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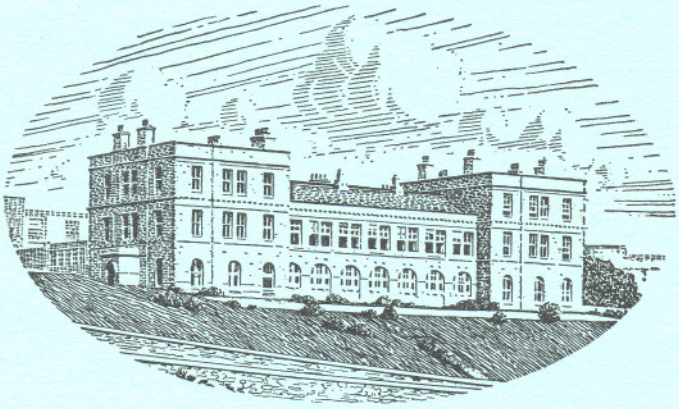

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ON A NEW MEDUSA, *KRAMPELLA DUBIA* N.G., N.SP.

By F. S. Russell, F.R.S.
The Plymouth Laboratory

(Text-figs. 1 and 2)

In a collection made with a 2 m stramin ring trawl at 47° 03′ N., 5° 47′ W. on 4 July 1956, with 800 fathoms of wire out, I have found a new species of medusa. This specimen is in a comparatively good state of preservation except that the stomach is badly damaged.

The umbrella is hemispherical and the jelly is moderately thick. The form of the stomach cannot be described for certain. Parts of it are to be seen as narrow strips hanging down from the upper ends of three of the radial canals. One of these strips is continued for a short distance along the subumbrella surface towards the summit. It has the form of two short curtains with a space between them which leads into the radial canal. It thus seems quite possible that the stomach is in fact an open cross with mouth lips extending along each arm as in *Staurophora*.

The four radial canals are broad and there is a ring canal. Along each of the four radial canals there are about sixteen fine strands of tissue running through the jelly and connecting the walls of the radial canals with the exumbrella surface, similar to those I have recorded (Russell, 1956) in *Amphinema krampi*.

The gonads are situated along almost the whole length of each radial canal. They are widely divided longitudinally.

There are four perradial and four interradial marginal tentacles each with a swollen conical basal bulb. The tentacles coil spirally.

Between the bases of each pair of marginal tentacles there are three or four small marginal cirrus-like tentacles, the actual sequence being 3, 3, 4, 3, 4, 3, 4, 4.

No marginal vesicles, cordyli, or sense organs can be seen, and there are no ocelli apparent.

There is a little yellowish brown pigment on parts of the gonads and this colour is rather prominent on what appear to be the mouth lips. Otherwise the medusa is colourless. It is about 3 mm in diameter, and is a male.

A drawing of this medusa as seen from the subumbrellar side is given in Fig. 1 *a*. A lateral view, drawn slightly ideally, is given in Fig. 1 *b* in which the possible outlines of the stomach are indicated.

One quadrant of the medusa was removed for sectioning. Examination of these sections adds the following additional information.

The strands of the tissue running from the outer walls of the radial canals to the exumbrella surface consist of rows of cells which may be two or three thick in places (Fig. 2*a*). At some points there may be as many as three strands starting from approximately the same position on the radial canal, and

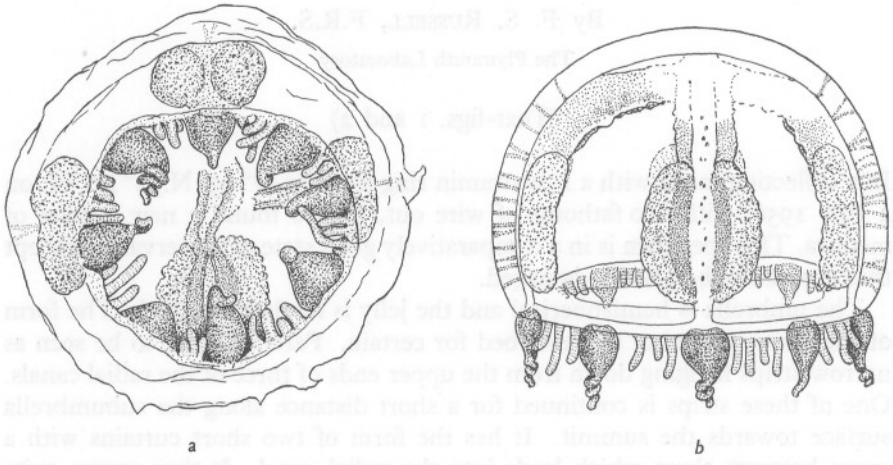

Fig. 1. *Krampella dubia* n.sp. *a*, viewed from subumbrellar side; *b*, lateral view slightly idealized, with suggested outlines of stomach.

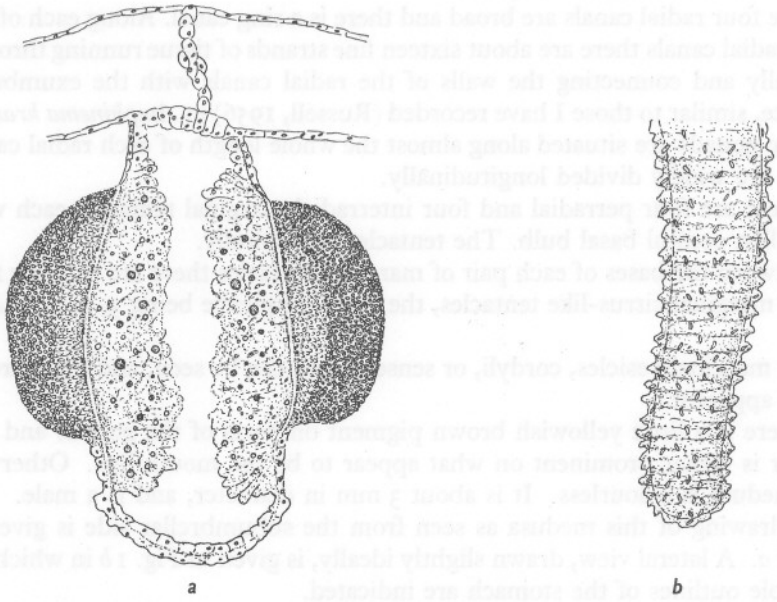

Fig. 2. *Krampella dubia* n.sp. *a*, section through radial canal and gonads, and showing strand of cells connecting wall of radial canal with exumbrella surface; *b*, marginal tentacula.

diverging to reach the exumbrella surface at three different spots. In no instance did there appear to be a definite canal surrounded by cells, though it is possible that there may be intercellular connexion of cavities between cells.

The radial canals carry the gonads on their lateral walls. They do not cover the whole of the walls dorso-ventrally, but begin a short distance from the subumbrella and are well separated ventrally (Fig. 2*a*). The endoderm of the greater part of the lateral wall consists of tall narrow digestive cells. Much of this tissue is in a disintegrated state, but in places the cell outlines can be seen.

The marginal tentacles are filled with cubical endoderm cells, and the basal bulbs and at any rate the proximal regions of the tentacles, are hollow.

The cirrus-like tentacles are cylindrical and hollow, having a single layer of cubical endoderm cells surrounding a central lumen. There are numerous small nematocysts evenly dispersed over them (Fig. 2*b*). They are evidently capable of extension since in their present state they are ringed with corrugations (Fig. 2*b*). From their structure they do not appear to be homologous with either cordyli or true marginal cirri which have a solid core of endoderm cells. It seems better to regard them as tentaculae or true tentacles of a different kind from the large tentacles.

I have examined the nematocysts, but not under oil immersion. There are two sizes; the larger, about 17 μ long undischarged, appeared to be an atrichous haploneme, and the smaller, about 9 μ long undischarged, a microbasic mastigophore. Both kinds were to be seen on the bases of the large marginal tentacles, but only the smaller kind on the tentaculae.

The systematic position of this medusa is problematical. It is evidently a Leptomedusa. The combination of characters, absence of marginal vesicles and possible cruciform shape of the stomach, might indicate affinities with the Laodiceidae. There are, however, no cordyli nor are the small cirrus-like tentacles true marginal cirri.

Until a complete specimen is obtained it seems unnecessary to say more.

I have much pleasure in naming the genus after my friend P. L. Kramp, while giving a specific name which alludes to its uncertain systematic position. I propose the name *Krampella dubia* n.g., n.sp.

The specimen has been deposited in the British Museum (Natural History) and given the registration number B.M. 1957.5.8.1.

My thanks are due to Captain C. A. Hoodless and the crew of R.V. *Sarsia* who collected the specimen; and to Dr J. S. Alexandrowicz who very kindly removed and sectioned one quadrant of the medusa.

REFERENCE

RUSSELL, F. S., 1956. On a new medusa, *Amphinema krampi* n.sp. *J. mar. biol. Ass. U.K.*, Vol. 35, pp. 371–3.

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THE LOSS OF MERCURY FROM STORED SEA-WATER SOLUTIONS OF MERCURIC CHLORIDE

By E. D. S. CORNER
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and F. H. RIGLER
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(Text-figs. 1 and 2)

To assess the efficiency of an anti-fouling composition it is necessary to determine the rate at which the poison leaches from the paint film into the surrounding sea water. With a paint containing mercury this estimation is difficult because sea-water solutions of mercuric chloride are unstable. Thus, when examined by the chloroform-dithizone procedure (Harris, 1946) these solutions have been found to lose as much as 80% of their mercury content in the course of a week (Robinson, private communication).

In the present work, ^{203}Hg-labelled mercuric chloride has been used for a quantitative and qualitative study of the loss of mercury from sea water, and the results of this investigation have demonstrated the considerable importance of bacteria as a factor in this process.

One of us (F. H. R.) is indebted to the National Research Council of Canada for a Research Fellowship to work at Plymouth, and the other wishes to acknowledge a Research Fellowship from International Paints Ltd. Both of us wish to express our thanks to Mr O. D. Hunt, Mr T. W. Robinson and Mr R. Robinson for their keen interest in this work, and to Dr H. W. Harvey, F.R.S., for his many helpful suggestions. We should also like to thank Dr B. C. Abbott for his advice on the use of radioactive materials, and Mr L. Hummerstone for the maintenance of the counting equipment.

PRELIMINARY EXPERIMENTS

Chloroform-dithizone titrations

Mercuric chloride was added to filtered Plymouth sea water to give a concentration of 0·1 mg Hg/l. ($0{\cdot}5 \times 10^{-6}$ M), and estimations were made daily by means of the chloroform-dithizone procedure to determine the quantity of mercury present in the solution. The results of experiments with plain sea water, and with sea water to which 40% formaldehyde had been added

(5 ml./l.), are shown in Table 1. For the purposes of tracer isotope studies it was thought necessary to use a higher concentration of mercuric chloride, and further estimations were therefore carried out using a sea-water solution of this compound containing 1 mg Hg/l. The results of this experiment are also included in Table 1. In these experiments, which were carried out at 16–18° C, it was found that after one week only a very small proportion of the mercury originally added to untreated sea water could be detected, but that 80% of the mercury could still be found in sea-water solutions containing formaldehyde.

TABLE 1. RATES OF LOSS OF MERCURY FROM SOLUTIONS OF MERCURIC CHLORIDE IN PLAIN SEA WATER AND IN SEA WATER CONTAINING FORMALDEHYDE

(Concentration of 40% HCHO = 5 ml./l. of sea water. Experiment carried out at 16° C)

	Chloroform-dithizone titres (ml.)		
	Plain sea water		Formaldehyde-treated sea water
Day	(0·1 mg Hg/l.)	(1·0 mg Hg/l.)	(0·1 mg Hg/l.)
0	26	240	25
1	24	230	24
2	20	210	24
3	11	120	24
4	—	50	—
5	—	12	—
6	—	9	—
7	5	—	20

Prevention of mercury loss by various bactericides

It seemed possible that the role of formaldehyde in preventing mercury loss might be chemical rather than bactericidal. Accordingly, estimations were made of the loss of mercury from solutions of mercuric chloride (1 mg Hg/l.) in sea water in which bacterial growth was prevented by several different methods. The results of this experiment are given in Table 2, which shows that, in addition to formalin, other treatments which would destroy bacteria or inhibit their growth, also prevented the loss of mercury from the sea water.

TABLE 2. LOSS OF MERCURY FROM SOLUTIONS OF MERCURIC CHLORIDE IN SEA WATER TREATED TO PREVENT BACTERIAL GROWTH

(Sea water saturated with chloroform and phenol; 40% formaldehyde used at a concentration of 5 ml./l.; penicillin and streptomycin each used at a concentration of 50 mg/l.)

Treatment	Percentage decrease in chloroform-dithizone titration after 1 week
None	74
Chloroform	0
Formaldehyde	0
Phenol	4
Penicillin and streptomycin	9
Autoclaving	5

QUANTITATIVE STUDIES USING TRACER ISOTOPES

To examine whether or not the decrease in the chloroform-dithizone titre represented an actual loss of mercury from the sea water, experiments were carried out with radioactive mercuric chloride.

MATERIALS AND METHODS

Radioactive mercury (^{203}Hg) was obtained from Harwell as mercuric oxide and converted into the chloride by treatment with 50% HCl. Certain technical difficulties encountered in the estimation of radioactive mercury have been described by Kelly, Thorpe, Threefoot & Burch (1950). In the present work it was found that the volatilization of mercury during the drying of radioactive samples was prevented if sodium sulphide was added to the solution before it was warmed to dryness on the planchette. Estimations of radioactivity were usually made with 0·1 ml. samples of the sea-water solution which, when dried, were found to contain about 3 mg solids/cm^2. The correction necessary for self-absorption in these samples was determined by comparing the number of counts/min. shown by samples prepared in sea water and in distilled water. This correction (2%) was then applied in all subsequent estimations of radioactivity in sea-water samples. As a precaution, the decay curve of the radioactive material was plotted from measurements of radioactivity made at suitable intervals and was found to be similar to that shown by ^{203}Hg (half-life = 47·9 days).

ESTIMATION OF MERCURY LOSS

Sufficient radioactive mercuric chloride was added to sea water containing glucose and ferric ammonium citrate (to promote the growth of bacteria) to give a concentration of 1 mg Hg/l. Simultaneous estimations of the mercury present in the sea water by titration with chloroform-dithizone and by measurement of the amount of radioactivity in samples (0·1 ml.) of the sea water were then made immediately after the mercuric chloride was added to the sea water and at suitable intervals during the subsequent week. In addition, simultaneous determinations were made of the quantity of mercury present on bacteria in the solution by passing a sample (10 ml.) through a millipore filter which was then examined for radioactivity.

The results of this experiment (see Fig. 1) showed that during the first 2 days the loss of mercury as determined by chloroform-dithizone titration was approximately the same as that estimated from measurements of radioactivity in the sea water. This correlation disappeared, however, once a significant amount of mercury had been taken up by the bacteria, and as this quantity neared and passed its maximum value the chloroform-dithizone procedure detected much less mercury than was found to be present in the sea water by estimations of radioactivity. It is interesting to note that in this

region of the curve the total amount of mercury present in the sea water was roughly the sum of the quantity taken up by bacteria and that detected by the chloroform-dithizone titrations, a finding which implied that the mercury held by the bacteria was not extracted by chloroform-dithizone. Of further interest was the finding that, during the latter part of the experiment, the quantity of mercury held by bacteria in suspension gradually diminished until, after 6 days, it had practically disappeared.

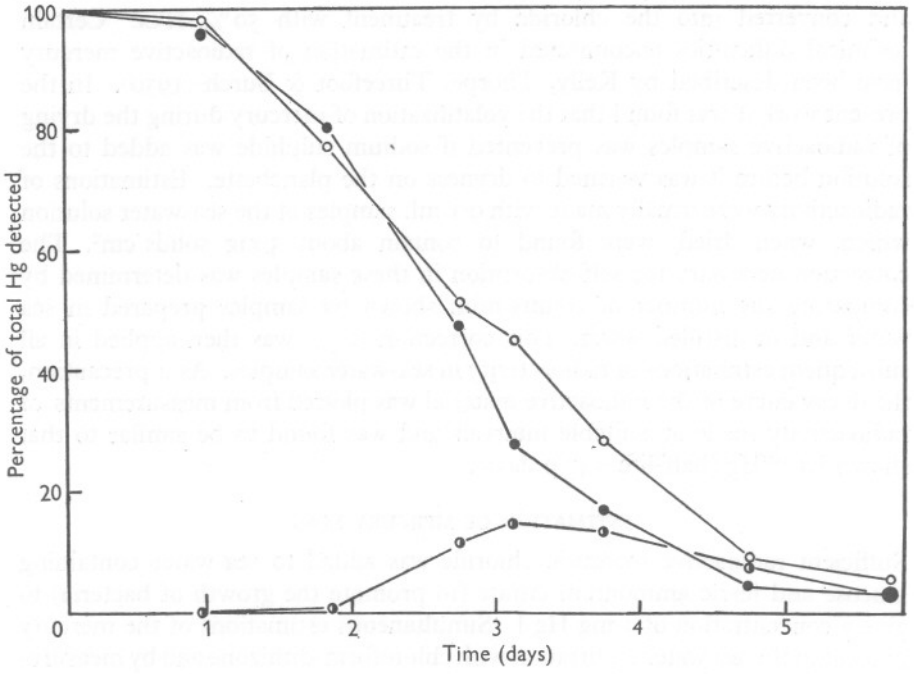

Fig. 1. The loss of mercury as mercuric chloride (1 mg Hg/l.) from sea water as estimated by chloroform-dithizone titrations (●—●), and measurements of radioactivity in solution (○—○). The amounts of mercury present on suspended bacteria are also shown (◑—◑).

LOCATION OF THE LOST MERCURY

Previous experiments had shown that the loss of mercury from stored sea-water solutions of mercuric chloride was genuine, and not simply the results of inadequacies in the chloroform-dithizone procedure. Further experiments were therefore made to locate the mercury which had been lost from solution.

Attachment to walls of storage vessel. In preliminary studies, flasks in which sea-water solutions of mercury had been stored were emptied and fumed out with conc. HNO_3. The acid extract and the cleaned glass were then examined for radioactivity. On no occasion did the mercury so detected account for

more than 1% of that lost. In later experiments, no preliminary treatment with acid was carried out: the flasks were emptied, drained, dried and smashed, and fragments of suitable size were immediately examined for radioactivity. When this procedure was used a much larger amount of mercury was detected, but this was still not enough to account for the total quantity lost. Because of this unexpected finding it became necessary to examine the possibility that some of the mercury had volatilized from solution.

Volatilization from solution. In these experiments a slow stream of air was passed over the sea-water solution and led out to the atmosphere through a series of traps containing various reagents. In the course of these studies the reagents used were ethanol, *o-cyclo*hexanone, distilled-water solutions of cysteine and sodium sulphide, ethyl ether, activated animal charcoal, alumina, powdered silver, acidified permanganate, potassium iodide and sodium hypobromite. However, only charcoal was effective in trapping a significant amount of volatile radioactive compound(s). When the decay curve of this radioactive material trapped on the charcoal was plotted it was found to correspond to that for ^{203}Hg. In different experiments the amounts of mercury detected on the charcoal varied from 5 to 25% of the quantity lost, the minimum value being obtained in an experiment with sea water containing nutrients, and the maximum with untreated sea water.

These preliminary studies led to three conclusions. The first was that some of the lost mercury had volatilized from solution and some had become attached to the walls of the glass vessel. The second was that the attached mercury could itself be converted into a volatile compound by treatment with conc. HNO_3. Thirdly, it appeared that the distribution of the lost mercury between glass and vapour largely depended upon the conditions under which bacteria developed in the solution. In order to examine these possibilities further, the following experiments were carried out.

