of Zoology, Queen Mary College, Mile End Road, London, E.* 1
1932 Harris, Prof. J. E., Ph.D., *Department of Zoology, The University, Bristol.* (**Council**, 1946–49, 1950→)
1946 Harris, T. R., 31 *All Saints Road, Wyke Regis, Weymouth, Dorset*
1939 Harrison, R. J., D.Sc., M.R.C.S., L.R.C.P., *Vinicombe, The Woodlands, Farnborough, Kent*
1929 Hart, T. J., D.Sc., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1934 Hartley, P. H. T., *Brightwell Rectory Cottage, Wallingford, Berks.*
1924 Harvey, H. W., Sc.D., F.R.S., *The Laboratory, Citadel Hill, Plymouth, Devon*
1933 Harvey, Prof. L. A., *Department of Zoology, University College of the South West, Exeter, Devon.* (**Council**, 1940–43)
1950 Haswell, G. A., 23 *Russell Avenue, Hartley, Plymouth, Devon*
1950 Haswell, Miss L. J., 23 *Russell Avenue, Hartley, Plymouth, Devon*
1952 Hawes, F. A. B., *c/o Grindlay's Bank,* 54 *Parliament Street, London, S.W.* 1
1939 Hayes, Dr F. R., *Dalhousie University, Halifax. N.S., Canada*

1939 Hayes, Mrs F. R., *Dalhousie University, Halifax, N.S., Canada*
1950 Hazevoet, A. C., *Vogelenzangstraat 19-I, Amsterdam West, Holland*
1949 Heaysman, Miss J. E. M., 69 *Brook Road, Merstham, Surrey*
1948 Hedley, Ronald H., *Remora, Quarry House Lane, Crossgate Moor, Durham City*
1931 Henderson, G. T. D., D.S.C., Ph.D., *Oceanographic Laboratory, 78 Craighall Road, Edinburgh 5*
1925 Hentschel, C. C., 7 *Dudley Court, Upper Berkeley Street, London, W. 1*
1939 Herklots, G. A. C., Ph.D., *Vanners, Chobham, Surrey*
1950 Herring Industry Board, 1 *Glenfinlas Street, Edinburgh 3*
1939 Hewer, H. R., Assistant Professor, *Department of Zoology, Imperial College of Science, London, S.W. 7*
1926 Hickling, C. F., C.M.G., Sc.D., *Colonial Office, Sanctuary Buildings, Great Smith Street, London, S.W. 1.* (**Council**, 1947–50)
1951 Hidaka, Prof. K., *Geophysical Institute, Tokyo University, Tokyo, Japan*
1926 Hill, Prof. A. V., C.H., O.B.E., Sc.D., F.R.S., 16 *Bishopswood Road, Highgate, London, N. 6.* (**Council**, 1925–29, 1930–33, 1934–37, 1938–41, 1942→; representing Royal Society, 1944→; **Vice-President**, 1948→)
*1949 Hill, D. K., *Postgraduate Medical School of London, Ducane Road, London, W. 12*
1939 Hill, M. D., *Uplands, near Ledbury, Herefordshire*
1947 Hill, M. N., Ph.D., 6 *St Eligius Street, Cambridge*
*1921 Hindle, E., Sc.D, F.R.S., *Zoological Society of London, Regent's Park, London, N.W. 8* (**Council**, 1946–49; representing British Association, 1950→)
1937 Hinton, M. A. C., F.R.S., *Glaister, Wrington, near Bristol, Somerset*
1926 Hobson, Prof. A. D., *King's College, Newcastle-upon-Tyne 1, Northumberland*
1948 Hockley, A. R., *Department of Zoology, The University, Southampton*
1939 Hodgkin, A. L., F.R.S., *Trinity College, Cambridge.* (**Council**, 1951–52)
1945 Hodson, W., *Rhodena, Penare Avenue, Prestatyn, Flints*
1947 Hollowday, E. D., F.R.M.S., 45 *Manor Road, Aylesbury, Bucks*
1948 Holme, N. A., *The Laboratory, Citadel Hill, Plymouth, Devon*
1939 Holmes, W., D.Phil., *Department of Zoology and Comparative Anatomy, University Museum, Oxford*
1948 Holsgrove, H. E., 67 *Bridwell Road, Weston Mill Estate, Plymouth, Devon*
1950 Honeker, C., 24 *Romney Road, New Malden, Surrey*
1951 Hornby, Miss C. E., 53 *Langley Drive, Wanstead, London, E. 11*
1933 Horne, F. R., *National Institute of Agricultural Botany, Huntingdon Road, Cambridge*
1950 Horridge, G. A., *St John's College, Cambridge*
1952 Horvath, C., 8649 *Clifton Way, Beverley Hills, Calif., U.S.A.*
1950 Howard, G. H., 14 *Westlands Avenue, Bargate, Grimsby, Lincs*
1948 Howe, Surg. Cdr. (D) D. C., R.N., *The Cottage, Pomphlett, Plymouth, Devon*
1950 Howells, D. V., 42 *Radstock Road, Reading, Berks*
1932 Howes, N. H., *Department of Zoology, University College, Gower Street, London, W.C. 1*
1952 Hoyle, G., *Department of Zoology, The University, Glasgow, W. 2*
1928 Hunt, O. D., *Corrofell, Newton Ferrers, Devon.* (**Council**, 1944–47, 1948–51, 1952→)
1947 Hunter, W. Russell, *Department of Zoology, The University, Glasgow, W. 2*
*1947 Hurrell, H. G., J.P., *Moorgate, Wrangaton, Devon*
1939 Hurst, C. P., *Landulph Rectory, Saltash, Cornwall*
*1920 Hutton, J. Arthur, *Woodlands, Alderley Edge, Manchester*
*1952 Hutton, Robert F., *The Laboratory, Citadel Hill, Plymouth, Devon*

1946 Iceland: *Atvinnudeild Háskólans (Fiskideild), Reykjavik, Iceland*
1945 Imperial Chemical Industries Ltd., *Nobel House, 2 Buckingham Gate, London, S.W. 1*
1952 Inglis, W. G., *Upper Kirkhill, Nigg, Aberdeen*

1952 Jackman, L. A. J., 44 *Old Torquay Road, Preston, Paignton, Devon*
1952 Jean, Prof. Yves, *School of Fisheries, Ste. Anne de la Pocatier, Kam., P.Q., Canada*
1945 Jeffries, H. S., *The Mill, Avoncliffe, Bradford-on-Avon, Wilts*
1935 Jenkin, Miss P. M., *Department of Zoology, The University, Bristol*
1934 Jepps, Miss M. W., D.Sc., *Department of Zoology, The University, Glasgow*
1949 Jeremy, W. H. R., 38 *Barnfield Road, Exeter, Devon*
1937 Jersey: Conservateur honoraire du Musée de la Société Jersiaise
*1924 Jesus College, *Oxford*
*1947 John, C. C., D.Sc, *Department of Fisheries, Colombo, Ceylon*
*1947 Johnson, D. S., 10 *St John's Road, Cambridge*
1944 Johnson, Dr F. R., *Osu Fisheries Station, P.O. Box 630, Accra, Gold Coast Colony*
*1948 Jones, C. Burdon, *Department of Zoology, University College of N. Wales, Bangor, Caern*
1950 Jones, Miss C. M., *Department of Zoology, University of Cape Town, Cape Town, S. Africa*
*1950 Jones, E. Idris, M.D., 6 *Kewferry Road, Northwood, Middlesex*
*1949 Jones, E. W. Knight, Ph.D., *Marine Biological Station, University College of N. Wales, Bangor, Caern*
1949 Jones, F. R. Harden, Ph.D., 9 *Clifton Crescent, Folkestone, Kent*
1952 Jones, Howell T., *St Cuthbert's Society, Durham University, 12 South Bailey, Durham City*
1948 Jones, J. D., *Nantyci, Llysonnen Road, Carmarthen, S. Wales*
1946 Jones, L. W. G., *Cumber House, Manor Road, Brixham, Devon*
1946 Jones, N. S., *Marine Biological Station, Port Erin, Isle of Man*
1949 Jones, R. J., 14 *Canning Road, Croydon, Surrey*
1936 Jones, Rodney R. M., *Tros-yr-Afon, Penmon, Anglesey*
1946 Jones, Prof. R. V., C.B., C.B.E., D.Phil., F.Inst.P., *Department of Natural Philosophy, Marischal College, Aberdeen*
1950 Jones, W. C., *King's College, Cambridge*
1951 Jones, W. E., 7 *Cambrian Place, Aberystwyth, Cardigan*
1947 Jörgensen, C. Barker, *Slettevej 8, Copenhagen Söborg, Denmark*
1952 Joysey, Mrs V. C., 25 *Hillside Avenue, Woodford Green, Essex*
1923 Judge, J. J., *Virginia House, Palace Street, Plymouth, Devon*
1950 Juniper, A. J., *The Polytechnic, Regent Street, London, W. 1*