INFLUENCE OF NUTRIENTS ON THE PATTERN OF MERCURY LOSS

A sample (200 ml.) of sea water containing 1 mg Hg/l. as ^{203}Hg-labelled mercuric chloride was added to each of two flasks. One of the samples was enriched with glucose (0·5 g/l.) and ferric ammonium citrate (1 mg/l.) to promote the growth of bacteria. No additions were made to the other sample. Each solution was examined daily for distribution of radioactivity between the solution, the suspended bacteria, and the walls of the vessel, the latter quantity being determined by estimating the radioactivity on a glass slide suspended vertically in the liquid.

The results of this experiment (Fig. 2) clearly show the influence of bacteria on mercury loss. Thus, compared with untreated sea water, the enriched sample lost mercury at a faster rate, the bacteria in it took up twice as much mercury as did those in the untreated sample, and about twice the quantity of mercury was lost to a glass slide suspended in the solution. There were,

however, certain similarities between the two samples. Thus the amount of mercury removed by suspended bacteria passed through a maximum value at a time when approximately 50% of the mercury had been lost from solution, and the quantity detected on the glass slide rose to a peak one day later. It seemed surprising that the amount of mercury taken up by the glass slide did not continue to increase throughout the whole experiment, and to check this observation, at the end of the experiment the flasks containing the untreated and the enriched samples were emptied, dried, and smashed, and fragments were examined for mercury in the usual way. When this was done 18% of the lost

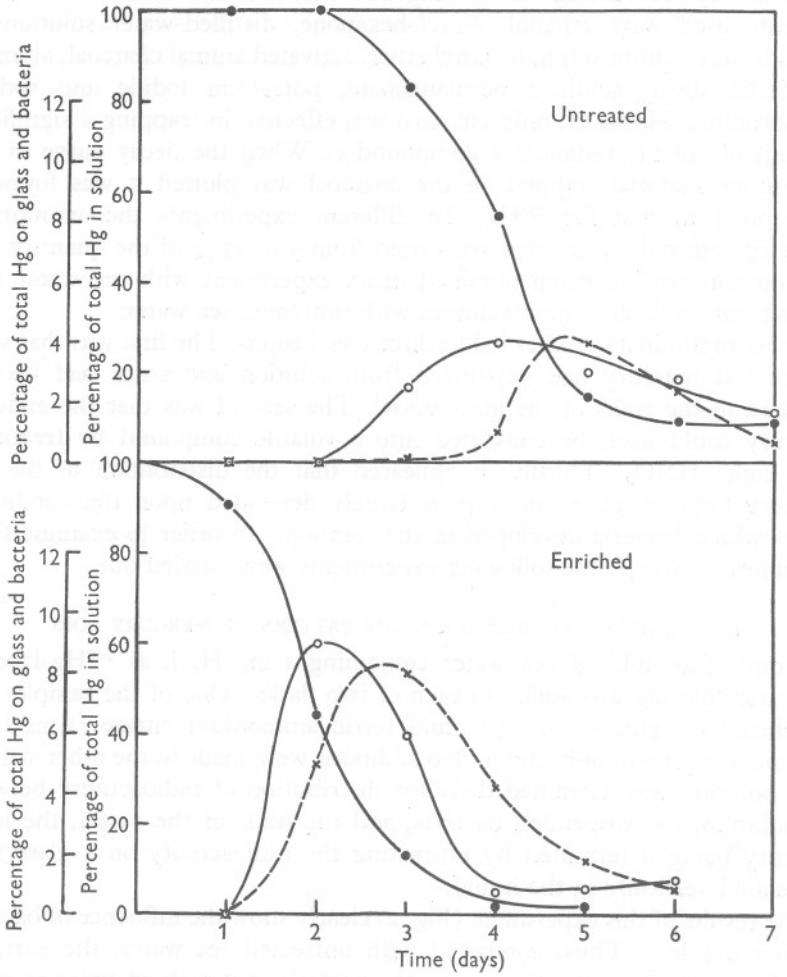

Fig. 2. Distributions of mercury between solution (●—●), suspended bacteria (○—○) and walls of the vessel (×- - -×) after mercuric chloride (1 mg Hg/l.) had been added to enriched (0·5 g glucose and 1 mg ferric ammonium citrate/l.) and untreated sea water.

mercury was detected on the flask which had contained the enriched sample and 9% on the flask which had held the untreated sample. As the values calculated from the radioactivity of the glass slides accounted for less than 1% of the mercury lost from each sample, it was obvious that during the latter half of the experiment, at least, measurement of the amount of mercury on a suspended glass slide was inadequate as an indication of the quantity adsorbed on the walls of the vessel. The reason for this discrepancy became clear when the distribution of mercury over the flask was examined at the end of the experiment, for whereas very little mercury could be detected on the sides, a large amount was found on the bottom of the vessel. It seemed, therefore, that most of the mercury which was lost from solution to the glass of the storage vessel was not fixed by sessile bacteria but sedimented either attached to bacteria themselves or as some insoluble derivative which they formed. Moreover, this sedimented mercury was very difficult to remove and was probably firmly attached to the bottom of the flask by the slimy bacterial film already present.

Next, an attempt was made to examine the possibility that mercury in a volatile form might be released by lysing the bacteria attached to the walls of the glass vessel. To do this, a sample of enriched sea water containing 1 mg Hg/l. was allowed to stand at room temperature for 6 days, after which the solution was removed from the flask and replaced by acetone. The flask was then sealed, a column of activated animal charcoal was inserted between the acetone and the atmosphere, and a current of air was passed through the system for a further 6 days. The charcoal was then extruded from the column, thoroughly mixed and samples (2–4 mg) then worked into a paste with absolute ethanol on planchettes. The samples were then slowly dried and examined for radioactivity. It was found in this experiment that the quantity of radioactivity on the charcoal column corresponded to 5% of the total amount of mercury originally added to the sea-water sample, and approximately one-third of the mercury attached to the glass of the vessel. An attempt to detect further quantities of volatile mercury by reassembling the apparatus with a column of fresh charcoal and continuing the experiment for a further 4 days was unsuccessful, for no additional quantity of volatile mercury was detected.

Further experiments were carried out in order to examine the influence of nutrients on the distribution of the lost mercury between the atmosphere and the surface of the glass vessel. In these experiments one enriched and one plain sea-water sample containing 1 mg Hg/l. (as ^{203}Hg-labelled mercuric chloride) were placed in each of two flasks. The flasks were then sealed and a current of air was passed over the surface of each solution and out to the atmosphere through a column of activated animal charcoal. In order to avoid dismantling the assemblies, daily estimations of mercury loss from the two solutions were obtained from measurements of the radioactivity in identical

samples prepared at the same time but left open to the atmosphere. When these estimations indicated that more than 80% of the mercury originally added to the solutions had been lost, the flasks equipped with charcoal columns were opened and each assembly was examined as follows. The sea water was removed from each flask which was then drained, dried and smashed, and fragments from the sides and bottom of the flask were then examined for radioactivity. Next, the charcoal was extruded from the column and examined for radioactivity. The results of these experiments are shown in Table 3, from which it is clearly seen that whereas a large proportion of the mercury lost from the plain sea-water sample was trapped on the

TABLE 3. INFLUENCE OF NUTRIENTS ADDED TO SEA WATER ON THE PATTERN OF MERCURY LOSS

(Experiment carried out for 6 days at room temperature)

	Enriched sea water (%)	Untreated sea water (%)
Total amount of mercury lost	86	55
Quantity adsorbed on charcoal	15	34
Quantity attached to glass	50	1
Percentage of lost mercury accounted for	76	64

charcoal column, only a small quantity was found on the glass. By contrast, however, in the case of the enriched sample, whereas a large amount of the lost mercury was detected on the glass, a considerably smaller fraction was found on the charcoal. In addition, it was found that the rate of loss of mercury from the plain sea-water solution contained in the flask equipped with a charcoal column was much slower than that from the solution which was exposed to the atmosphere. Thus, although measurements of the radioactivity present in this latter sample indicated that more than 80% of the mercury had gone from the solution in 6 days, similar determinations carried out on the other solution showed that, after 6 days, only 55% of the mercury originally added had been lost.

The experiments just described demonstrated that bacteria influence the loss of mercury from sea-water solutions both quantitatively and qualitatively. Thus, sea water enriched with nutrients loses mercury much faster than untreated sea water, and the distribution of the mercury between volatile compounds and the glass surface of the vessel is markedly different in the two cases, for whereas nutrients favour attachment to the glass, absence of nutrients favours volatilization. In conclusion, it should be stated that in none of these experiments has all the lost mercury been detected. However, it has been shown that part of the mercury on bacteria attached to the glass can be released as a volatile compound when these bacteria are lysed, and this finding draws attention to the possibility that some of the mercury may be volatilized from the flasks when these are dried prior to examination for radioactivity.

DISCUSSION

The results of the present study have emphasized the importance of bacteria as a factor determining the loss of mercury from stored sea-water solutions of mercuric chloride. Consequently, when leaching rates of mercury from anti-fouling compositions are measured, care should be taken to prevent the growth of bacteria in the sea water in contact with the paint film. For not only do bacteria reduce the chloroform-dithizone titres by removing mercury from solution as a volatile compound (or compounds), they also cause a large quantity of the mercury to concentrate at the surface of the glass vessel, in which form it is no longer extracted into chloroform-dithizone.

At present it is not clear why part of the mercury is volatilized from the solution, and part is attached to the walls of the vessel; and, further, why the relative amounts of these fractions are changed by the presence of nutrients in the sea water. However, an observation by Ruska (1947) that certain bacteria can convert mercuric chloride into at least two products may provide a possible answer. For if the bacteria which arise in stored sea water convert the mercury into more than one compound then it is possible that the relative amounts of the compounds produced might depend on the conditions under which the bacteria develop. However, further speculation along these lines is not likely to be profitable until the identities of these compounds have been determined.

SUMMARY

The disappearance of mercury from stored sea-water solutions of mercuric chloride has been studied by means of the chloroform-dithizone procedure and by the use of radioactive mercury (^{203}Hg).

When sea water is enriched with nutrients facilitating the growth of bacteria, the rate at which mercury is lost from the solution is markedly increased. On the other hand, when the sea water is treated in various ways which prevent the development of bacteria, the loss of mercury from solution is considerably reduced.

Rates of loss of mercury measured by the chloroform-dithizone procedure and by the use of tracer isotopes are in good agreement only in the early stages of the experiments. Thus, at a time when approximately half the mercury has been lost, titrations with chloroform-dithizone only account for about 50% of the mercury determined by measurements of radioactivity. Further findings have suggested that this discrepancy arises from the fact that a considerable amount of the mercury is taken up by bacteria and converted into a form which is not detectable with chloroform-dithizone.

A comparison has been made of the patterns of mercury loss from plain sea water and from sea water containing nutrients promoting the growth of bacteria. The mercury lost from the former medium is produced mainly as a volatile compound, only a very small fraction being attached to the glass

surface of the containing vessel. By contrast, a large amount of the mercury lost from the latter medium is attached to the glass and a significantly smaller fraction is volatilized. Some of the mercury attached to bacteria on the walls of the containing vessel can be released in the form of a volatile compound when the bacteria are lysed.

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THE MODES OF ACTION OF TOXIC AGENTS

II. FACTORS INFLUENCING THE TOXICITIES OF MERCURY COMPOUNDS TO CERTAIN CRUSTACEA

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(Text-figs. 1–3)

It is well known that certain alkylmercuric halides are more toxic than inorganic mercury to a number of widely different test organisms, such as fungi (Yoshiyuki & Shintani, 1942), zooplankton (Hoffman, 1950), bacteria (Okamoto & Nagayama, 1952) and molluscs (Bond & Nolan, 1954). However, although the considerable toxicities of the organomercury compounds have often been observed, their modes of action seem to have attracted little attention.

In a recent investigation (Corner & Sparrow, 1956) the toxicities of ethylmercuric chloride and mercuric chloride were compared using two crustacean species as test animals. It was found that whereas the alkylmercuric compound was far more toxic than mercuric chloride to *Artemia salina* (L.), an animal highly resistant to mercury poisoning, the difference between the toxicities of the two compounds to *Elminius modestus* Darwin, a much less resistant species, was far smaller. These findings led to the view that rates of penetration are important factors influencing the toxicities of mercury compounds, and further evidence in support of this concept has now been obtained from the present work. The relative toxicities of a number of organomercury compounds to *Artemia* and to *Elminius* have been measured, and a study made of the extent to which these values are related to the lipoid solubilities of the compounds and their abilities to interact with proteins.

EXPERIMENTS

GENERAL METHODS

Animals

Artemia salina was reared in the laboratory. Larvae were collected 24 h after they had hatched, concentrated in a small volume of filtered sea water, and samples of the concentrate were added to the various toxic media under

test. Adults of *Elminius modestus* were obtained from rocks at Tinside, below the Plymouth Laboratory. They were placed in filtered sea water and the larvae liberated were collected after 1 h and added to the toxic solutions.

Poisons

The organomercury compounds used were the first five members of an homologous series of primary alkylmercuric chlorides and, in addition, *iso*-propyl-, *iso*-amyl- and phenylmercuric chlorides. Inorganic mercury was

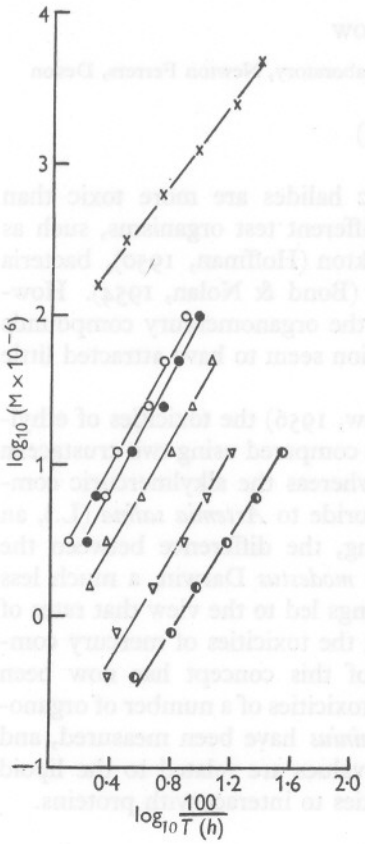

Fig. 1

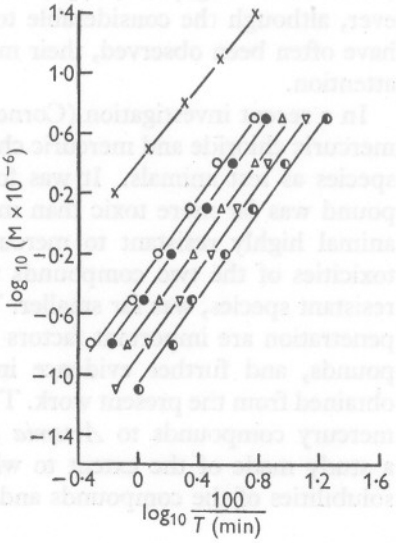

Fig. 2

Fig. 1. Toxicities of mercuric chloride (×—×), methylmercuric chloride (○—○), ethylmercuric chloride (●—●), *n*-propylmercuric chloride (△—△), *n*-butylmercuric chloride (▽—▽) and *n*-amylmercuric chloride (◐—◐) to *Artemia* larvae in sea water, pH 8·1.

Fig. 2. Toxicities of mercuric chloride (×—×), methylmercuric chloride (○—○), ethylmercuric chloride (●—●), *n*-propylmercuric chloride (△—△), *n*-butylmercuric chloride (▽—▽) and *n*-amylmercuric chloride (◐—◐) to *Elminius* larvae in sea water, pH 8·1.

used as mercuric chloride and mercuric iodide. It was found that the organo-mercury compounds were only slightly soluble in sea water, and that as the homologous series was ascended, solubility decreased. In order to obtain a known concentration of each compound in sea water a concentrated solution in warm ethanol (*o-cyclo*hexanone in the case of phenylmercuric chloride) was first prepared, and a measured volume of the solution was then added to the sea water. In this way, sea-water solutions of methyl-, ethyl-, *n*-propyl- and *iso*-propylmercuric chlorides equivalent to 10 mg Hg/l. (5×10^{-5} M) were prepared: the other mercury compounds were used at half this concentration. In all experiments with both species of test animals control tests showed that the quantities of ethanol and *o-cyclo*hexanone present in the toxic solutions had no significant toxic effect.

RELATIVE TOXICITIES

The methods used in toxicity experiments with *Artemia* and *Elminius* were those described in an earlier paper (Corner & Sparrow, 1956). The data from experiments using mercuric chloride and the homologous series of organo-mercury compounds are shown in Fig. 1 (*Artemia*) and Fig. 2 (*Elminius*). By plotting the logarithm of the molar concentration against the logarithm of the reciprocal of the time at which 50% of the animals died (TD_{50}) a linear relationship was found for each poison with each test animal. From these data

TABLE 1. RELATIVE TOXICITIES OF VARIOUS MERCURY COMPOUNDS TO *ARTEMIA*

Standard mercuric chloride solution equivalent to 200 mg Hg/l. (10^{-3} M). TD_{50} values were 12·5 h (Expt. 1) and 16 h (Expt. 2).

Mercury compound	No. of times as toxic as mercuric chloride	
	Expt. 1	Expt. 2
CH_3HgCl	15	15
C_2H_5HgCl	18	17
n-C_3H_7HgCl	47	54
n-C_4H_9HgCl	300	294
n-$C_5H_{11}HgCl$	930	980
i-C_3H_7HgCl	—	25
i-$C_5H_{11}HgCl$	—	450
C_6H_5HgCl	17	23
HgI_2	29	24

TABLE 2. RELATIVE TOXICITIES OF VARIOUS MERCURY COMPOUNDS TO *ELMINIUS*

Standard mercuric chloride solution equivalent to 1 mg Hg/l. (5×10^{-6} M). $TD_{50} = 1$ h.

Mercury compound	No. of times as toxic as mercuric chloride	Mercury compound	No. of times as toxic as mercuric chloride
CH_3HgCl	4·7	i-C_3H_7HgCl	2·4
C_2H_5HgCl	6·8	i-$C_5H_{11}HgCl$	16
n-C_3H_7HgCl	9·7	C_6H_5HgCl	4·3
n-C_4H_9HgCl	16	HgI_2	4·6
n-$C_5H_{11}HgCl$	20		

the concentration of each poison which killed 50% of the test animals in the same time was calculated and compared with that of mercuric chloride as a standard. The ratios of these equitoxic concentrations were then used to determine the relative toxicities of the poisons to each species, and the results are shown in Table 1 (*Artemia*) and Table 2 (*Elminius*). In the course of experiments with *Artemia*, determinations of relative toxicities were made on several occasions over a period of about 6 months, using different batches of test animals at different room temperatures. It was found, however, that the relative toxicities of the poisons, using mercuric chloride as a standard, were fairly consistent (see Table 1).

STUDIES WITH CYSTEINE AND REDUCED GLUTATHIONE

Studies of the nature of heavy metal poisoning have shown that mercury compounds are usually far less toxic to the test material when they are used in the presence of substances which contain a sulphydryl group. Thus, in studies of the inactivation of papain (Hellerman & Perkins, 1934), urease (Hellerman, Chinard & Deitz, 1943; Evert, 1952), succinoxidase (Barron & Kalnitsky, 1947), invertase (Gemmill & Bowman, 1950), amylase and phosphorylase (Ewart, Siminovitch & Briggs, 1953) and yeast carboxylase (Stoppani, Actis, Deferrari & Gonzalez, 1953) it has been found that the inhibitory powers of mercury compounds are much less when the enzyme is protected by such compounds as BAL, cysteine, reduced glutathione and thioglycollic acid. Further, even when the enzyme has been inhibited, the addition of a sulphydryl compound to the system can restore enzymatic activity. Analogous studies carried out with other test material have shown that cysteine and reduced glutathione counteract the inhibitory effects of mercury compounds on the growth of bacteria (Jude, Nordmann, Girard, Nordmann, Servant & Gauchery, 1952) and partially prevent the toxic effects of mercury and copper on *Daphnia magna* (see Holm-Jensen, 1948).