1952 Kabata, Z., 35 *Hilton Street, Aberdeen*
1951 Kampa, E. M., Ph.D. (Mrs B. P. Boden), *Bermuda Biological Station, St Georges West, Bermuda*
1948 Katterns, L. B., 115 *Feltham Hill Road, Ashford, Middlesex*
1945 Katz, Max, Ph.D., 3636 *Bellecrest Avenue, Cincinnati, 8, Ohio, U.S.A.*
1951 Kay, Miss E. A., *Box 522, Kolva, Kanai, Territory of Hawaii, U.S.A.*
1940 Keilin, Prof. D., Sc.D., F.R.S., *Molteno Institute, Cambridge.* (**Council,** 1940–43)
1950 Keir, Ronald S., *Newfoundland Fisheries Research Station, Water Street East, St Johns, Newfoundland*

1946 Kelley, D. F., 17 *Bainbridge Avenue, Hartley, Plymouth, Devon*
1949 Kennedy, G. Y., Ph.D., F.R.I.C., *Department of Cancer Research, University Field Laboratory, Blackbrook Road, Sheffield* 10
1946 Kenya: The Game Warden, *Game Department, P.O. Box* 241, *Nairobi*
1951 Kerslake, Miss J., 17 *Hardman Road, Kingston-upon-Thames, Surrey*
1950 Keynes, R. D., Ph.D., *Physiological Laboratory, Cambridge*
1949 Kimmins, B. J., 19 *Cranleigh Gardens, Bristol* 9
1928 King, Mrs A. Redman, *Mixton House, Lerryn, Lostwithiel, Cornwall*
1947 Kingsbridge Modern Secondary School, *Kingsbridge, Devon*
1949 Kingston Technical College, *Kingston Hall Road, Kingston-upon-Thames, Surrey*
1927 Kirtisinghe, P., *Department of Zoology, University of Ceylon, Colombo* 3, *Ceylon*
1950 Kisch, B. S., C.I.E., 38 *Boulevard Thiers, St Jean-de-Luz, B.P., France*
1930 Kitching J. A., O.B.E., Ph.D., *Department of Zoology, The University, Bristol*
1939 Knight, Miss Margery, D.Sc., *University Hall for Women Students, Holly Road, Fairfield, Liverpool.* (**Council**, 1943–46)
1945 Knowles, F. G. W., D.Phil., *Marlborough College, Marlborough, Wilts*
1950 Korn, M. E., 62 *Aberdare Gardens, Hampstead, London, N.W.* 6
1950 Kott, Miss P., *C.S.I.R.O. Fisheries Division, Cronulla, N.S.W., Australia*
1948 Kow, Tham Ah, *c/o Fisheries Department, 4th Floor, Fullerton Building, Singapore*
1949 Kristensen, Dr Ingvar, *Zoölogisch Station, den Helder, Holland*