Because of these findings, it seemed of interest to examine the possibility that the toxic effects of some of the mercury compounds used in the present work might be diminished when cysteine or reduced glutathione was added to the toxic solutions: further, that after the test animals had been poisoned, subsequent treatment with thiol compounds might facilitate their recovery. The following experiments were, therefore, carried out.

Protection studies

Using *Elminius* as the test animal, each of six mercury compounds was examined for toxicity when used alone, and when used with a tenfold excess of reduced glutathione. It was found that the thiol compound completely abolished the toxicity of mercuric chloride, and considerably reduced those of methyl-, ethyl- and *n*-propylmercuric chlorides. By comparison, however, its

influence on the toxicity of *n*-butylmercuric chloride was much less, and still less with *n*-amylmercuric chloride (see Table 3).

When a similar study was made with *Artemia*, mercuric chloride could not be used because of the large amounts of glutathione needed to provide a tenfold excess of a lethal concentration of the poison. The results of experiments with the other mercury compounds, however, showed that the toxicities of methyl-, ethyl-, *n*-propyl- and *n*-butylmercuric chlorides were considerably reduced by both cysteine and reduced glutathione, the latter compound being

TABLE 3. THE EFFECT OF REDUCED GLUTATHIONE ON DEATH-RATES OF *ELMINIUS* IN SOLUTIONS OF VARIOUS MERCURY COMPOUNDS

Each poison used at a concentration giving a TD_{50} of 1 h. Reduced glutathione used in tenfold excess of each mercury compound.

Mercury compound	Percentage increase in TD_{50}	Mercury compound	Percentage increase in TD_{50}
$HgCl_2$	∞*	*n*-C_3H_7HgCl	800
CH_3HgCl	900	*n*-C_4H_9HgCl	420
C_2H_5HgCl	870	*n*-$C_5H_{11}HgCl$	410

* Animals died no faster than controls.

TABLE 4. EFFECTS OF CYSTEINE AND REDUCED GLUTATHIONE ON THE TOXICITIES OF MERCURY COMPOUNDS TO *ARTEMIA*

Each poison used in a concentration giving TD_{50} of 10 h. Thiol compounds used in tenfold excess of each poison.

	Percentage increase in TD_{50}	
Mercury compound	Cysteine	Reduced glutathione
CH_3HgCl	84	240
C_2H_5HgCl	87	260
n-C_3H_7HgCl	89	280
n-C_4H_9HgCl	92	270
n-$C_5H_{11}HgCl$	20	96

the more effective of the two. Moreover, as in the experiments with *Elminius*, it was found that the protection which either thiol compound provided against poisoning by *n*-amylmercuric chloride was noticeably less than that observed when any of the other four mercury compounds was used (see Table 4).

Recovery studies

Elminius larvae were placed in sea-water solutions of mercuric chloride (1 mg Hg/l.) and *n*-amylmercuric chloride (0·05 mg Hg/l.) for measured times. The toxic solutions were then centrifuged, the supernatants were decanted off and the larvae were suspended in fresh sea water. After a second centrifuging, half the animals were transferred to plain sea water and the remainder to a sea-water solution of reduced glutathione (5×10^{-5} M). The rates of death of the two sets of animals were then compared. It was found that animals which had 'died' (i.e. become completely quiescent) in the toxic

media did not recover after they had been transferred either to plain sea water or to sea water containing glutathione. It was also observed that, of the animals which had lost their ability to move freely in the toxic solutions, a few completely recovered their mobility when they were transferred to the new media, and the remainder continued to die at a very slow rate. However, of the latter animals, those placed in sea water containing glutathione died much more slowly than the larvae transferred to plain sea water (Table 5).

TABLE 5. EFFECT OF REDUCED GLUTATHIONE ON *ELMINIUS* PREVIOUSLY TREATED WITH MERCURY

GSH = reduced glutathione (5×10^{-5} M) in sea water (SW).

Mercury compound	Time of immersion (min)	Second medium	TD_{50} in second medium (h)
$HgCl_2$	15	SW	29
	15	GSH	42
	30	SW	14
	30	GSH	21
n-$C_5H_{11}HgCl$	15	SW	17
	15	GSH	26
	30	SW	9
	30	GSH	21

TABLE 6. EFFECT OF REDUCED GLUTATHIONE ON *ARTEMIA* PREVIOUSLY TREATED WITH MERCURY

GSH = reduced glutathione (5×10^{-4} M) in sea water (SW).

Mercury compound	Time of immersion (h)	Second medium	TD_{50} in second medium (h)
$HgCl_2$	4	SW	108
		GSH	115
n-$C_5H_{11}HgCl$	4	SW	45
		GSH	57

An experiment identical with the one just described was carried out with *Artemia*. It was found that the influence of reduced glutathione on the death-rate of the animals was negligible (see Table 6).

INHIBITION OF UREASE BY VARIOUS MERCURY COMPOUNDS

Mention was made earlier of studies of the effects of heavy metals on enzymes. These investigations were primarily concerned with establishing whether or not a certain enzyme possessed sulphydryl groups, and the extent to which such groups influenced catalytic activity. More recently, however, Okamoto & Nagayama (1952) have compared the relative abilities of a number of mercury compounds as inhibitors of catalase and as bactericides in order to test the possibility that there was a correlation between their abilities to react with proteins and their potencies as antibacterial agents. No correlation was found. In the present work, similar experiments were carried out to see

whether or not the affinities of mercury compounds for protein, estimated from their abilities to inhibit urease, might be correlated with the toxicities of these compounds to *Artemia* and *Elminius*.

Because the purpose of this study was simply to compare the toxicities of a number of substances to urease, it was not thought necessary to prepare the enzyme in pure crystalline form. Commercial preparations, however, were found to be much too inactive and, accordingly, the enzyme was obtained by aqueous-acetone extraction of Jack-bean meal in the manner described by Sumner (1926). This procedure usually gave a preparation with an activity of 0·20 Sumner units/mg. Various concentrations of each mercury compound in ethanol were added to solutions (5 ml.) of the enzyme (10 Sumner units) in 0·01 M phosphate buffer, pH 6·7 (the amounts of ethanol used had no influence on enzyme activity). Each mixture was allowed to stand for 15 min at room temperature and its ureolytic activity was then compared with that of a control solution, using the colorimetric method of Van Slyke & Archibald (1944). In this way, the extent of the inactivation caused by each concentration of each mercury compound was measured, and the quantity of each poison required to cause a 50% loss of ureolytic activity was estimated. The potencies of the various compounds studied as inhibitors of urease, expressed in terms of that of mercuric chloride as a standard, are shown in Table 7.

TABLE 7. RELATIVE POTENCIES OF VARIOUS MERCURY COMPOUNDS AS INACTIVATORS OF UREASE

Mercury compound	No. of times as effective as mercuric chloride	Mercury compound	No. of times as effective as mercuric chloride
CH_3HgCl	0·76	i-C_3H_7HgCl	0·63
C_2H_5HgCl	0·66	i-$C_5H_{11}HgCl$	0·95
n-C_3H_7HgCl	0·70	C_6H_5HgCl	0·95
n-C_4H_9HgCl	0·76	HgI_2	1·09
n-$C_5H_{11}HgCl$	0·88		

ETHER: SEA-WATER PARTITION COEFFICIENTS OF MERCURY COMPOUNDS

From a study of the permeability of rabbit skin to ethyl-iodide, methanol, ethanol, thiourea, glycerol, urea and glucose, Treherne (1956) found that the rates of penetration of these compounds were closely related to the corresponding ether: water partition coefficients. This result provided quantitative demonstration of an earlier view put forward by Calvery, Draize & Laug (1946) and by Rothman (1943) that the lipoid solubility of the penetrating substance was an important factor in the mechanism of skin permeability.

Because of the possibility that penetration of a lipoid barrier might be an important factor influencing the toxic actions of mercury compounds, it was considered worth while to examine whether or not a close parallel could be found between the ethyl ether: sea-water partition coefficients of these poisons

and their toxicities. Accordingly, the following experiments were carried out using *Elminius* as the test animal.

Each mercury compound was dissolved in sea water to give a concentration corresponding to 1 mg Hg/l. (5×10^{-6} M). A volume of this solution (50 ml.) was then shaken with an equal volume of ethyl ether for 1 min in a separating funnel. After the two phases had separated the lower one was run off and a stream of air was passed through it for 20 min to remove the ether. The quantity of the mercury compound left in this ether-free solution was then determined by comparing its toxicity to *Elminius* with that of a series of sea-water solutions containing known amounts of the mercury compound. The quantity so determined, when subtracted from the amount originally added to the sea water (1 mg Hg/l.), gave the amount extracted by the ether. The ratio of this latter quantity to that remaining in the sea water was then estimated as the partition coefficient.

Because the toxicity data for the mercury compounds had been expressed in terms of mercuric chloride as a standard poison, it was thought necessary to express their lipoid solubilities in a similar way. For this reason it was important that an accurate value should be obtained for the ethyl ether:sea-water partition coefficient of mercuric chloride. It was found, however, that the accuracy of the bio-assay method proved inadequate in the case of mercuric chloride because only a relatively small quantity of this compound was extracted into the ether phase. Accordingly, the value for mercuric chloride was obtained from the use of tracer isotopes. As details concerning the use of radioactive mercury are given elsewhere (Corner & Rigler, 1957), only a brief description of the experimental procedure is included in the present account. ^{203}Hg-labelled mercuric chloride was added to sea water to give a concentration equivalent to 1 mg/l., and estimates of radioactivity in samples (0·1 ml.) were immediately made. After the sea water (50 ml.) had been extracted with an equal volume of ether for 1 min it was again examined for radioactivity in order to determine the quantity of mercury which had been extracted by the ether. From these data the partition coefficient was estimated in the usual way and was found to be 0·26.

Further experiments were carried out with ^{203}Hg-labelled mercuric chloride and *n*-amylmercuric chloride in order to examine the possibility that the aeration of sea-water solutions of mercury compounds in order to remove traces of ether might cause volatilization of the compounds and lead to further errors in the bio-assay method. In these experiments, small quantities of ether were added to sea-water solutions of the two mercury compounds (each equivalent to 1 mg ^{203}Hg/l.) and the media were aerated until the amounts of ether in them were sufficiently small to have no influence on the viability of the test animals (20 min). Determinations of radioactivity in these solutions after aeration had taken place showed that no loss of mercury had occurred and this procedure, therefore, introduced no errors into the bio-assay method.

The partition coefficient for each mercury compound, expressed in terms of that for mercuric chloride as a standard, is shown in Table 8.

TABLE 8. RELATIVE VALUES OF ETHYL ETHER:SEA-WATER PARTITION COEFFICIENTS OF VARIOUS MERCURY COMPOUNDS

Experimental conditions as given in text. Value for standard $HgCl_2$ solution (5×10^{-6} M) = 0·26 at 15° C.

Mercury compound	No. of times partition coefficient greater than that of mercuric chloride	Mercury compound	No. of times partition coefficient greater than that of mercuric chloride
CH_3HgCl	15·9	*i*-C_3H_7HgCl	42
C_2H_5HgCl	63	*i*-$C_5H_{11}HgCl$	1641
n-C_3H_7HgCl	255	C_6H_5HgCl	360
n-C_4H_9HgCl	879	HgI_2	18·9
n-$C_5H_{11}HgCl$	2490		

RESULTS

Ferguson (1939) has drawn attention to the fact that the logarithms of equitoxic concentrations of members of an homologous series decrease linearly as the series is ascended, and that a similar relationship holds when certain physical constants (e.g. water solubility, vapour pressure, etc.) of these compounds are expressed in the same way. In the present work it has been found that if the toxicity data for ethyl-, *n*-propyl-, *n*-butyl- and *n*-amylmercuric chlorides are plotted in the manner shown in Fig. 3, linear relationships exist when the compounds are tested with either *Artemia* or *Elminius*. Differences between toxicities to *Artemia*, however, are far greater than those observed when *Elminius*, which is much more readily poisoned, is used as the test species. These observations confirm and extend the results of some earlier experiments (Corner & Sparrow, 1956) which have shown that orders of difference between the toxicities of certain mercury compounds to a test animal are much greater when the animal used is one which is highly resistant to mercury poisoning. It will also be seen from Fig. 3 that stepwise increments in toxicity to *Artemia*, but not to *Elminius*, approximate to corresponding increments in lipoid solubility, consistent with the view that toxicity to *Artemia* is much more influenced by lipoid solubility than is toxicity to *Elminius*.

Two secondary alkylmercuric halides have been studied in the present work, and these poisons have been found to be significantly less toxic than the corresponding primary compounds to both the test species. Nevertheless, as with the primary compounds, the lipoid solubilities of *iso*-propyl- and *iso*-amylmercuric chlorides are more closely related to their toxicities to *Artemia* than to their toxicities to *Elminius*. Similar results have also been obtained in experiments with methylmercuric chloride and mercuric iodide. An exception, however, is phenylmercuric chloride, which possesses a much greater lipoid solubility than might be expected from its toxicity to either species.

It has been found that thiol compounds protect both *Elminius* and *Artemia* from poisoning by mercuric chloride and primary alkylmercuric chlorides. However, further experiments have shown that when the lipoid solubility of the poison is very high (e.g. *n*-amylmercuric chloride) thiol compounds provide less protection than when the poison used is one of low lipoid solubility (e.g. mercuric chloride). Interest also attaches to the additional finding that when lipoid solubilities greatly influence the toxicities of organomercury

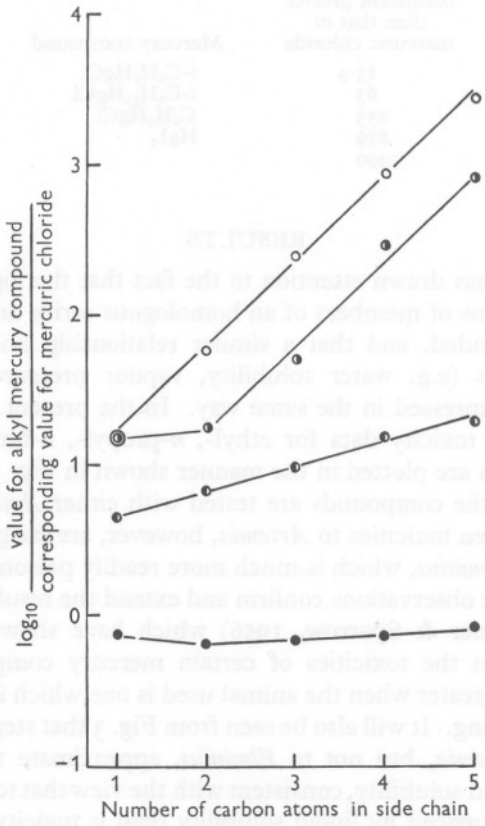

Fig. 3. Toxicity and other data for primary alkylmercuric chlorides. Lipoid solubility, ○—○; toxicity to *Artemia*, ◑—◑; toxicity to *Elminius*, ◐—◐; potency as urease inhibitor, ●—●.

compounds (experiments with *Artemia*) protection of the test animal by thiols is much smaller than under conditions where lipoid solubilities are of less importance (experiments with *Elminius*). Further, when in complementary studies the test animals have been given preliminary treatments with mercury compounds and measurements subsequently made of their rates of death in plain sea water, it has been found that adding reduced glutathione to the sea water has little effect on the viability of *Artemia*, but a marked influence on

that of *Elminius*. A possible explanation of this finding is that the ability of a given poison to interact with proteins on the surface of the test animal may play a more important part in determining its toxicity to *Elminius* than its toxicity to *Artemia*. A further possibility is that reduced glutathione may be able to penetrate *Elminius* but not *Artemia* and inactivate some of the mercury poison after it has reached tissues inside the test animal.

Finally, it is obvious from Fig. 3 that differences between the toxicities of mercury compounds to either *Artemia* or to *Elminius* are significantly greater than corresponding differences between the potencies of the poisons as inhibitors of urease, a finding which lends further support to the view that, in general, the toxicities of these compounds are influenced by their lipoid solubilities far more than by their abilities to combine with proteins.

DISCUSSION

Of the possible mechanisms of action of organomercury poisons, one is that the compounds may interact with the surface of the test animal, and another is that these poisons may penetrate into the tissues and inhibit metabolism. If the poisons exerted their toxic action solely by acting on the surface of the animal it might be expected that a reasonable correlation would be found between the toxicities of the poisons to the test animal and their abilities to combine with proteins. However, neither in the present work, nor in studies made by other workers (Okamoto & Nagayama, 1952) has any correlation been found. Moreover, if surface effects alone are responsible for the toxicities of organomercury compounds it would seem unlikely that great differences would be found between the resistances of different test species to the poisons. In this, and a previous study (Corner & Sparrow, 1956), however, the resistance of *Artemia* to mercury poisons has been found to be of a much higher order than that of *Elminius*.

If, however, in order to penetrate the test animal organomercury compounds had to pass through a lipoid barrier, it would be expected that the toxicities of these compounds would largely depend on their lipoid solubilities: and, further, that the importance of lipoid solubility in determining toxicity would vary with different animals according to whether or not a lipoid barrier was dominant among the factors involved in resistance. In general, the findings made in the present study have shown that the toxicities of organomercury compounds are, in fact, related to the lipoid solubilities of these poisons: and, in addition, that whereas this correlation is close in the case of *Artemia*, it is less so in experiments with *Elminius*. These findings are, therefore, consistent with the view that the mechanism of action of an organomercury compound involves penetration of the test animal.

It is necessary, however, to consider the possibility that in order to act on the animal, the poison may not have to penetrate into the tissues and inhibit metabolic changes, but may exert its toxic effects by some physical mechanism

as soon as it has entered the lipoid barrier. Although the results of the present work provide no definite information on this point it is possible that the anomalous findings made with phenylmercuric chloride are best explained by assuming that interference with metabolism in the tissues of the animal does, in fact, occur. Thus, if phenylmercuric chloride exerted its toxic action once it had entered the lipoid barrier, it is difficult to see why the toxicity of this poison should be so much smaller than one might expect from its considerable lipoid solubility. On the other hand, if this compound became involved in metabolic processes, then it would be possible to account for its reduced toxicity by assuming that it underwent changes in the tissues which resulted in its detoxication. Although mechanisms of detoxication in *Artemia* and *Elminius* are completely unknown, it is possible that these animals may be able to carry out some of the reactions whereby other species are known to detoxicate administered organic compounds (cf. Young, 1939; Williams, 1949). Thus, it is possible that phenylmercuric chloride, like certain other aromatic compounds, might be conjugated *in vivo* with cysteine and so rendered less toxic. In addition, hydroxylation of the aromatic ring might occur, followed by conjugation of the product so formed with sulphuric or glucuronic acids.

Many of the conclusions drawn from the results of the present study are based on the assumption that *Artemia* is able to survive in the presence of large concentrations of mercury compounds simply because these poisons penetrate the species very slowly. It is possible, however, that mercury compounds may enter *Artemia* at rates commensurate with those at which they penetrate *Elminius*, a species which is much more readily poisoned, and that *Artemia* is highly resistant to the poisons either because it possesses a very efficient means of detoxicating them, or because it can tolerate far higher concentrations of the poisons in its tissues. In order to examine these possibilities further, a study is at present being made in which ^{203}Hg-labelled mercuric and *n*-amylmercuric chlorides are being used to measure the rates of uptake of these compounds by *Artemia* and *Elminius*.

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SUMMARY

A study has been made of the toxicities of mercuric chloride, mercuric iodide and methyl-, ethyl-, *n*-propyl-, *n*-butyl-, *n*-amyl-, *iso*-propyl-, *iso*-amyl- and phenylmercuric chlorides to larvae of the crustaceans *Artemia salina* and *Elminius modestus*. With both species it has been found that all the mercury compounds are more toxic than mercuric chloride, that primary alkylmercuric chlorides are more toxic than the corresponding secondary compounds, and that as the homologous series of primary compounds is ascended, toxicities increase. In addition, it has been found that *Elminius* is much more readily poisoned than *Artemia* by each mercury compound, and that differences between the toxicities of the poisons to *Elminius* are much smaller than corresponding differences observed in experiments with *Artemia*.

It has been found that the toxicities of primary alkylmercuric chlorides to both species are considerably less when cysteine and reduced glutathione are added to the toxic media. However, these thiol compounds give less protection against poisoning by the higher homologues. Other experiments have shown that when the animals are given a preliminary immersion in toxic solutions of mercuric chloride and *n*-amylmercuric chloride, and are then transferred to fresh sea water containing reduced glutathione, the influence of the thiol compound on the subsequent death-rate of *Elminius* is significant, but negligible in the case of *Artemia*.

Measurements have been made of the potencies of the compounds as inhibitors of urease in order to estimate their abilities to combine with proteins. No correlation has been found between these abilities and the toxicities of the compounds to either test species.

The lipoid solubilities of the compounds have been estimated from measurements of their ethyl ether : sea-water partition coefficients. In general, a good measure of agreement has been found between the relative lipoid solubilities of both primary and secondary alkylmercuric chlorides and their respective toxicities to *Artemia*. In addition, it has been found that although this correlation is not so exact for *Elminius*, nevertheless, compounds with high lipoid solubilities have usually been found to be more toxic. However, phenylmercuric chloride is an exception in that its lipoid solubility is much higher than would be expected from its toxicity to either test species.

The results of this study, which in general are consistent with the view that organomercury compounds act by penetrating the test animals, have been discussed.

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THE AGE AND GROWTH OF THE SCALLOP, *PECTEN MAXIMUS* (L.), IN MANX WATERS

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(Text-figs. 1–9)

MATERIAL AND METHODS

An important fishery for the scallop, *Pecten maximus* (L.), is carried on during the winter months round the Isle of Man. A knowledge of the age and growth of the scallop would be useful should conservation become necessary with regard to the fishery.

Regular samples of scallops were obtained at roughly weekly or fortnightly intervals throughout the period October 1950–October 1952 from two areas off Port Erin. These were one-quarter to one-half a mile off Bay Fine (Station 1) and one-quarter to one-half a mile off Bradda Head (Station 2) respectively, the depth in each area being 13–16 fm. (23·8–29·3 m) (see chart, Fig. 1). A few samples were obtained from each of three other stations, in 9–11 fm. (16·5–20·1 m) off Gob-yn-Ushtey (Station 3), in 19–20 fm. (34·7–36·6 m) on the Breast (Station 4), and in 28–29 fm. (51·2–53·0 m) $3\frac{1}{2}$ miles W.S.W. of the Chicken Rock (Station 5).

Excepting a few from commercial fishermen, all samples were taken by the research vessels *William Herdman*, *Cypris* and *Runa* of the Marine Biological Station, Port Erin, towing toothed scallop dredges. The bag of the commercial dredge used by the 64 ft. R.V. *William Herdman* had a belly of rings of $\frac{1}{4}$ in. (6·4 mm) steel, with an internal diameter of $3\frac{1}{4}$ in. (82 mm), joined together by small steel ties, and a back of sisal netting measuring 2–3 in. (51–76 mm) from knot to knot. The cross-bar was 6 ft. (1·83 m) long and carried teeth, $3\frac{1}{2}$ in. (89 mm) apart, which protruded $1\frac{3}{4}$ in. (44 mm). Such a dredge captures only a few small scallops, and it was assumed that the size of the rings and mesh of the bag were the effective factors in selection. A smaller dredge was fitted with an inner lining of $\frac{3}{8}$ in. (9·5 mm) mesh shrimp netting in an attempt to catch smaller members of the scallop population. This small-mesh dredge had a cross-bar 4 ft. (1·22 m) long, carrying teeth 3 in. (76 mm) apart which protruded 2 in. (51 mm). The *Cypris* and *Runa*, which are considerably smaller than the *William Herdman*, used 4 ft. (1·22 m) and 3 ft. (0·91 m) dredges, both commercial and small-mesh. Baird & Gibson (1956) have since suggested that tooth-spacing is the effective agent in size selection, but the small-mesh dredge, nevertheless, took numbers of small

scallops by digging deep into the bottom and filling up with gravel and shells, thus acting as a complete bottom sampler.

Individual hauls varied in duration from 7 to 20 min. and in speed of towing from 2 knots (by the *Cypris* and *Runa*) to 3 knots (by the *William Herdman*).

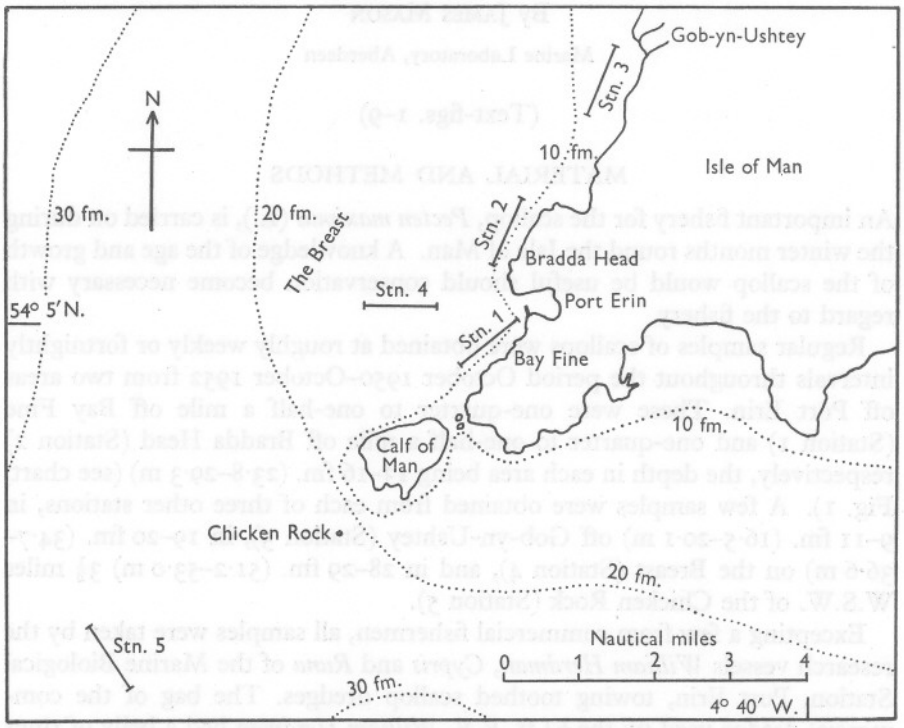

Fig. 1. Chart of S.W. Isle of Man, showing the sampling stations. Depth contours in fathoms.

Various measurements were made on the scallops caught. The over-all length (anterior-posterior axis), breadth (dorso-ventral axis), and thickness (lateral axis) were measured on a specially designed measuring board. The over-all length and breadth are in reality the length and breadth of the rounded, or right, valve of the shell, which overlaps the flat, or left, valve. Dividers were used to measure the distance from the umbo to the edge of the flat valve, and to each of the annual growth rings (see below) on the flat valve along the dorso-ventral axis. All measurements were to the nearest millimetre below the value shown on the scale.

AGE-ANALYSIS

The growth-rings

The shell of *Pecten maximus* bears distinct concentric growth-rings, which are white in colour and translucent. They show more clearly on the reddish brown flat valve than on the white round valve. They occur regularly and in approximately the same position on most shells.

In addition, the shell bears numerous regularly occurring concentric striae, 0·1–0·3 mm apart, which are prominent and raised over most of the shell, but less so in a slightly concave area within 20–25 mm of the umbo. These striae are the result of the manner in which the shell is enlarged by the deposition of new material at its edge (Coker, Shira, Clark & Howard, 1921), so that each one represents the edge of the shell at the time of its deposition. The striae tend to become worn on the round valve of the shell, which is in contact with the sea-bed, and, on account of this, they were examined on the upper, flat valve.

The growth-rings are ½ mm or less wide, and are made up of striae which are crowded together about 0·05 mm apart and less prominent than elsewhere. Immediately outside a ring, on the side away from the umbo, the striae become more raised, assume a pale brown colour, and become farther (about 0·3 mm) apart. After a few millimetres the striae take on a darker hue, and become gradually closer together until, just before the next ring, they are about 0·1 mm apart. This description applies to the shell between the second and third rings from the umbo. Farther from the umbo, both the growth rings and the striae are somewhat closer together, but a similar series of changes is seen.

Dakin (1909) considered that the growth-rings may indicate the age of the shell. Priol (1930) and Elmhirst (1945) also considered that they were laid down annually. Tang (1941), working on *P. maximus* at Port Erin, found that a ring is laid down in April, May or June, and said that, while it is not certain that all rings are laid down at yearly intervals, there is probably a good deal of agreement between the number of rings and the age of the scallop. I examined the edge of the flat valve of the shell throughout the year, and found that only one ring is laid down each year, in the spring.

The growth-ring is narrow and is laid down slowly, taking perhaps several weeks, but its deposition is followed at once by rapid growth, so that any growth-ring near the edge of the shell has very recently been laid down. In each month the number of scallops was noted which had a ring within 3 mm of the edge of the flat valve. Growth becomes slower in older scallops, and the later growth-rings become close together and difficult to distinguish, and so only scallops which had fewer than five growth-rings were included. The results are shown in Fig. 2. The somewhat low percentages are due to the long period of time (March–May) during which rings are laid down, so that some scallops have acquired more than 3 mm of new growth before others have commenced to lay down their ring.

Evidence that only one ring was laid down each year was afforded also by a tagging experiment. Six living tagged scallops were recaptured which had spent one spring in the sea, and each of these had one more ring than when it was released. Of thirty-seven scallops recaptured before they had spent a spring in the sea, none had acquired a further ring. Occasionally a disturbance-ring was found on these scallops where the edge of the shell was at the time of tagging, being probably caused by a retraction of the mantle edge away from the edge of the shell during tagging. Such a ring differs from an annual ring in that it has no small, crowded striae, and that the striae on either side of it are equally spaced. Such false rings also occur occasionally in nature.

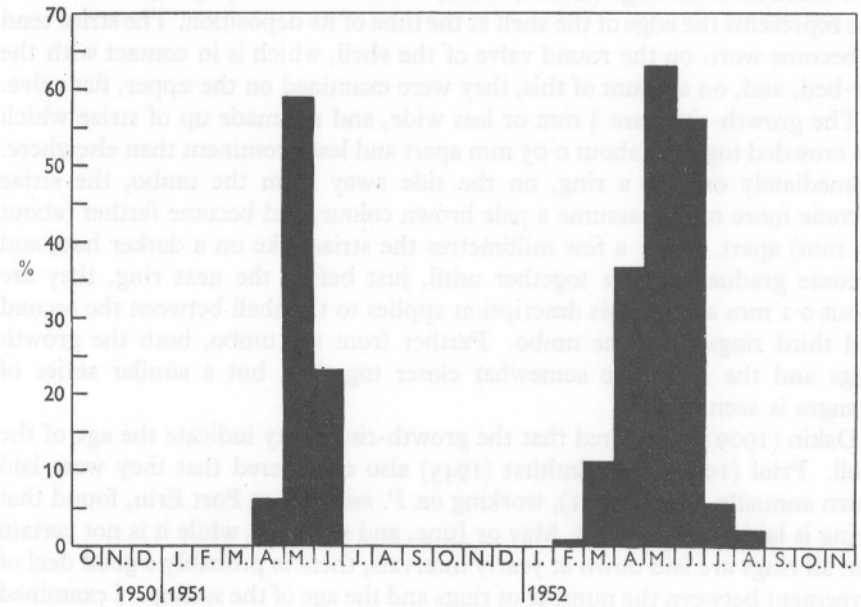

Fig. 2. Percentages of scallops with fewer than five growth-rings, which had a growth-ring within 3 mm of the edge of the shell (3592 scallops examined).

Gibson (1956), by means of a similar tagging experiment, obtained evidence of the annual nature of the growth-rings on the shell of *P. maximus* in Irish waters.

In subsequent pages, the area of shell between two successive annual growth-rings, or between the umbo and the first ring, will be called a growth-band. A scallop is aged by the number of growth-rings and the presence or absence of new growth outside the outermost ring. Thus 5+ indicates that the shell has five rings, with new growth outside the fifth, while 4 indicates that the fourth ring has just been laid down at the edge of the shell.

Length of life

Tang (1941) recorded a scallop, captured off Port Erin, which had twenty-two growth-rings; the oldest one I caught had eighteen rings.

GROWTH

THE FIRST GROWTH-BAND

If the size-frequency of the first growth-band is plotted, a bimodal distribution is obtained; Bradda and Bay Fine scallops with from 1 to 15 rings were used for this investigation. The results are presented in Fig. 3, the widths being in 2 mm groups. The modal values are 19 and 39 mm respectively, and

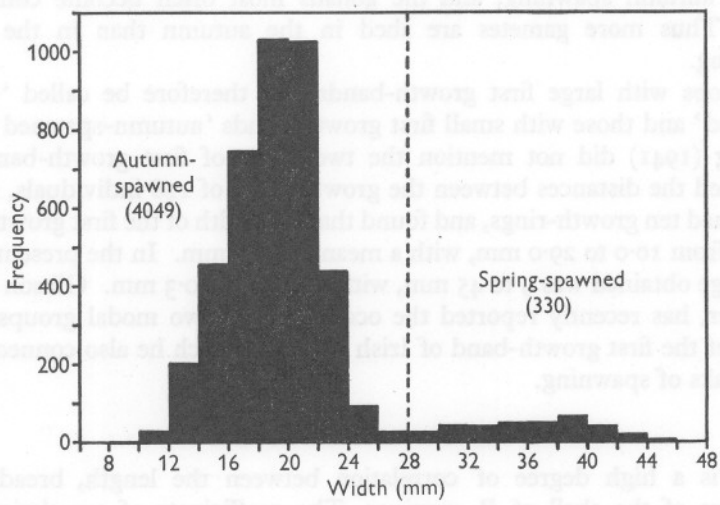

Fig. 3. Width-frequency of the first growth-band.

the curve is divided arbitrarily at 28 mm, giving two groups of scallops, a majority with small, and a minority with large, first growth-bands. Of 4379 scallops examined, 4049, or 92·5% had small, and 330, or 7·5% had large, first growth-bands.

The two types of first growth-band can be correlated with the breeding cycle of the scallop. *P. maximus* in Manx waters has two main spawnings each year, a spring spawning in April or May and an autumn spawning in late August or September, while there is a small summer spawning in July or early August. Growth of the scallop ceases in December, and the resumption of growth in spring results in the appearance of the growth-ring (see later, p. 485). Spring-spawned scallops would thus grow for a greater length of time before the first cessation of growth than would autumn-

spawned individuals. It is suggested that most of the scallops forming the minor group, those with large first growth-bands, arise from the spring spawning, and that most of those forming the major group, those with small first growth-bands, arise from the autumn spawning, while a few of the latter probably arise from the small summer spawning.

Although there are many possible factors which can influence the success of a brood, the difference in the numbers of scallops constituting the two groups can to some extent be accounted for by the amount of spawn released in each spawning. Only those which have just deposited, or are about to deposit, their fourth or any subsequent growth-ring, take part in the spring spawning, and their gonads become only partially spent. On the other hand, mature scallops of all ages (those with two or more growth-rings) take part in the autumn spawning, and the gonads most often become completely spent. Thus more gametes are shed in the autumn than in the spring spawning.

Scallops with large first growth-bands will therefore be called 'spring-spawned' and those with small first growth-bands 'autumn-spawned'.

Tang (1941) did not mention the two types of first growth-band. He measured the distances between the growth-rings of 128 individuals, each of which had ten growth-rings, and found that the width of the first growth-band varied from 10·0 to 29·0 mm, with a mean of 19·0 mm. In the present study, the range obtained was 9 to 45 mm, with a mean of 20·3 mm. Gibson (1956), however, has recently reported the occurrence of two modal groups in the width of the first growth-band of Irish scallops, which he also connects with two peaks of spawning.

THE ANNUAL GROWTH RATE

There is a high degree of correlation between the length, breadth and thickness of the shell of *P. maximus*. The coefficients of correlation were worked out on 614 scallops of all ages from 0+ to 13+. The coefficient of correlation between length and breadth is 0·9937, and that between length and thickness is 0·9597. Furthermore, a high degree of correlation exists between the length of the scallop and the breadth of the flat valve. The coefficient of correlation, worked out on 414 scallops of all ages from 0+ to 13+, is 0·9954. The scallop, in fact, grows proportionately in all dimensions, and retains virtually the same shape throughout its life, with the exception of a concavity on the upper valve during the first year or so. The annual increment of any one of these dimensions will, therefore, give a reliable indication of the rate of growth from one year to another.

Growth curves for *P. maximus* have been drawn, using Bradda and Bay Fine scallops, from the two following measurements: (i) position of successive annual growth-rings on the flat valve, and (ii) annual increase in length, breadth and thickness of the whole shell.

(i) Since each growth-ring represents the position of the edge of the shell at the end of an annual growth period, it is possible to measure directly on the shell of any scallop, the breadth of the flat valve of that scallop at the end of each growth period in its life. By measuring the distances of the various growth-rings from the umbo it is possible to draw up a growth curve. The

TABLE 1. MEAN DISTANCES OF THE GROWTH-RINGS FROM THE UMBO (FLAT VALVE)

		Growth-rings					
		1	2	3	4	5	6
Autumn-spawned scallops	Number measured	4049	3519	2791	1888	1130	526
	Mean distance (mm)	19·0	48·0	76·4	94·6	104·9	112·3
Spring-spawned scallops	Number measured	330	247	141	60	32	25
	Mean distance (mm)	36·2	65·8	88·1	101·8	109·1	113·4

		Growth-rings				
		7	8	9	10	11
Autumn-spawned scallops	Number measured	207	132	67	40	31
	Mean distance (mm)	114·2	119·2	121·6	123·9	126·1
Spring-spawned scallops	Number measured	18	—	—	—	—
	Mean distance (mm)	114·6	—	—	—	—

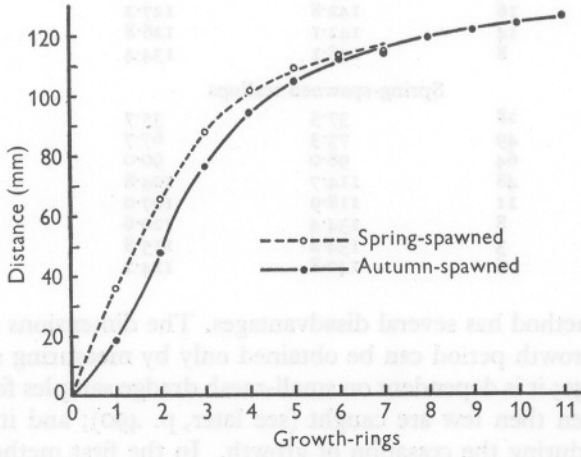

Fig. 4. Mean distances of the growth-rings from the umbo (flat valve).

results are shown in Table 1 and Fig. 4. Only the first eleven rings were measured in autumn-spawned scallops because of the crowding together of the later rings and the small numbers of older scallops obtained. Few spring-spawned scallops were found with more than seven rings.

(ii) Growth curves were drawn by plotting the length, breadth and thickness of scallops measured during the cessations of growth in the winters of

1950–51 and 1951–52; figures for the two winters were combined. No scallop was measured which showed new growth at the edge of the shell. In this method, a scallop which has no growth rings has completed its first growth period, one with one ring has completed two growth periods, and so on. Autumn-spawned scallops with eleven or fewer growth-rings and spring-spawned scallops with seven or fewer rings were used. The results are given in Table 2 and Fig. 5.

TABLE 2. LENGTH, BREADTH AND THICKNESS DURING THE CESSATION OF GROWTH OF AUTUMN- AND SPRING-SPAWNED SCALLOPS

(Data from small-mesh samples, December 1950–March 1951 and December 1951–April 1952, supplemented in the older age-groups by data from commercial samples.)