1950 La Rochelle: Station Océanographique, *Pavillon du Port-Le Gabut, La Rochelle* (*Charente-Maritime*), *France*
1950 Lasker, Reuben, *Hopkins Marine Station, Pacific Grove, Calif., U.S.A.*
*1925 Lebour, Miss M. V., D.Sc., *Kean Hill, Cawsand, near Plymouth, Devon*
1947 Leehane, J. D. B., 14 *Wyndham Street East, Plymouth, Devon*
1935 Le Mare, D. W., *Fisheries Department, Federation of Malaya and Singapore, Penang, Malaya*
1948 Letts, J. K., 183 *Windmill Lane, Greenford, Middlesex*
1951 Lewis, J. B., *Marine Laboratory, University of Miami, Coral Gables, Florida, U.S.A.*
1952 Lewis, J. R., *Department of Zoology, University College of Wales, Aberystwyth, Cardigan*
1951 Lightowlers, F., 109 *Bradford Road, Brighouse, Yorkshire*
1932 Lisbon: Instituto de Biologia Maritima, *Cais do Sodré, Lisbon, Portugal*
1952 Lister-Bradney, J., Ph.D., 25 *Palmerston Road, Westcliff-on-Sea, Essex*
1949 Lodge, Miss S. M., Ph.D., *Marine Biological Station, Port Erin, Isle of Man*
1950 Longhurst, A. R., *Landford Cottage, Landford, Wilts*
1948 Lovegrove, T., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1950 Lowenstein, Prof. O. E., Ph.D., *Department of Zoology, The University, Birmingham*, 15. (**Council**, 1952→)
1926 Lowndes, A. G., Sc.D., F.R.I.C., *c/o The Laboratory, Citadel Hill, Plymouth, Devon*
1950 Lowy, J., Ph.D., *The Laboratory, Citadel Hill, Plymouth, Devon*
1931 Lucas, C. E., D.Sc., *Marine Laboratory, Wood Street, Torry, Aberdeen.* (**Council**, 1949–52)
1930 Lumley, Adrian, *Beechcroft, Udney Park Road, Teddington, Middlesex*
1938 Lysaght, Miss A. M., Ph.D., 6 *Cumberland Gardens, London, W.C.* 1

1938 MacDonald, R., 112 *Antrim Road, Belfast, N. Ireland*
1935 Mackenzie, Col. W., O.B.E., *c/o Messrs Peel and Co. Ltd., P.O. Box* 331, *Alexandria, Egypt*
1929 Mackinnon, Prof. D. L., D.Sc., 44 *St Leonard's Terrace, Chelsea, London, S.W.* 3. (**Council**, 1938–42)
1937 Mackintosh, N. A., C.B.E., D.Sc., 7 *Hinde House, Hinde Street, London, W* 1. (**Council**, 1946–49, 1951→)
1947 Macnae, William, *Department of Zoology, Rhodes University College, Grahamstown, S. Africa*
*1925 Magdalen College, *Oxford*
1951 Malkin, J. J. S., 33 *Elton Parade, Darlington*
1948 Mansfield, A. W., 32 *Newton Road, Wimbledon, London, S.W.* 19
1952 Mansfield, Lt.-Col. K. F., *Luckwell Bridge, Wheddon Cross, Minehead, Somerset*