No. of completed growth-bands	No. measured	Mean length (mm)	Mean breadth (mm)	Mean thickness (mm)
		Autumn-spawned scallops		
1	4	21·2	20·0	5·2
2	173	53·5	50·1	14·7
3	574	87·7	80·8	23·4
4	361	108·1	98·5	28·7
5	330	118·6	107·3	31·2
6	245	128·0	114·9	34·0
7	103	131·8	117·7	35·2
8	40	136·8	122·8	36·0
9	40	137·9	124·0	36·9
10	16	142·8	127·2	38·9
11	14	142·1	126·8	38·6
12	8	148·1	134·4	41·8
		Spring-spawned scallops		
1	28	37·5	35·7	10·4
2	49	73·3	67·7	19·1
3	64	98·0	90·0	26·0
4	48	114·7	104·8	30·8
5	11	118·9	107·0	30·7
6	8	134·4	120·6	35·8
7	3	134·2	115·8	36·3
8	6	140·8	124·2	36·3

The second method has several disadvantages. The dimensions at the end of a particular growth period can be obtained only by measuring scallops of that particular age; it is dependent on small-mesh dredge samples for younger scallops, and even then few are caught (see later, p. 490); and it must use scallops caught during the cessation of growth. In the first method, on the other hand, all the growth-rings can be measured on every shell; scallops from the commercial dredge can be used, since information about the early years of the scallop's life can be obtained from older shells; and scallops caught at any time of the year can be used.

In the first method, data from scallops of different year-classes are grouped together, thereby masking any variation in growth rate there may be from year to year. Such variation could be shown by measuring one particular growth-band, say the third, in scallops of all ages in one particular season.

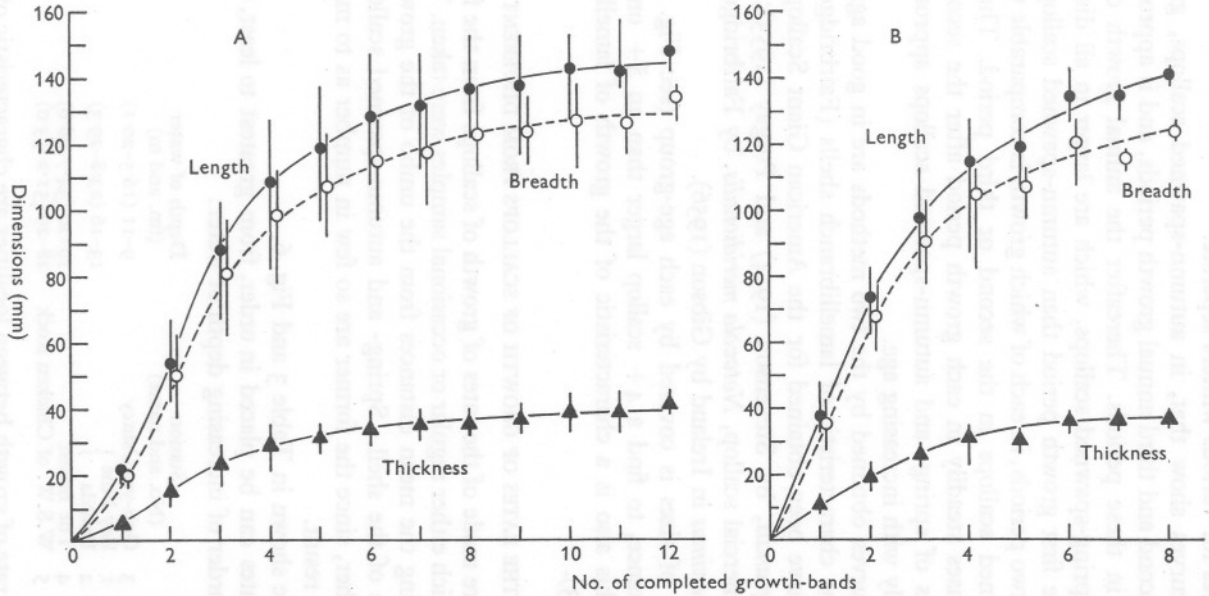

Fig. 5. Length, breadth and thickness of scallops of various ages measured during the cessation of growth. Vertical lines represent the range of sizes in each age-group. Data for breadth are displaced slightly to avoid confusion with length data. (A) Autumn-spawned scallops. (B) Spring-spawned scallops.

The second method would also afford a means of comparing the rates of growth in different years if sufficient scallops were measured to allow of keeping the figures for various winters separate.

The growth curves show that, in autumn-spawned scallops, growth is greatest in the second and third annual growth periods, and is approximately equal in extent in these periods. Thereafter the annual growth decreases progressively. Spring-spawned scallops, which are larger in all dimensions at the end of the first growth period than autumn-spawned scallops, grow most in the first two periods, in each of which growth is comparable with that of autumn-spawned scallops in the second or third period. The annual increment decreases steadily in each growth period after the second. The mean dimensions of spring- and autumn-spawned scallops approach each other more closely with increasing age.

The growth curves obtained by the two methods are in good agreement, and are of a type characteristic of lamellibranch shells (Fairbridge, 1953). Similar curves have been obtained for the American Giant Scallop, *Placopecten* (*Pecten*) *grandis*, by Stevenson (1934) and Posgay (1953); for the Tasmanian commercial scallop, *Notovola meridionalis*, by Fairbridge (1953); and for *Pecten maximus* in Ireland by Gibson (1956).

A large range of sizes is covered by each age-group (see Fig. 5); it is possible, for instance, to find a 4+ scallop larger than an 8+ one in the same sample. This also is a characteristic of the growth of lamellibranchs (Fairbridge, 1953).

COMPARISON OF THE RATES OF GROWTH OF SCALLOPS FROM DIFFERENT DEPTHS

Comparisons were made of the rates of growth of scallops from the five areas (p. 473) from which either regular or occasional samples were taken. This was done by measuring the mean distances from the umbo of the growth-rings on the flat valve of the shell. Spring- and autumn-spawned scallops were considered together, since the former are so few in number as to make little difference to the result.

The results are shown in Table 3 and Fig. 6.

The growth rates can be placed in order, from greatest to least, to correspond with the order of increasing depth of water:

Station (No. and name)	Depth of water (fm. and m)
3 Gob-yn-Ushtey	9–11 (16·5–20·1)
1 Bay Fine 2 Bradda	13–16 (23·8–29·3)
4 The Breast	19–20 (34·7–36·6)
5 W.S.W. of Chicken Rock	28–29 (51·2–53·0)

Differences in rate of growth between localities are characteristic of lamellibranchs (Fairbridge, 1953). Several factors have been suggested to account for local differences of growth rate in pectinid and other molluscan species,

TABLE 3. MEAN DISTANCES FROM THE UMBO OF GROWTH-RINGS ON THE FLAT VALVE OF THE SHELL

(Spring- and autumn-spawned scallops combined.)

		Growth-rings									
		1	2	3	4	5	6	7	8	9	10
Bay Fine (Stn. 1)	Number measured	1977	1732	1385	1013	633	277	108	51	22	12
	Mean distance (mm)	19·6	48·4	76·6	94·8	105·2	112·7	118·3	123·1	125·4	128·4
Bradda (Stn. 2)	Number measured	2402	2034	1547	935	529	274	117	90	51	31
	Mean distance (mm)	20·8	49·9	77·2	94·7	104·7	112·0	110·4	116·9	119·5	121·9
Gob-yn-Ushtey (Stn. 3)	Number measured	117	117	100	96	91	75	62	40	11	10
	Mean distance (mm)	22·3	54·8	83·9	102·3	112·6	118·4	122·0	124·6	129·9	132·0
Breast (Stn. 4)	Number measured	116	116	114	100	88	48	28	22	11	5
	Mean distance (mm)	19·4	46·0	70·4	87·5	96·7	103·2	109·3	112·3	114·7	117·5
Chicken (Stn. 5)	Number measured	100	100	100	100	100	93	85	58	28	27
	Mean distance (mm)	18·7	39·8	62·4	82·0	95·1	101·8	105·5	108·9	110·7	111·5

including currents (Gutsell, 1930; Fairbridge, 1953), temperature (Coe & Fox, 1944) and the nature of the sea bed (Fairbridge, 1953).

Gibson (1956) found that scallops living on sheltered beds grew more quickly than those on exposed beds, and suggested that this is due to excessive particle bombardment interfering with feeding on the latter beds. This could not be the cause of the differences in growth rate between different areas in the present study, since all the areas were exposed.

In the present study, scallops living in the shallowest water were found to grow more quickly than those in deeper water. It is suggested below (p. 489) that the growth of *P. maximus* is influenced by temperature. It is of interest

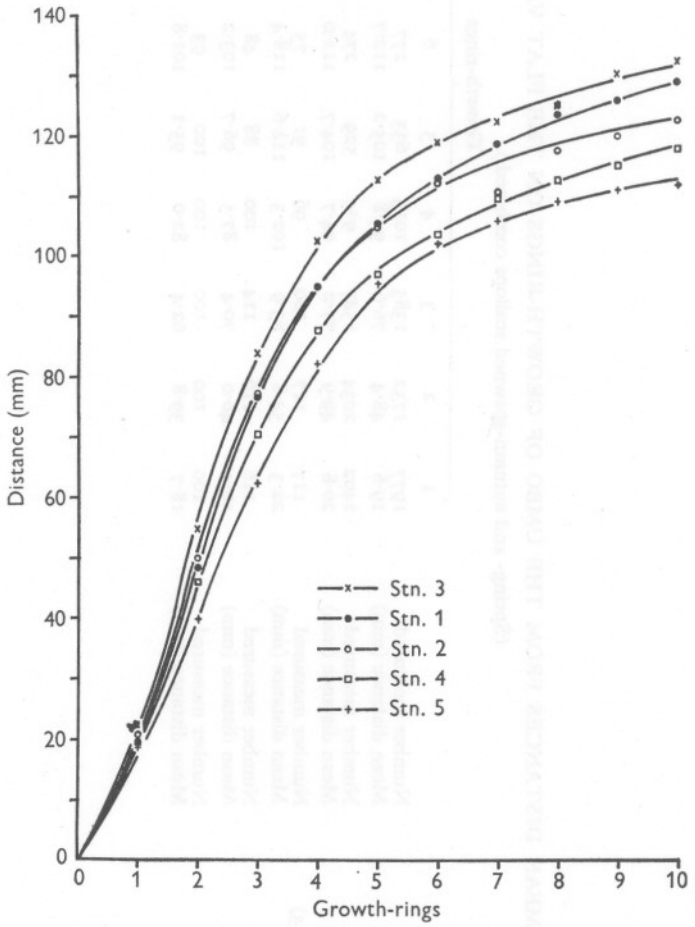

Fig. 6. A comparison of the rates of growth of scallops from five areas (see chart, Fig. 1). The graph shows the mean distances from the umbo of the growth-rings on the flat valve of the shell. Data for spring- and autumn-spawned scallops are combined.

in this connexion that from May to August, when the scallop is growing most rapidly, bottom temperatures inshore are higher than those offshore,[1] probably resulting in a higher rate of growth on the shallower, inshore beds.

THE ANNUAL PERIOD OF GROWTH

The period of growth was determined by measuring throughout the year the width of shell outside the outermost growth-ring on the flat valve of the shell of Bradda scallops, spring- and autumn-spawned scallops being treated separately. Autumn-spawned scallops with 0–5 growth-rings were used, but insufficient spring-spawned scallops were obtained with more than three rings. Since the annual growth-ring is laid down some time in March, April or May, it is necessary to consider the period March 1951–May 1952 in order to cover a complete growth period. The monthly measurements are, where necessary, reinforced by data from the corresponding month of the other year. Samples taken in the small-mesh dredges were used, supplemented in the larger sizes by scallops from commercial samples.

The results (Table 4 and Fig. 7) show that growth commences in March, April or May, and is most rapid from June to September or October, when it begins to slow down, stopping altogether from December until the following March, April or May. These results agree well with those of Gibson (1956), who found that growth of *P. maximus* in Irish waters ceases from November to February.

With two exceptions, all the scallops which had not yet deposited their first growth-ring were obtained between December and May, after the completion of their early growth. The exceptions were two scallops, 3·5 and 3·0 mm long, which were found on the Bradda bed in August 1952. These probably arose from the small spawning of July 1952, but since this is not certain they were not included in Table 4 and Fig. 7. No suggestion can be advanced at present to explain my inability to find more young specimens; Elmhirst (1945) found many between 0·7 and 4·0 mm attached to *Laminaria saccharina* in the Firth of Clyde in July and August.

POSSIBLE FACTORS CAUSING CESSATION OF GROWTH AND THE DEPOSITION OF THE ANNUAL RING

The growth of an animal is the total result of many interacting factors, of which temperature is well known to be important. With scallops, Belding (1931) found that growth of *Pecten irradians* ceased during the cold winter months, and was resumed in May when the temperature of the water had reached 45–50° F (7–10° C). But other factors may have to be taken into account—for instance alternate scarcity and abundance of food (see Thompson, 1942). It has been suggested that in *P. irradians*, cessatian of growth is caused in

[1] Data kindly provided by Mr D. J. Slinn. The temperatures were taken on the Bay Fine bed and at a position near the Chicken Rock bed (Station 5).

TABLE 4. GROWTH OF SHELL (IN MM) BEYOND THE LAST-FORMED ANNUAL RING, THROUGHOUT THE YEAR

Number of growth-rings		M.	A.	M.	J.	J.	A.	S.	O.	N.	D.	J.	F.	M.	A.	M.
Autumn-spawned scallops, age-groups 0 to 5																
0	Number measured	—	—	—	—	—	—	—	—	—	1	1	2	—	—	4
	Mean growth	—	—	—	—	—	—	—	—	—	19·5	15·5	20·5	—	—	22·3
1	Number measured	—	—	—	4	—	2	3	3	9	9	6	12	31	7	—
	Mean growth	—	—	—	9·5	—	22·5	24·0	26·0	30·4	31·9	30·7	31·2	30·1	31·3	—
2	Number measured	1	27	38	20	15	8	9	7	35	5	9	50	5	37	12
	Mean growth	1·0	2·2	4·9	7·9	12·7	18·8	21·3	25·0	27·5	28·4	30·1	30·4	30·4	30·9	30·0
3	Number measured	3	24	74	127	36	17	80	66	52	19	45	90	49	45	9
	Mean growth	2·0	1·9	2·9	4·6	7·6	11·5	14·1	15·9	17·8	18·8	17·8	18·0	18·6	18·9	18·5
4	Number measured	—	29	49	52	16	8	13	24	9	8	16	12	13	5	22
	Mean growth	—	2·0	1·7	2·3	5·2	6·3	9·4	10·4	12·2	11·4	11·6	12·2	12·0	13·6	10·7
5	Number measured	—	3	12	58	43	27	22	20	32	9	35	22	21	33	16
	Mean growth	—	0·3	1·5	1·6	3·3	4·4	5·0	6·2	7·5	7·1	7·3	6·8	7·8	7·8	7·3
Spring-spawned scallops, age-groups 0 to 3																
0	Number measured	—	—	—	—	—	—	—	—	—	—	1	2	13	—	2
	Mean growth	—	—	—	—	—	—	—	—	—	—	30·0	33·5	34·2	—	36·5
1	Number measured	—	1	1	1	—	—	—	5	7	8	2	13	8	5	—
	Mean growth	—	4·0	3·0	10·0	—	—	—	25·2	26·6	30·4	29·5	31·2	28·1	33·0	—
2	Number measured	1	19	10	6	5	12	7	5	2	—	11	6	32	13	—
	Mean growth	1·0	2·5	4·7	7·3	9·4	15·8	17·6	19·8	21·5	—	22·5	20·8	21·7	23·7	—
3	Number measured	—	1	13	10	6	1	12	17	15	6	8	9	7	8	2
	Mean growth	—	1·0	1·8	3·0	6·8	8·0	10·7	10·3	12·1	14·0	13·1	12·1	12·9	14·5	15·0

Rhode Island waters by spawning (Risser, 1901), and in North Carolina waters by gonad development (Gutsell, 1930). Gonad development is also suggested in *Chlamys varia* (Dalmon, 1935) and in *Notovola meridionalis* (Fairbridge, 1953). Tang (1941), working on *Pecten maximus* at Port Erin, assumed that the growth-ring which was laid down in April, May or June represented not the resumption but the cessation of growth. Finding more than 50% of scallops with running gonads in these months, he stated, erroneously, that the cause

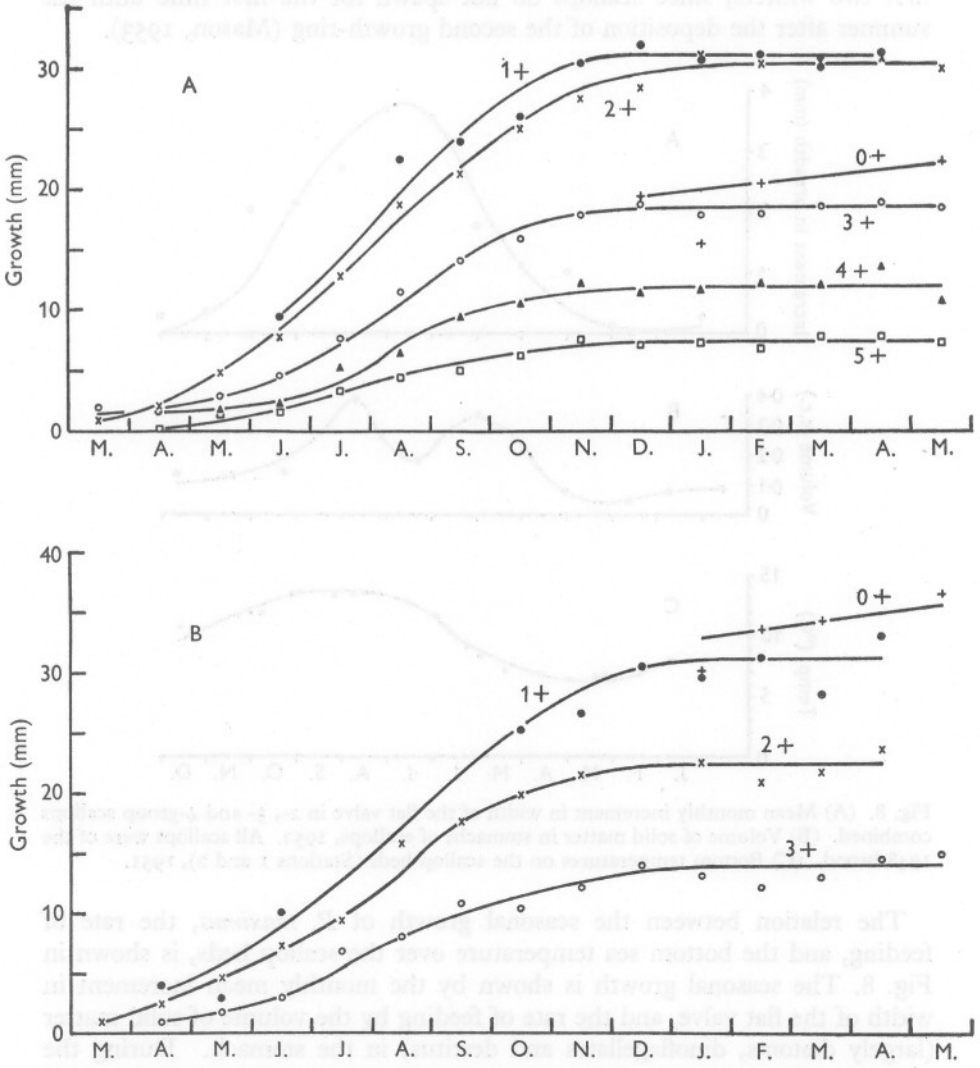

Fig. 7. Growth of shell (in mm) beyond the last-formed annual ring, throughout the year. (A) Autumn-spawned scallops, age-groups 0–5. (B) Spring-spawned scallops, age-groups 0–3.

of cessation of growth may be correlated with the poor condition after the formation of gametes and spawning.