*1928 Manton, S. M., Sc.D., F.R.S. (Mrs J. P. Harding), 18 *Ennerdale Road, Richmond, Surrey*
1948 Marcotte, Alexandre, D.Sc., *Marine Bioogical Station, Grand River, Gaspé Co., P.Q., Canada*
1951 Marshall, C. J., M.D., F.R.C.S., *Penhaven, The Drive, Mevagissey, Cornwall*
1949 Marshall, Douglas, M.P., *Lanwithan House, Lostwithiel, Cornwall*
1951 Marshall, K. E., 6 *Holcombe Road, Blackpool, Lancs*
*1947 Marshall, Miss S. M., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1951 Mason, J., *Marine Biological Station, Port Erin, Isle of Man*
1939 Matthews, L. Harrison, Sc.D., *Zoological Society of London, Regent's Park, London, N.W.* 8. (**Council**, 1944–47, 1949–52)
1937 Mayne, Cyril F., O.B.E., F.R.C.S., *c/o Barclays Bank Ltd., Plymouth, Devon*
1949 McCarthy, Miss D. F., 70 *Halton Terrace, Kensington Park, Adelaide, S. Australia*
1951 McCarton, Miss L., 89 *Eglantine Avenue, Malone Road, Belfast, N. Ireland*
1910 McClean, Capt. W. N., 39 *Phillimore Gardens, London, W.* 8
*1929 McEwen, Mrs Lawrence, *Isle of Muck, Isle of Eigg, Inverness-shire*
1948 McIntyre, A. D., *Marine Laboratory, Wood Street, Torry, Aberdeen*
1950 McIntyre, J. M., 75 *Harcourt Terrace, Kensington, London, S.W.* 10
*1948 Menon, M. Devidas, *Parvathi Nivas, Diwans Road, Ernakulam, United States of Cochin and Travancore, S. India*
1950 Messenger, K. G., *Uppingham School, Rutland*
1951 Messent, R. K., 13 *Sedberg Street, Preston, Lancs*
1939 Metropolitan Water Board, 177 *Rosebery Avenue, London, E.C.* 1
1951 Metz, P., *Eremitagevej* 4, *Taarbaek pr Klampenborg, Denmark*
1950 Mexico: Department of Physiology, National University, *Apartado Postal* 13699, *Mexico, D.F.*
1947 Miami University Marine Laboratory, *Coral Gables, Florida, U.S.A.*
1951 Michelmore, Miss M. S. J., *Rowhorne House, Whitestone, Exeter, Devon*
1951 Mij tot Exploitatie van Kooksovengassen (Mekog), *Ijmuiden, Holland*
1923 Milford Haven Trawler Owners Association, Ltd., *Milford Haven, Pembs*
1949 Millar, R. H., Ph.D., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
1946 Miller, Cyril J., 42 *Westbourne Road, Peverell, Plymouth, Devon*
1949 Millott, Prof. N., Ph.D., *Department of Zoology, University College of West Indies, Mona, Liguanea, Jamaica*
1949 Mistakidis, M. N., *Oyster Research Station, Burnham-on-Crouch, Essex*
1947 Mitchell, E. L., *Hillside, Chapel Street, Camelford, Cornwall*

1947 Mitra, G. N., *Assistant Director of Fisheries, Cuttack (Orissa), India*
1952 Mohamed, Prof. Abdel Fattah, Ph.D., *Oceanography Department, Faculty of Science, Farouk I University, Maharram Bey, Alexandria, Egypt*
1951 Mohr, J. L., Ph.D., *Department of Zoology, University of Southern California, Los Angeles 7, Calif., U.S.A.*
1940 Moore, Hilary B., Ph.D., *Marine Laboratory, Miami University, Coral Gables, Florida, U.S.A.*
1949 Morton, J. E., *Department of Zoology, Queen Mary College, Mile End Road, London, E. 1*
1931 Mount Desert Island Biological Laboratory, *Salisbury Cove, Maine, U.S.A*
1938 Mowbray, Louis L., *Curator, Bermuda Government Aquarium, Flatts, Bermuda*
1942 Moynahan, Dr E. J., *Wayside, Jordans, near Beaconsfield, Bucks*
1952 Munn, R. B., 11002 *East Saragossa Street, Whittier, Calif., U.S.A.*

1952 Naylor, E., *Marine Biological Station, Port Erin, Isle of Man*
1933 Neale, Morley H., C.B.E., *Chaffcombe House, Chard, Somerset.* (**Council**, 1934–36, 1939–42, 1943–46, 1947–50; **Vice-President**, 1951→)
1934 Neale and West, *Trawler Owners, Wharf Street, Cardiff*
1939 Needham, Joseph, Sc.D., F.R.S., *Gonville and Caius College, Cambridge*
1947 Newell, G. E., Ph.D., *Department of Zoology, Queen Mary College, Mile End Road, London, E 1*
1951 Newfoundland Fisheries Research Station, *Water Street East, St John's, Newfoundland*
1947 Newton, Prof. Lily, Ph.D., *Department of Botany, University College of Wales, Aberystwyth, Cardigan.* (**Council**, 1947–50)
1930 Nicholls, A. G., Ph.D., *C.S.I.R.O. Division of Fisheries, Stowell, Hobart, Tasmania*
1950 Nicol, J. A. C., D.Phil., *Trevean, George Lane, Plympton St Maurice, Devon*
1947 Nisbet, R. H., 8 *Lichfield Road, Woodford Green, Essex*
1948 Nobbs, Miss G. E. D., 4 *Clifton Estate, Plympton, Devon*
1949 Norris, E., *Biology Department, Kingston Technical College, Kingston Hall Road, Kingston-upon-Thames, Surrey*
1951 North Carolina, University of, *Fisheries Research Laboratory, Morehead City, N. Carolina, U.S.A.*
1950 North, J., 316 *Lee High Road, Lewisham, London, S.E.* 13
1952 Nunn, G., F.R.I.C., *Cleeve House,* 10 *Tyrells Close, Chelmsford, Essex*
1948 Nunn, S. M., *The Laboratory, Citadel Hill, Plymouth, Devon*
1950 Nurse, F. R. (Mrs R. M. Allison), *Biology Department, Canterbury University College, Christchurch, New Zealand*

1934 Oakley, Dr C. L., 58 *Cumberland Road, Bromley, Kent*
1930 Olive, G. W., C.B.E., *Dauntsey's School, West Lavington, near Devizes, Wilts*
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1937 Omer-Cooper, J., *Zoological Department, Rhodes University College, Grahamstown, S. Africa*
1939 Ommanney, F. D., Ph.D., *P.O. Box* 669, *Zanzibar, E. Africa*
1949 Orkin, P. A., *Natural History Department, The University, Aberdeen*
1947 Orr, A. P., D.Sc., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*
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1951 Oxford: Department of Zoology and Comparative Anatomy, *University Museum, Oxford*

1951 Pacific Biological Station, *Nanaimo, B.C., Canada*
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*1923 Pantin, C. F. A., Sc.D., F.R.S., *Trinity College, Cambridge*. (**Council**, 1930–32, 1933–36, 1937–40, 1941–44, 1945–49, 1951→ representing Cambridge University, 1946–49, 1951→)
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1937 Parry, D. A., Ph.D., *Department of Zoology, Downing Street, Cambridge*
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*1920 Pass, A. Douglas, *Wooton Fitzpaine, Charmouth, Dorset*
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1950 Powell, H. T., *Marine Station, Keppel Pier, Millport, Isle of Cumbrae*

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THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

THE ASSOCIATION was founded in 1884 to promote accurate researches leading to the advancement of zoological and botanical science and to an increase in our knowledge of the food, life, conditions and habits of British fishes. The work of the Association is controlled by a Council elected annually by its subscribing members.

Professor T. H. Huxley took the chair at the initial meeting held in the rooms of the Royal Society and was elected the first President. Among those present were Sir John Lubbock (afterwards Lord Avebury), Sir Joseph Hooker, Professor H. N. Moseley, Mr G. J. Romanes, and Sir E. Ray Lankester who, after Professor Huxley, was for many years president of the Association. It was decided that a laboratory should be established at Plymouth, where a rich and varied fauna is to be found.

The Plymouth Laboratory was opened in June 1888. The cost of the building and its equipment was £12,000 and, since that date, a new library and further laboratory accommodation have been added at an expenditure of over £25,000.

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. Accounts of the laboratory and aquarium and the scope of the researches will be found in Vol. XXVII (p. 761) and Vol. XXXI (p. 193) of this *Journal*.

The laboratory is open throughout the year and its work is carried out by a fully qualified research staff under the supervision of the Director. 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, physiology and other branches of science. Arrangements are made for courses for advanced students to be held at Easter, and marine animals and plants are supplied to educational institutions.

Work at sea is undertaken by two research vessels and by a motor boat, and these also collect the specimens required in the laboratory.

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

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CAMBRIDGE UNIVERSITY PRESS
LONDON: BENTLEY HOUSE, N.W.1
NEW YORK: 32 EAST 57TH STREET, 22
CANADA AND INDIA: MACMILLAN

Printed in Great Britain at the University Press, Cambridge
(Brooke Crutchley, University Printer)