Spawning cannot be an effective factor in causing the cessation of growth of *P. maximus*, since spawning occurs in April or May and in July, August and September, all during the period of growth, while growth ceases from December to March, during which period there is no spawning. Spawning cannot possibly be responsible for the cessations of growth in the animal's first two winters, since scallops do not spawn for the first time until the summer after the deposition of the second growth-ring (Mason, 1953).

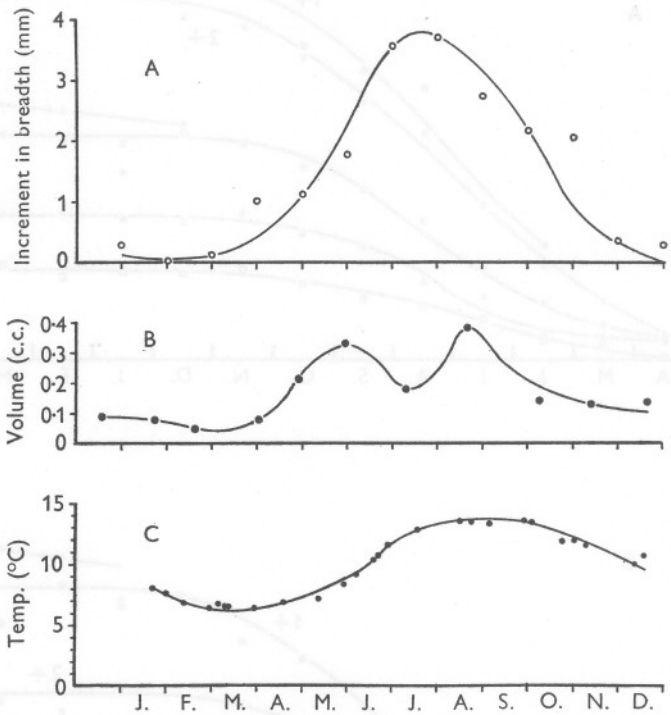

Fig. 8. (A) Mean monthly increment in width of the flat valve in 2-, 3- and 4-group scallops combined. (B) Volume of solid matter in stomachs of scallops, 1952. All scallops were of the 1948 brood. (C) Bottom temperatures on the scallop beds (Stations 1 and 2), 1951.

The relation between the seasonal growth of *P. maximus*, the rate of feeding, and the bottom sea temperature over the scallop beds, is shown in Fig. 8. The seasonal growth is shown by the monthly mean increment in width of the flat valve, and the rate of feeding by the volume of solid matter (largely diatoms, dinoflagellates and detritus) in the stomach. During the cessation of growth, the sea temperature is at its annual minimum, and the rate of feeding is at its lowest. The latter may be due to cold, to lack of

available food, or to both. Gonad development occurs throughout the year, but most slowly in winter, possibly owing to low temperature, low rate of feeding, or both.

It is likely that several factors act together to cause the annual cessation of growth of *Pecten maximus*. The following hypothesis is tentatively suggested. During the cold of winter, body processes occur slowly, and feeding is sufficient for slow gonad development, but not growth, to occur. With the higher temperature of summer the body processes are speeded up, and feeding is sufficiently high for more rapid gonad development and also growth to occur, even during the slight drop in feeding in July. (Too much significance should probably not be attached to the July minimum, as only one sample of stomach contents was obtained between May and August.)

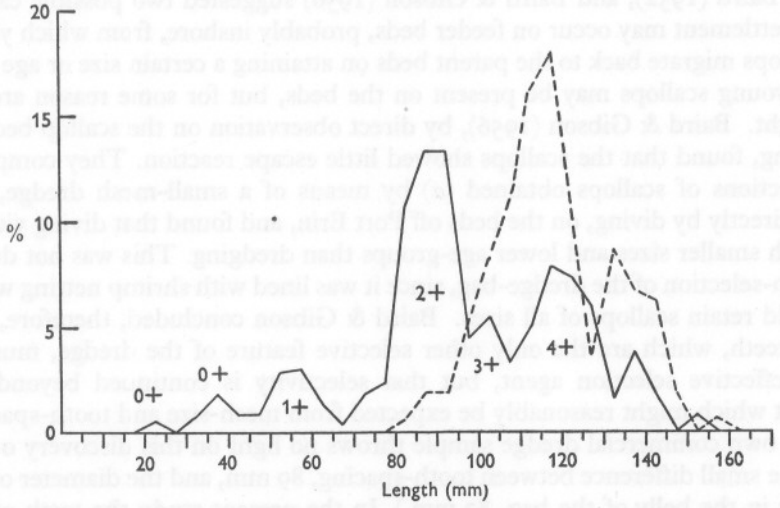

Fig. 9. Length-frequency of Bradda scallops in samples; March 1951. R.V. *William Herdman*. Length in 5 mm groups. ——, 4 ft. small-mesh dredge (398 scallops measured); – – –, 6 ft. commercial dredge (161 scallops measured).

LENGTH-FREQUENCY AND THE SCARCITY OF YOUNG SCALLOPS

Comparisons were made of the length-frequencies of scallops taken in the 6 ft. commercial and 4 ft. small-mesh dredges (see above, p. 473) on the Bradda bed by R.V. *William Herdman* in March 1951 (Fig. 9). The samples were made up of the contents of several dredge hauls, each of 15 min duration in the case of the commercial dredge, and of 7 min duration in the case of the small-mesh dredge, which quickly filled with gravel and shells.

The commercial dredge, which is typical of Manx commercial scallop dredges, exercises a selective action, which begins to act at 95–100 mm (Fig. 9). There is no selection of scallops more than 100 mm long, but few less than 95 mm long are taken. None less than 80 mm long was caught in

March 1951, but the commercial dredge occasionally retained a few smaller scallops among the stones and shells in the bag. On the average the scallop attains a size of 100 mm late in its fourth growth period, so that most scallops spawn in at least two years before they can be caught.

The length-frequency curve for the small-mesh dredge shows a number of peaks, of which the first few each consist entirely or almost entirely of scallops of one age-group (Fig. 9). The most abundant age-group in the sample was that composed of scallops with two growth-rings. It would be expected that the youngest scallops would be most abundant, decreasing in abundance with increasing age. The contrary results appeared to imply that a proportion of the younger, and therefore smaller, scallops, was being missed.

A scarcity of young scallops in dredge samples was noted also by Priol (1930) and Baird (1952), and Baird & Gibson (1956) suggested two possible causes. (i) Settlement may occur on feeder beds, probably inshore, from which young scallops migrate back to the parent beds on attaining a certain size or age; and (ii) young scallops may be present on the beds, but for some reason are not caught. Baird & Gibson (1956), by direct observation on the scallop beds by diving, found that the scallops showed little escape reaction. They compared collections of scallops obtained (*a*) by means of a small-mesh dredge, and (*b*) directly by diving, on the beds off Port Erin, and found that diving yielded much smaller sizes and lower age-groups than dredging. This was not due to mesh-selection of the dredge-bag, since it was lined with shrimp netting which would retain scallops of all sizes. Baird & Gibson concluded, therefore, that the teeth, which are the only other selective feature of the dredge, must be the effective selection agent, but that selectivity is continued beyond the point which might reasonably be expected from mesh-size and tooth-spacing. (My own commercial dredge sample throws no light on this discovery owing to the small difference between tooth-spacing, 89 mm, and the diameter of the rings in the belly of the bag, 82 mm.) In the present study the teeth of the small-mesh dredge must have dug deep into the sea bottom, since the bag rapidly became full of fine gravel, shells, stones and other objects. This means that the teeth were ineffective as a selective agent, and the dredge acted as a complete bottom-sampler. Even so it collected less than the expected proportion of young (0+ and 1+) scallops. In fact my small-mesh dredge sample compared closely with the sample collected by hand, from visual observation, by Baird & Gibson. It would appear, therefore, that fewer 0+ and 1+ scallops than expected are actually on the beds.

As Baird & Gibson pointed out, few 0+ scallops would be expected in their collections, which were taken in July 1953, since 90–95% of scallops at Port Erin are autumn-spawned. It is still difficult, however, to account for the relative shortage of 1+ scallops in Baird's & Gibson's collections and of 0+ and 1+ scallops in my small-mesh dredge samples taken in March and at all other times of the year.

This paper is based on parts of a thesis[1] presented to the University of Liverpool in 1953 for the degree of Ph.D. The work was carried out at the Marine Biological Station, Port Erin, while I held a Herdman Studentship and Liverpool University Research Fellowship. I wish to thank the Director, Mr J. S. Colman, for suggesting the problem to me, for his constant guidance and valuable criticisms, and for reading the manuscript. Mr A. B. Bowers and Mr A. D. McIntyre also read the manuscript and made helpful suggestions. I am grateful for the help given by the scientific staff, students and technical staff of the Marine Biological Station, particularly by Mrs D. I. Williamson and Miss M. MacLeod. Lastly, I wish to thank the Masters and crews of the R.V. *William Herdman* and the M.B.'s *Cypris* and *Runa*.

SUMMARY

Growth-rings on the shell of the scallop (*Pecten maximus*) are laid down annually, in spring, and so can be used to determine the age.

Scallops grow from spring to December, and cease growing in winter. The resumption of growth in the spring is marked by the appearance of the annual growth-ring at the edge of the shell.

The first year's growth is of one of two types. A few scallops have shells which show a large first year's growth, 28 mm or more wide, while the great majority have shells which show a small first year's growth, less than 28 mm wide. These two types probably depend on the two principal spawning periods of the scallop, most of the former arising from the spring spawning and most of the latter from the autumn one.

The growth curve of *P. maximus* is of a type characteristic of lamellibranch shells. The annual growth is greatest in the first two or three years of life, after which it decreases steadily.

Scallops grow more quickly in shallow water than in deeper water.

Possible causes of the annual cessation of growth are discussed.

A paucity of young scallops was noted in the dredge samples, as previous workers have reported. No reason can be given.

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SEA CURRENTS OFF THE NORTHUMBERLAND COAST

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(Text-fig. 1)

The non-periodical currents off the southern Northumberland coast are in general weak and variable and can with safety be ignored by the prudent navigator. For the student of the region's ecology, however, they are of greater significance, and it is of some importance that as exact a knowledge as possible of their speed and direction should be available. The present account is concerned with water movements close to the surface a mile or so offshore; deep currents, it is hoped, will form part of a separate study.

Earlier investigations have usually formed part of much wider surveys in the North Sea and the results have tended to be rather generalized for the small region between the River Tyne entrance (55° 01′ N., 1° 24′ W.) and Newbiggin Point (55° 11′ N., 1° 30′ W.) at present under consideration. Perhaps in consequence of this, different workers have produced conflicting results, although the work of Tait in particular has shown (Tait, 1937) that there may be considerable seasonal and even yearly fluctuations in the currents of the northern North Sea.

The main question at issue is whether the residual current flows along the Northumberland coast in a southerly or a northerly direction. A few instances of the differing conclusions reached will illustrate this. Fulton (1897), deriving his conclusions from drift bottle recoveries, held that it ran to the southward. Böhnecke, quoted by Meek (1926), and basing his conclusions on salinity curves, believed that it ran to the northward. Meek himself, in a paper in which he described the charting of the North Sea currents as 'the most fundamental problem of all' (in relation to fisheries biology), strongly refuted Böhnecke's conclusions. Like Fulton he believed in a southerly current and offered in evidence replies to a letter he sent to fishery officers, etc., up and down the coast inquiring whether, in their region, the ebb or flood ran the stronger. This appeal to common observation brought him a response from Northumberland stating that 'the flood tide is the stronger, the current going in a southerly direction'. But he failed to ask an equally important question, whether the ebb or flood ran the longer, and his argument is the weaker for this omission.

Tait's results, based on numerous drift bottle returns, were more complex.

His final chart (1937) indicated a southerly drift about 15 miles offshore and a northerly counter-current running closer inshore. However, he remarked earlier (1930) that the correspondence between superficial water displacement and wind direction and velocity, particularly in shallow water areas adjacent to land may at times be very close. Since the prevailing winds on the Northumberland coast are westerlies this suggests, allowing for Coriolis force, a mean vector current in the shallow, coastal waters running approximately south-east.

In view of these differing accounts it is difficult to decide from the literature alone what is the true nature of the residual currents off Northumberland. In April 1956 I began a survey in the hope of providing sufficient information from purely local waters to solve this problem. The method I employed was the old and well tried one of following the movements of a free-floating buoy having little windage, and plotting its track. As in all direct methods of measuring currents in the North Sea it was necessary for each observation to extend over a period of at least half a lunar day so that tidal effects could be eliminated. Observations were begun at various states of tide and continued for between 12 and 13 h, the exact period to be spent tracking the buoy being determined from an inspection of the tide tables.

The buoy used was a fisherman's dan buoy to which was attached a drogue to reduce leeway. During the work a number of drogues were lost and because of this they were progressively strengthened in construction. In particular it was found that the connexion between buoy and drogue was subjected to considerable stress in heavy weather, which broke wires and opened shackles. In its most recent form (Fig. 1) the buoy had spliced round it a short sling of 2 in. rope and to this sling was shackled 14 ft. of 1 in. circumference wire. The wire was in turn shackled to an eyebolt in the bottom of the drogue. The drogue itself was in the form of an open ended box whose framework consisted of four wooden uprights each 4 ft. 6 in. by 2 in. by 2 in., and diagonal bars of steel 5 ft. long and $\frac{1}{2}$ in. in diameter at each end. Details of these diagonals are shown in Fig. 1. The drogue was given a covering of no. 4 canvas.

The effective depth at which the current was measured by this instrument was assumed to be about 12 ft., i.e. the depth of the mid-point of the drogue. The effects of water movement on the buoy and wire were disregarded since it was felt that they would not be significantly different from those acting on the drogue. Consideration was, however, given to the effect of wind action on the buoy and this will be referred to later. In fact, the effect was negligible.

At sea the buoy's position was fixed every 45 min. by horizontal and vertical sextant angles of conspicuous marks ashore. At the time of each fix the force and direction of the wind were estimated, short notes were made on the weather and state of the sea, and a sounding was taken. Owing to the proximity of the coast positions were accurate to within at least 0·1 mile and usually much better.

From April 1956 nineteen complete runs were made with the free-floating

buoy over a period of 12 months. The incomplete run of 4 December 1956 has also been included, an estimate being made of the last 2 h of the run. The observations were spread as evenly as possible over the year and at least one

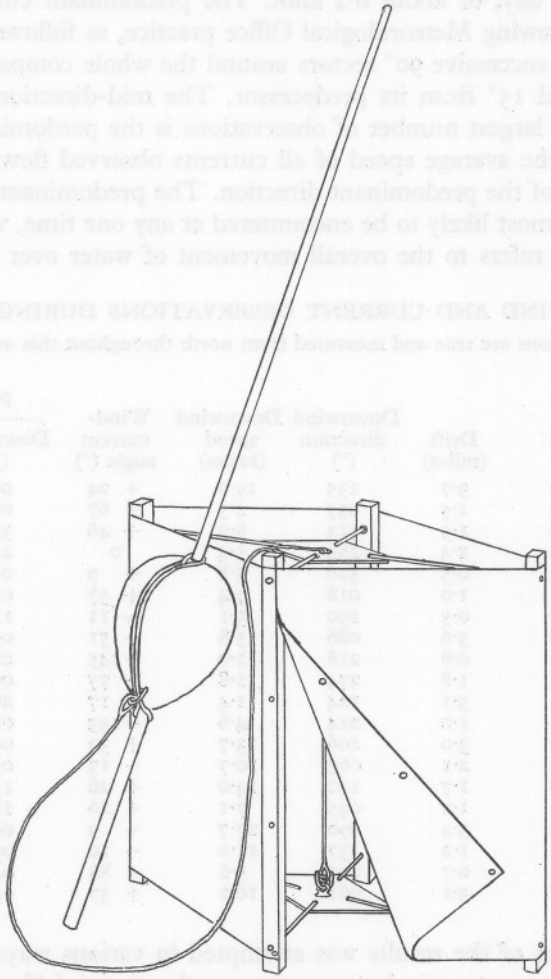

Fig. 1. Diagram of the buoy and drogue used in the investigations. A flap of canvas is raised to show the attachment of the wire to the drogue.

run was made in each month except February 1957. As far as practicable the work was conducted in all states of weather; it should be noted, however, that projected runs were cancelled on days with strong north-easterly winds when the Northumberland coast becomes a lee shore.

From the results obtained (Table 1) certain values may immediately be calculated. First, the mean vector current or resultant direction and speed

works out at 114° and 1·30 miles per half lunar day or about 0·1 knot. Secondly, the mean vector wind during the observations is 273°, 5·4 knots. Thirdly, the predominant direction and speed of current is 120° and 2·5 miles per half lunar day, or about 0·2 knot. The predominant current has been calculated, following Meteorological Office practice, as follows: observations are totalled in successive 90° sectors around the whole compass, each sector being displaced 15° from its predecessor. The mid-direction of the sector containing the largest number of observations is the predominant direction. The speed is the average speed of all currents observed flowing within 45° on either side of the predominant direction. The predominant current refers to the current most likely to be encountered at any one time, while the mean vector current refers to the overall movement of water over a period.

TABLE 1. WIND AND CURRENT OBSERVATIONS DURING THE YEAR

Directions are true and measured from north throughout this account

Date 1956–7	Set (°)	Drift (miles)	Downwind direction (°)	Downwind speed (knots)	Wind-current angle (°)	Winds in preceding 24 h: Downwind (°)	Winds in preceding 24 h: Speed (knots)
3 Apr.	159	3·7	135	19·0	+ 24	090	4·1
16 Apr.	102	1·5	035	2·5	+ 67	076	2·6
20 Apr.	359	1·9	313	8·0	+ 46	339	3·3
25 Apr.	189	1·3	189	5·4	0	221	3·8
2 May	335	0·5	326	5·8	+ 9	011	4·0
3 May	075	1·0	018	7·4	+ 57	027	2·8
14 June	179	0·5	190	3·1	− 11	124	6·7
19 June	137	5·6	086	15·8	+ 51	054	6·9
24 July	003	0·8	218	1·0	+145	089	5·1
27 July	351	1·8	274	1·8	+ 77	097	11·9
7 Aug.	141	3·1	124	1·4	+ 17	263	1·3
9 Aug.	061	1·0	214	4·6	−153	088	6·5
13 Sept.	138	3·0	106	13·7	+ 32	090	6·5
23 Oct.	082	2·1	069	10·7	+ 13	050	11·4
26 Oct.	156	1·7	130	14·0	+ 26	136	17·3
13 Nov.	071	1·1	045	7·1	+ 26	115	8·0
4 Dec.	099	3·4	090	27·7	+ 9	090	20·0
10 Jan.	127	1·2	137	11·2	− 10	090	14·7
22 Jan.	087	0·7	003	5·6	+ 84	044	9·7
27 Mar.	118	3·1	061	16·2	+ 57	055	7·6

Interpretation of the results was attempted in various ways. No obvious relationship appears to exist between a current's set and drift and the moon's phase or the tidal range at the time of observation. Similarly, there is no clear relationship between a current and the departure of a tide from its predicted level as measured on a tide gauge at the River Tyne entrance. It remains to be seen whether two tide gauges widely separated would reveal a slope of the sea and hence a current-generating force. Density differences in the region are in general too small to cause horizontal currents of any importance.

The only valid relationship revealed by the results appears to be that between current and wind. Currents are listed in Table 1 against the direc-

tions towards which the winds blew (henceforward called downwinds), obtained from the trigonometric summation of the $\frac{3}{4}$-hourly wind observations. Column 6 of this table shows the difference in degrees between current set and downwind, marked positive if the current ran to the right of downwind and negative if it ran to the left. Columns 4 and 6 are rearranged in Table 2 with downwinds increasing clockwise from north. It will be seen that the current ran consistently into the quadrant to the right of downwind except in the five downwind records 137° to 218°; these records are anomalous and will be dealt with later. The remaining currents show a mean deflexion of 40°

TABLE 2. DOWNWIND DIRECTIONS AND WIND-CURRENT ANGLE

Downwind (°)	Wind-current angle (°)	Downwind (°)	Wind-current angle (°)
003	+84	130	+ 26
018	+57	135	+ 24
035	+67	137	− 10
045	+26	189	0
061	+57	190	− 11
069	+13	214	−153
086	+51	218	+145
090	+ 9	274	+ 77
106	+32	313	+ 46
124	+17	326	+ 9

with standard deviation 26°. The figures are in close agreement with many open ocean records, e.g. at the ocean weather ship station 'I' (Hay, 1954), where eighteen observations, each of 5 days' duration, showed a deflexion of 42° with standard deviation 42°. For comparison, current sets were related to winds recorded during the 24 h preceding each observation, wind data being obtained from 3-hourly readings of an anemometer at Tynemouth. The relationship here was less good, with deflexion 20° and standard deviation 59°. From this it seems likely that the onset of a given wind and the appearance of the induced current are separated in time by only a very few hours.

A relationship can also be established between wind and current speeds using the data in columns 3 and 5 of Table 1. For all observations $U_s = 1{\cdot}30$ miles per half lunar day, $U_a = 67$ miles per half lunar day, where U_s represents residual current velocity and U_a residual wind velocity.

Following Thorade (Proudman, 1953, p. 176) and employing a mean latitude (ϕ) of 55° 06′ N. we obtain the equation

$$\frac{U_s(\sin\phi)^{\frac{1}{2}}}{U_a} = 0{\cdot}018.$$

For this expression Thorade found the value 0·0126 and Ekman 0·019.

There appears to be no basic current independent of wind such as has been found in the southern North Sea from an analysis of lightship current records (Lawford & Veley, 1955).

With regard to the five observations which were excluded from the deflexion calculations, if the mean deflexion is applied to each wind all the sets become onshore, for between the Tyne and Newbiggin the trend of the coast is about north-west to south-east. But only very small onshore sets were recorded; potential onshore sets, then, are deflected by the coastline, those to the south of south-west being deflected anticlockwise and those to the north of south-west clockwise.

Throughout this account it has been assumed that the current observations were made during a fair sample of the wind speeds experienced during the year. Table 3 shows that this is approximately true. Wind-speed estimations

TABLE 3. 9 A.M. WIND FORCES AT CULLERCOATS AND AT SEA, EXPRESSED AS PERCENTAGE OF TOTAL OBSERVATIONS

	At Cullercoats	At sea
Observations ...	237	20
Calm	1·7	0
Force 1	12·2	15
Force 2	21·7	25
Force 3	26·2	20
Force 4	19·4	25
Force 5	10·1	10
Force 6	5·9	0
Force 7	2·1	5

TABLE 4. 9 A.M. WIND DIRECTIONS AT CULLERCOATS AND AT SEA, EXPRESSED AS PERCENTAGE OF TOTAL OBSERVATIONS

	At Cullercoats	At sea
Observations ...	237	20
Calm	1·7	0
000–089°	14·3	10
090–179°	20·2	5
180–269°	28·2	25
270–359°	35·5	60

made on the 20 sea-going days at 9 a.m. are compared with estimations made at corresponding times at Cullercoats on 237 occasions. Wind directions (Table 4) do not correspond so closely, and it is clear that too many north-west winds and too few south-east winds are represented in the sea observations. This has had a small effect on the figures given for residual and predominant currents; if a residual current is worked for the 237 shore observations and a deflexion of $+21°$ is allowed, as was found for residual winds and currents at sea the result, using Thorade's formula, is 110°, 0·06 knot, which is not very different from the 114°, 0·1 knot already found.

Finally, an answer must be given to the question of whether the buoy used in the investigations was seriously affected by the wind. It would be simple to discover this by attaching a current meter to the drogue, when the total reading would be due to wind drift, but for the very low speeds (certainly less than 10 ft a minute) which would have to be measured in a horizontal direction alone; so this solution is impracticable at sea. It might have been

possible to test the buoy's downwind movement in one of the Tyne docks were it not suspected that the dock water itself is always in slow motion. Short of wind tunnel experiments I was forced to fall back on observation and inference from the buoy's movement at sea.

In low winds I examined the drogue underwater. It hung down vertically from the buoy and did not move away from small fragments of paper which I placed near it. In high winds direct underwater observation was not possible but the buoy's track was often so far away from downwind as to make it seem unlikely that it was carrying much leeway. Attention is drawn to the record of 19 June, where a westerly wind of force six blew for more than 6 h. The buoy ran 51° to the right of downwind and parallel to the coast. Unless leeway was being cancelled by a large onshore current, already seen to be very unlikely, this track represents true water movement. Even in a strong breeze, then, leeway is negligible.

My acknowledgements are due to the Tyne Improvement Commissioners for access to tide gauge information at South Shields, to the Coast Guards of Tynemouth for providing wind records and to Dr H. O. Bull and Dr J. N. Carruthers for valued advice. Especially is my gratitude due to R. Harrison, skipper of the R.V. *Alexander Meek* of the Dove Marine Laboratory, for the many patient hours he spent at sea with me in all weathers on this work.

SUMMARY

Observations have been made of the surface currents off the Northumberland coast over a period of 12 months, using a free-floating buoy. A mean vector current was found, setting 114° at 0·1 knot. Currents flowed into the quadrant to the right of downwind except when this would have directed them ashore. A relationship is established between wind speed and current speed.

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VITAMIN A AND CAROTENOIDS IN CERTAIN INVERTEBRATES

VI. CRUSTACEA: PENAEIDEA

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Fisher (1957) has pointed out the possible connexion between the richness in vitamin A and the pelagic existence of species of the orders Amphipoda and Mysidacea of the malacostracan Crustacea. The most striking example is seen in the Eucarida, of which the more benthic Decapoda are nearly all poorer in vitamin A than the pelagic Euphausiacea. In the Decapoda, species of the suborder Natantia do, however, lead a more or less pelagic life. Of its two constituent groups the Penaeidea swim more actively than the Caridea. The Penaeidea were believed by Calman (1910) to be primitive decapods and similarities in larval development indicated a possible affinity with the Euphausiacea. Gordon (1955) has recently produced further evidence of this relationship, particularly between euphausiids and sergestids, from the structure of the petasma, spermatophores, thelycum and photophores in the two groups. Taxonomically as well as ecologically, then, the penaeids may be said to lie between the rest of the decapods and the euphausiids, and we wished to compare these groups in their biochemical relationships so far as vitamin A and carotenoids were concerned. Moreover, some species of penaeids are the basis of important fisheries and knowledge of their vitamin A content might be of some economic value.

Published work on vitamin A and carotenoids in penaeids is confined almost entirely to that of Grangaud and his colleagues at Algiers on *Aristeomorpha foliacea* and *Aristeus antennatus*. These workers reported in several papers, summarized by Grangaud (1951) and Grangaud & Massonet (1951), on the anti-xerophthalmic activity of astaxanthin isomers from these species. Grangaud, Massonet & Sansac (1954) also mentioned the presence of vitamin A in concentrations of 5–10 i.u./g in the eyes and ovaries and of 30 i.u./g in the intestines of *Aristeomorpha foliacea*, *Aristeus antennatus* and *Parapenaeus longirostris*. In an earlier paper we reported vitamin A at a concentration of 5·7 i.u./g in the eyes of *Trachypenaeus membranaceus* from Naples (Fisher, Kon & Thompson, 1953).

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MATERIAL AND METHODS

Apart from *Trachypenaeus membranaceus* just mentioned we have analysed samples of thirteen species of penaeids, of which seven belong to the family Penaeidae and six to the Sergestidae. Details of these samples are given in Table 1.

Carotenoids and vitamin A were measured by the recent modification (Fisher, Kon & Thompson, 1956) of our usual method (Fisher, Kon & Thompson, 1952). None of the groups analysed contained enough specimens for biological assay or for the separation of vitamin A isomers carried out for some other Eucarida (Fisher, Kon & Plack, 1957; Wald & Brown, 1956–7; Wald & Burg, 1956–7).

RESULTS

Detailed results for the Penaeidae are shown in Table 2 and those for the Sergestidae in Table 3.

DISCUSSION

The results in the tables show that, apart from *Gennadas borealis*, all the species analysed contained vitamin A in at least one sample. The concentration of the vitamin in the Penaeidae was relatively low and its distribution varied. In some species it was confined to the eyes, in others to the bodies, and only in *Parapenaeopsis atlantica* was it found in both eyes and bodies. In the Sergestidae, vitamin A concentrations in most species tended to be higher than in the Penaeidae, but distribution varied in the different species.

All species of both families contained appreciable quantities of carotenoids and some, for example, *Petalidium foliaceum*, were very rich in them. The more actively pelagic sergestids usually contained only astaxanthin or its esters with an occasional trace of xanthophylls. There was a greater variety of carotenoids in the penaeids. Fisher, Kon & Thompson (1954) reported a similar difference between decapods with several different carotenoids and the more pelagic euphausiids in which only astaxanthin or its derivatives were found.

The results show that the concentration of vitamin A in penaeids is similar to those in other Natantia. Fisher (1957) has shown that, of the species we have examined, more Penaeidea (13 out of 14 listed in his paper) contain vitamin A than Caridea (29 out of 36). The results now presented indicate that Sergestidae with a more oceanic existence may be richer in vitamin A than Penaeidae, but more individuals of more species must be analysed in order to establish any such relationship.

Taken as a whole the vitamin A values for the Sergestidae would place them between the other Penaeidea (and other Decapods) and the Euphausiacea, a biochemical classification in agreement with current taxonomical views. *Penaeus aztecus*, the basis of an important shrimp fishery in Texas, contained modest amounts of vitamin A, all in the eyes and so of no importance in human nutrition.

TABLE 1. SPECIES, NUMBERS, SOURCES AND METHODS OF PRESERVATION OF PENAEIDS ANALYSED

Sample no.	Species	No. of specimens per sample	Locality	Ship	Date	How caught	Method of preservation
1	*Amalopenaeus elegans* Smith	16	39° 39′ N., 12° 08′ W.	*Discovery II*	16. xi. 1954	2 m stramin net	BF
2	*A. elegans* Smith	4	Bay of Biscay	*Sarsia*	18–24. vii. 1955	2 m stramin net	BF
3	*Funchalia woodwardi* Johnson	3	Madeira	—	17. v. 1955	From stomach of sword-fish	DA
4	*Gennadas borealis* Rathbun	7	32° 45′ N., 117° 38′ W.	*Paolina T*	4. iv. 1956	Isaacs-Kidd mid-water trawl	BF
5	*G. parvus* Bate	4	Bay of Biscay	*Sarsia*	28–30. iv. 1955	2 m stramin net	BF
6	*G. parvus* Bate	27	North Atlantic	*Discovery II*	vi. 1955	2 m stramin net	BF
7	*G. parvus* Bate	107	Bay of Biscay	*Sarsia*	18–24. vii. 1955	2 m stramin net	BF
8	*Parapenaeopsis atlantica* Balss	25	Gold Coast	—	Spring 1955	—	DS
9	*Penaeus aztecus* Ives	44	Gulf of Mexico	—	24. vi. 1952	—	DA
10	*Plesiopenaeus edwardsianus* (Johnson)	1	Madeira	—	1. vi. 1955	Deep fishing line	DA
11	*Petalidium foliaceum* Bate	29	32° 45′ N., 117° 38′ W.	*Paolina T*	4. iv. 1956	Isaacs-Kidd mid-water trawl	BF
12	*Sergestes arcticus* Kröyer	4	North Atlantic	*Discovery II*	16. xi. 1954	2 m stramin net	BF
13	*S. arcticus* Kröyer	4	North Atlantic	*Discovery II*	vi. 1955	2 m stramin net	BF
14	*S. arcticus* Kröyer	1	58° 54′ N., 13° 44′ W.	*George Bligh*	20. vii. 1955	Prawn trawl	BF
15	*S. arcticus* Kröyer	289	Bay of Biscay	*Sarsia*	18–24. vii. 1955	2 m stramin net	BF
16	*S. atlanticus* Milne Edwards	2	North Atlantic	*Discovery II*	16. xi. 1954	2 m stramin net	DA
17	*S. atlanticus* Milne Edwards	12	North Atlantic	*Discovery II*	vi. 1955	2 m stramin net	DA
18	*S. bisulcatus* Wood-Mason	6	32° 45′ N., 117° 38′ W.	*Paolina T*	4. iv. 1956	Isaacs-Kidd mid-water trawl	BF
19	*S. robustus* Smith	6	North Atlantic	*Discovery II*	16. xi. 1954	2 m stramin net	BF
20	*S. robustus* Smith	12	Bay of Biscay	*Sarsia*	18–24. vii. 1955	2 m stramin net	BF
21	*S. similis* Hansen	15	North Pacific	*Horizon*	26. v. 1953	1 m silk net	DS
22	*S. similis* Hansen	25	32° 45′ N., 117° 38′ W.	*Paolina T*	4. iv. 1956	Isaacs-Kidd mid-water trawl	BF

BF: boiled (Fisher, Kon & Thompson, 1952) and kept frozen until arrival at Shinfield laboratory.

DA: eyes dissected off and both parts preserved separately in alcohol; kept at low temperature, sent by air to London and immediately taken to Shinfield.

DS: dissected as above and preserved in alcohol, but sent by sea to England. *Parapenaeopsis atlantica* was stored in ship's refrigerator but *Sergestes similis* came by ordinary surface mail.

TABLE 2. OIL, VITAMIN A AND CAROTENOIDS IN SOME PENAEIDAE

Sample no.	Species	Av. wt. (mg)	Oil (%)	Vitamin A				Total carotenoids		β-carotene (μg/g)	Other carotenoids
				μg/spec.	μg/g	% ester	% alcohol	μg/spec.	μg/g		
1	*Amalopenaeus elegans*										
	Eyes (pairs)	0·14	9·1	0	0	0	0	0·28	2000	0	A
	Bodies	66	4·1	0·054	0·83	100	0	17	260	0	AE
	Total	66	4·1	0·054	0·82	100	0	17	270	0	AE
2	*A. elegans*										
	Eyes (pairs)	0·10	—	0	0	0	0	0·075	750	0	A
	Bodies	74	0·34	0	0	0	0	3·7	50	0	A
	Total	74	0·34	0	0	0	0	3·8	50	0	A
3	*Funchalia woodwardi*										
	Eyes (pairs)	240	3·1	0	0	0	0	2·8	12	0	A
	Bodies	17500	10	1·7	0·098	100	0	506	29	0·19	AE, C
	Total	17800	11	1·7	0·097	100	0	509	29	0·19	AE, C
4	*Gennadas borealis*										
	Eyes (pairs)	0·40	11	0	0	0	0	1·4	3500	0	A
	Bodies	350	12	0	0	0	0	9·0	26	0	AE
	Total	350	12	0	0	0	0	10	30	0	AE
5, 6	*G. parvus*										
	Eyes (pairs)	0·13	19	0·012	88	0	100	0·38	2900	0	AE
	Bodies	69	3·2	0	0	0	0	3·9	57	0	AE, X
	Total	69	3·3	0·012	0·17	0	100	4·3	62	0	AE, X
7	*G. parvus*										
	Whole specimens	12	4·6	0	0	0	0	2·3	190	0	AE, X
8	*Parapenaeopsis atlantica*										
	Eyes (pairs)	57	2·9	0·11	1·9	100	0	0·53	9·3	0	AE
	Bodies	6100	0·73	0·19	0·032	0	100	93	15	0·086	AE, C, X
	Total	6100	0·77	0·30	0·049	37	63	94	15	0·085	AE, C, X
9	*Penaeus aztecus*										
	Eyes (pairs)	51	11	0·22	4·3	67	33	0·96	19	0	A
	Bodies	4000	0·66	0	0	0	0	56	14	0·013	AE, C, X
	Total	4000	0·79	0·22	0·054	67	33	57	14	0·013	AE, C, X
10	*Plesiopenaeus edwardsianus*										
	Eyes (pairs)	470	3·5	0·69	1·5	100	0	50	150	0	AE
	Body	138000	10	0	0	0	0	19000	140	Trace	AE, C, X
	Total	138500	10	0·69	0·0050	100	0	19000	140	Trace	AE, C, X
—	*Trachypenaeus membranaceus**										
	Eyes (pairs)	100	3·0	0·23	2·2	—	—	0·54	5·3	0	A
	Bodies	8700	—	—	—	—	—	—	—	—	
	Total	8800	—	—	—	—	—	—	—	—	

* Result previously reported by Fisher *et al.* (1953) for comparison.

A = astaxanthin; AE = astaxanthin or its esters; C = carotene; X = xanthopyll.

TABLE 3. OIL, VITAMIN A AND CAROTENOIDS IN SOME SERGESTIDAE

Sample no.	Species	Av. wt. (mg)	Oil (%)	Vitamin A				Total carotenoids		Carotenoids present
				μg/spec.	μg/g	% ester	% alcohol	μg/spec.	μg/g	
11	*Petalidium foliaceum*									
	Eyes (pairs)	0·57	27	0	0	0	0	0·51	900	AE
	Bodies	180	14	0·37	2·0	10	90	60	330	AE, X
	Total	180	14	0·37	2·0	10	90	60	330	AE, X
12	*Sergestes arcticus*									
	Eyes (pairs)	0·88	2·9	0	0	0	0	5·0	5700	AE
	Bodies	170	2·2	0	0	0	0	11	65	AE
	Total	170	2·2	0	0	0	0	16	94	AE
13	*S. arcticus*									
	Eyes (pairs)	0·40	—	0	0	0	0	0·17	420	A
	Bodies	31	3·2	0	0	0	0	1·8	58	AE
	Total	31	3·2	0	0	0	0	2·0	63	AE
14	*S. arcticus*									
	Eyes (pairs)	1·0	30	0	0	0	0	0	0	—
	Body	23	17	0	0	0	0	3·0	130	AE
	Total	24	18	0	0	0	0	3·0	120	AE
15	*S. arcticus*									
	Eyes (pairs)	0·65	12	0·0065	10	50	50	0·0048	7·4	A
	Bodies	99	2·1	0·024	0·24	25	75	3·7	37	AE, X
	Total	100	2·1	0·031	0·31	32	68	3·7	37	AE, X
16	*S. atlanticus*									
	Eyes (pairs)	1·3	—	0·24	184	100	0	1·1	820	A
	Bodies	320	3·4	0	0	0	0	47	140	A
	Total	320	3·4	0·24	0·74	100	0	48	150	A
17	*S. atlanticus*									
	Eyes (pairs)	0·33	—	0·078	238	100	0	0·12	360	A
	Bodies	91	1·3	0	0	0	0	4·1	44	AE
	Total	91	1·3	0·078	0·85	100	0	4·2	46	AE
18	*S. bisulcatus*									
	Eyes (pairs)	6·3	9·5	0	0	0	0	1·4	220	A
	Bodies	510	5·1	3·4	2·3	80	20	127	84	AE, X
	Total	520	5·2	3·4	2·2	80	20	128	84	AE, X
19	*S. robustus*									
	Eyes (pairs)	0·37	4·5	0	0	0	0	0·63	1700	AE
	Bodies	74	0·22	0	0	0	0	11	140	AE
	Total	74	0·25	0	0	0	0	11	150	AE
20	*S. robustus*									
	Eyes (pairs)	0·84	—	0	0	0	0	0	0	—
	Bodies	230	6·0	0·092	0·40	67	33	5·7	25	AE, X
	Total	230	6·0	0·092	0·40	67	33	5·7	25	AE, X
21	*S. similis*									
	Whole specimens	52	2·9	0	0	0	0	0·65	12	AE
22	*S. similis*									
	Eyes (pairs)	2·7	—	0·076	28	63	37	0	0	—
	Bodies	210	3·1	0·55	2·6	83	17	20	97	AE, X
	Total	210	3·1	0·63	3·0	80	20	20	96	AE, X

β-carotene absent from all groups. A = astaxanthin; AE = astaxanthin or its esters; X = xanthophyll.

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SUMMARY

Vitamin A and carotenoids were measured in six species of Penaeidae and seven species of Sergestidae.

Vitamin A was present in at least one sample of all species except *Gennadas borealis* at concentrations mostly of the same order as previously found in other Decapoda, but usually higher in the Sergestidae than in the Penaeidae.

Carotenoids in the Penaeidae included astaxanthin and its esters, carotenes and xanthophylls, but only astaxanthin or its esters with occasional traces of xanthophylls were found in the Sergestidae.

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THE IRON CONTENT OF SEA WATER

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Concentrations of iron in sea water up to about 3 mg Fe/l. have been reported, most of the figures being in the range 10–100 μg Fe/l. The published analyses, with notes on the methods used where these are known, are summarized by Lewis & Goldberg (1954), who list thirty-nine sources up to 1953.

It is well known that much of the iron is in particles which can be removed by filtration. Attempts have been made to estimate the chemically more reactive and presumably biologically more available fraction of the metal. Often the coarser particles have been filtered off before analysis, and reagents of varying potency have been used to bring iron into solution for colorimetric determination. These procedures have sometimes excluded determination of the total concentration of iron in the water. It is known, however, that the phytoplankton can utilize particulate material for its requirements of iron (Allen & Nelson, 1910; Harvey, 1927; Goldberg, 1952).

Methods intended to determine total iron in sea water have been described by Thompson, Bremner & Jamieson (1932); Thompson & Bremner (1935); Cooper (1935, 1948); Rakestraw, Mahncke & Beach (1936); and Lewis & Goldberg (1954). Thompson and his collaborators evaporated the water with excess of sulphuric acid and heated to fuming, and Lewis & Goldberg used perchloric acid in a similar way. These methods should undoubtedly be effective, as should that used by Rakestraw *et al.* when applied to unfiltered water. Cooper, in his method for 'total iron' (for which expression he made specific reservations) used a less drastic attack and heated the sample with hydrochloric acid (0·008 N) and some bromine, excess of bromine being later boiled off. Some analyses of suspended matter in sea water (Armstrong & Atkins, 1950) showed that in surface water from a position in the English Channel there were present from 42 to 210 μg Fe/l. These amounts were so much greater than those previously found at the same position, by direct analysis, that it seemed desirable to make more analyses and to re-examine the analytical methods.

ANALYTICAL CONSIDERATIONS

Methods using wet ashing with sulphuric or perchloric acids should serve well for referee analyses. They are not, however, very convenient for routine use and reagent blanks tend to be high. A simple alternative way of bringing iron into solution which could be used for large batches of samples was sought. A possible method came from the observation that when the suspended

matter is filtered from sea water, the iron can be extracted completely from the solid residue with cold 1 N hydrochloric acid. This concentration is unmanageably great for acidification of a sea water sample of about 100 ml., so attempts were made to use 0·1 N acid. At this level blanks are low and partial neutralization is easier. 0·1 N acid was ineffective in the cold, although boiling for 1 h dissolved more than 90% of the iron present. Solution of iron appeared to be complete however when the acidified sample was heated in an autoclave for 5 h at 140° C. Since the treatment extracted appreciable and varying amounts of iron from borosilicate glassware, fused silica flasks had to be used. It proved convenient to add 1 ml. of concentrated hydrochloric acid to 85 ml. of sea water to give a concentration of 0·12–0·14 N. After digestion and adjustment of volume the addition of 10 ml. (20%, w/v) sodium acetate brought the solution to pH $3{\cdot}8 \pm 0{\cdot}2$, which was suitable for colorimetric determination.

Of the many very satisfactory colorimetric reagents for iron, 1:10 phenanthroline seemed to be the most suitable. It was extensively tested by Fortune & Mellon (1938), who found it effective (with ferrous iron) in the pH range 2–9. Of fifty-five ions which these authors tested for interference none of the undesirable ones, with the possible exception of fluoride, is present in sea water in troublesome quantity. 2-2′-Dipyridyl, of similar sensitivity and also interference-free, has a narrower pH range of 3·5–8·5 (Hill, 1930). It could be used, but extra sodium acetate might be desirable to raise the pH somewhat (since colour development tends to be slow at the higher acidities) and this would undoubtedly increase blanks.

Some tests with 1:10 phenanthroline were made to see whether fluoride would interfere with iron determinations at pH 3·8, and it was found that there was no effect up to a concentration of 7·6 mg F/l. (400 μg atom F/l.). This is 5 or 6 times the usual concentration in sea water, which is stated to be about 1·4 mg F/l. (74 μg atom F/l.) (Thompson & Taylor, 1933).

It was found that 1:10 phenanthroline could be used with confidence and that the method prescribed by Fortune & Mellon, using hydroxylamine hydrochloride for reduction of ferric iron, could be followed closely with sea water. The depth of colour, which does not fade, is unaffected by the salts in the water, and Beer's Law is obeyed in a simple filter absorptiometer.

METHOD

Apparatus

Polyethylene sample bottles. Fused silica flasks, 100 ml. Autoclave for temperature 140° C (40 p.s.i. or 2·8 kg/cm²). This should be of non-ferrous construction. Absorptiometer to take 10 cm cuvettes or longer. Glassware should be cleaned with strong hydrochloric acid before use and reserved for this work.

Reagents

Standard iron solution. 1 ml. ≡ 0·0001 g Fe. Dissolve 0·702 g $FeSO_4.(NH_4)_2SO_4.6H_2O$ in 1%, v/v, HCl and make to 1 l. with 1%, v/v, acid.

Sodium acetate 20%, *w/v*. Dissolve 200 g $CH_3COONa.3H_2O$ in water, make to 1 l., shake with about 10 ml. chloroform to saturate and filter on No. 42 Whatman paper.

Hydroxylamine hydrochloride 10%, *w/v*. Dissolve 10 g $NH_2OH.HCl$ in water and make to 100 ml.

1:10 *phenanthroline* 0·1%, *w/v*. Dissolve 0·25 g 1:10 phenanthroline in hot water, cool and make to 250 ml.

Analysis of sea water

Measure 85 ml. of the properly collected (see below) and well-shaken sample into a 100 ml. silica flask and add 1·0 ml. conc. HCl, preferably with a syringe pipette. Cover the flask and heat for 5 h in an autoclave at 140° C. After cooling, adjust the volume to 86 ml., transfer to a 150 or 250 ml. borosilicate flask and add 10 ml. 20% sodium acetate and 1 ml. 10% $NH_2OH.HCl$, using pipettes. Mix the solution, and measure the absorbance in a 10 or 15 cm cuvette at about 510 mμ (Ilford no. 603 or combination of 303 and 404 filters). This reading will allow correction for slight turbidity of the solution. Return the solution from the cuvette to the flask, add 3 ml. 0·1% 1:10 phenanthroline solution, mix, and measure the absorbance again after 10 min. The difference between the two readings, when corrected for the absorbance of the blank, measures the iron content of the sample.

Blank determination

Carry 85 ml. of iron-free distilled water through the same procedure. If it is found that release of iron from the flasks is negligible digestion of blanks may of course be omitted.

Calibration

In a series of 100 ml. graduated flasks, place measured amounts of the standard iron solution (or of a freshly prepared known dilution of it), to give a range of known iron concentrations. They may be chosen on the assumption that about 60μg Fe in 100 ml. are required to give an absorbance of 1·0 in a 10 cm cuvette in a filter absorptiometer at about 510 mμ. Add distilled water to a volume of about 80 ml., and then add HCl, sodium acetate, $NH_2OH.HCl$ and 1:10 phenanthroline in the quantities given above. Adjust the volumes to 100 ml., mix and measure absorbance after 10 min. Construct a calibration curve. This should be a straight line. If so, it is convenient to recalculate the slope as the concentration of iron in an 85 ml. sea-water sample required to give an absorbance of 1·00. The product of this factor and the corrected absorbance of a treated sea-water sample is the concentration of iron in the sample. Calibration should be repeated occasionally as a check on the constancy of the absorptiometer. If the curve is linear a check at one iron concentration is enough.

TESTS OF METHOD

The effectiveness of the digestion in extracting iron from refractory marine material was tested by comparing the amount brought into solution by digestion with that found after ignition and fusion with potassium bisulphate. For this test two samples, one of marine silt and the other of equal parts of dried whole fish meal and dried ground sea weed, were homogenized by grinding. Fibrous material in the second sample was removed with a 100-mesh sieve. Portions of 50–100 mg were weighed and assayed by the two methods. The

results, expressed as iron contents of the samples, are given in Table 1, and show that recovery of iron by the digestion method was sensibly complete.

For trials with sea water, two carboys of freshly collected water were well shaken and kept vigorously stirred whilst samples were drawn off by siphon. From each carboy three samples of 2 l. each were taken for filtration as described below, and three sets of eight samples for replicate determinations

TABLE 1. RECOVERY OF IRON FROM MARINE MATERIALS

Material	Iron content (%)							
	Ignition and bisulphate fusion				Acid digestion at 140° C			
Silt	1·26	1·28	1·26	1·25	1·24	1·27	1·25	1·27
Sea weed and fish meal	0·061	0·077	0·060	0·069	0·079	0·078	0·067	0·060

TABLE 2. COMPARISON OF METHODS FOR DETERMINATION OF TOTAL IRON IN SEA WATER

(Iron found, μg Fe/l.)

	Filtration, bisulphate fusion, etc.	Acid digestion at 140° C	Fuming with H_2SO_4 (Thompson *et al.*)	HCl and Br_2 (Cooper)
Carboy A	89	81	71	13
	100	78	100	15
	83	83	98	21
	—	80	83	15
	—	82	83	17
	—	89	79	18
	—	93	76	19
	—	95	84	13
Mean	91	85	84	16
	S.D.	±6	±9	±3
Carboy B	140	106	130	50
	164	152	132	34
	118	139	168	6
	—	143	137	9
	—	140	140	17
	—	145	137	21
	—	142	132	22
	—	139	132	21
Mean	141	138	138	23
	S.D.	±14	±12	±14

by the digestion method (85 ml.), Thompson & Bremner's sulphuric acid method (100 ml.) and Cooper's 'Total Iron' method (150 ml.). The 2 l. samples were filtered on 'Gradocol' membrane filters (A.P.D. approx. 1 μ) and the filtrates reserved. Each membrane with the suspended matter on it was ignited in platinum and the residue fused with bisulphate. Iron in the melt was determined, blanks being carried through all stages. To the iron concentrations thus found were added those found in the filtrates by the digestion method. Any material passing the filter was necessarily very finely subdivided and was assumed to be readily dissolved. (The amount of iron

found in these filtrates varied from 4 to 8 μg Fe/l., and may be compared with the 2–5·5 μ Fe/l. found after filtration through 'Millipore' membranes of 0·5 μ A.P.D. by Lewis & Goldberg.) This procedure gave an independent estimate of total iron in the samples, although it is probably not very accurate because so much manipulation is involved.

The samples for digestion were carried through the method described above. Those for test by Thompson & Bremner's method were heated to fuming as prescribed in the original method. Silica flasks were used. The colorimetric finish with thiocyanate, however, was set aside in favour of the 1:10 phenanthroline procedure after neutralization of excess acid with ammonia, iron in this reagent being allowed for. The samples for Cooper's 'Total Iron' method were treated as described in his 1948 paper, dipyridyl being used.

The results are given in Table 2. Taking into consideration the marked scatter in the figures it can be seen that the filtration, Thompson & Bremner's and the new digestion methods agree well, but that the HCl-bromine 'Total Iron' method is not rigorous enough, as Cooper himself surmised (1948, p. 281).

COLLECTION OF SAMPLES

Circumspection is obviously needed when samples are taken from a steel ship and in a hydrographic water bottle on a steel wire. Ordinary glass sample-bottles are unsuitable, even after washing with acid, since they are appreciably attacked by sea water. Iron in the glass is released, remaining on the walls of the bottle, probably as a film of ferric hydroxide, but easily contaminating the sample. Moreover, Goldberg (1952) showed that iron added to sea water is rapidly adsorbed by glass. Polyethylene bottles, though not ideal, may be used. Analysis of some new bottles showed the plastic to be iron-free, but it should be remembered that the bottles may be made on iron or steel moulds. It is advisable to wash out all bottles with strong hydrochloric acid before use (a little wetting agent such as cetyl ammonium bromide with the acid is helpful) and to test for extractable iron by filling with 0·1 N-HCl and heating for several hours in a water bath at 100° C and then determining iron in the solution. It has been noticed that polyethylene bottles which had been used repeatedly for collection of water for other analyses had an internal deposit of ferruginous material which came out only after prolonged acid treatment.

Deposition of iron on the walls of polyethylene bottles takes place rapidly from raw sea water. Experiments showed that in a week one-quarter of the iron originally present was so deposited; storage for 4 weeks showed losses of one-half to two-thirds. The iron deposited is difficult to recover, only half of it being removed by standing with 0·1 N-HCl for several days with occasional shaking. It is advisable therefore to complete iron determinations soon after collection. When this cannot be done the samples should be acidified when

collected. For long storage it would probably be advisable to use the full amount of acid, i.e. 1·0 ml. conc. HCl per 85 ml. of sample, but for 3 weeks' storage a smaller amount is sufficient. Table 3 shows the effectiveness of addition of 1 ml. of 10%, v/v, HCl per 100 ml. sample. This amount of acid may be disregarded when acidifying before digestion and its contribution to the reagent blank is usually negligible.

TABLE 3. IRON DETERMINATIONS ON SUBSAMPLES OF SEA WATER BEFORE AND AFTER STORAGE FOR 3 WEEKS WITH ADDITION OF 1 ML. (10%, V/V) HCl PER 100 ML.

Before storage	74, 94, 92, 81, 105, 86, 85, 88, 67, 88	Mean 86	S.D. ± 11 μg Fe/l.
After 3 weeks' storage	105, 83, 86, 86, 80, 81, 86, 88, 88, 84	Mean 86	S.D. ± 7 μg Fe/l.

VARIABILITY OF RESULTS

Tables 2 and 3 include standard deviations. The sets of samples analysed are hardly random ones, but subsamples of larger portions which were vigorously stirred whilst subsampling. Those of Table 2 were, as stated, from carboys (20–25 l.), whilst those of Table 3 were from a bucket (8 l.). A set of ten samples, each of 85 ml., from ten consecutive buckets of water taken from the sea surface at Station E 1 whilst the ship was stopped gave a mean iron content of 65 ± 22 μg Fe/l. Sampling took about 15 min.

The variability of replicate iron determinations has been discussed by other workers, and was turned to account by Cooper (1948) who assessed, by statistical treatment, the size and distribution of iron-containing particles in the water. Lewis & Goldberg (1954) were at some pains to obtain replicate samples from deep water and gave a statistical analysis of their data from nine Pacific Ocean stations.

RESULTS OBTAINED

Iron concentrations found by the digestion method in samples from the Plymouth Laboratory stations L2 to L6 and at the International Hydrographic Station E 1 during 1955 and 1956 are given in Table 4. As would be expected there is appreciably more iron in the coastal waters. There is a seasonal variation, more iron being found in the winter months, which may be caused by the increased run-off from the land and greater turbulence in winter. There is often, at Station E 1, more iron at the surface, as observed by Cooper (1948). Iron concentrations are very much higher than those reported by Cooper for 1933 and 1934 and 1946 and 1947. This is ascribable to the difference in the analytical methods.

Results from two other stations in the English Channel and from three positions off the Brittany coast in the northern part of the Bay of Biscay are given in Table 5. Figures from four deep-water stations in the Bay of Biscay are given in Table 6.

TABLE 4. IRON CONTENT OF SEA-WATER SAMPLES FROM POSITIONS NEAR PLYMOUTH 1955–6

(In μg Fe/l.)

St. no.	N. lat.	W. long.	Miles from Plymouth	Depth (m)	1955 18 Jan.	16 Feb.	15 Mar.	12 Apr.	9 May	13 June	13 July	11 Aug.	15 Sept.	18 Oct.	17 Nov.	21 Dec.
L2	50° 20′	4° 10′	2	0	203	160	58	146	—	33	64	157	53	169	177	424
L3	50° 18′	4° 11′	5	0	82	174	59	65	—	21	17	92	35	176	129	212
L4	50° 15′	4° 13′	8	0	90	107	67	68	—	7	16	100	157	94	102	100
L5	50° 11′	4° 18′	12	0	92	92	43	111	—	8	11	140	115	85	77	59
L6	50° 06′	4° 21′	17	0	124	326	60	25	—	5	30	107	97	65	62	94
E1	50° 02′	4° 22′	22	0	78	111	39	89	13	13	1	58	75	25	127	100
				5	49	77	23	36	17	198	6	31	22	19	26	26
				10	60	61	27	15	19	19	4	24	29	33	22	38
				20	—	—	—	—	—	—	3	51	15	48	35	64
				25	85	77	31	17	15	7	—	—	—	—	—	—
				50	34	90	26	50	21	16	7	31	57	84	56	83
				70	73	108	29	84	46	25	4	60	28	175	54	87
Integral mean, Station E1				—	61	92	28	41	22	28	5	42	36	72	45	70

St. no.	Depth (m)	1956 17 Jan.	21 Feb.	26 Mar.	11 Apr.	16 Apr.	24 Apr.	22 May	23 July	22 Aug.	25 Sept.	23 Oct.	13 Nov.	10 Dec.	Mean
L2	0	239	129	209	106	103	54	69	40	84	70	104	120	86	127
L3	0	150	60	101	86	108	27	45	21	64	65	38	86	74	83
L4	0	121	60	33	129	98	19	32	73	57	37	30	42	64	71
L5	0	83	56	35	88	100	16	42	53	54	20	30	47	46	63
L6	0	76	64	31	52	50	28	38	75	76	13	44	64	78	70
E1	0	28	57	31	16	20	7	15	69	126	77	24	31	48	51
	5	36	36	10	9	13	5	50	14	134	20	8	32	31	37
	10	35	31	10	9	11	4	31	25	10	21	7	34	31	24
	20	37	26	20	11	13	8	13	21	15	18	10	43	23	27
	25	—	—	—	—	—	—	—	—	—	—	—	—	—	
	50	52	36	13	14	12	7	20	28	16	18	8	53	79	36
	70	75	32	18	20	22	19	16	33	25	17	13	59	41	46
Integral mean, Station E1	—	46	33	16	13	14	9	20	26	29	20	12	47	48	35

TABLE 5. IRON CONTENT OF SEA-WATER SAMPLES FROM POSITIONS IN ENGLISH CHANNEL AND OFF BRITTANY COAST

(Depth in metres. Iron content in μg Fe/l.)

49° 27′ N., 4° 42′ W. 14 Nov. 1956		48° 34′ N., 5° 13′ W. 14 Nov. 1956		48° 18′ N., 5° 18′ W. 14 Nov. 1956	
Depth	Iron	Depth	Iron	Depth	Iron
0·5	45	0	66	0	90
5	33	5	30	5	27
10	45	10	56	10	25
20	34	20	52	20	31
50	37	50	53	50	35
90	19	100	14	100	35
		110	35	105	41

47° 50′ N., 5° 22′ W. 14 Nov. 1956		47° 35′ N., 4° 20′ W. 15 Nov. 1956	
Depth	Iron	Depth	Iron
0	61	0	126
5	61	10	26
10	62	20	28
20	61	50	40
50	49	75	24
100	86	100	109
125	158	105	126

TABLE 6. IRON CONTENT OF SEA-WATER SAMPLES FROM POSITIONS IN THE BAY OF BISCAY

(Depth in metres. Iron content in μg Fe/l.)

48° 00′ N., 10° 05′ W. 29 Apr. 1955		47° 33′ N., 07° 27′ W. 8 May 1955		46° 27′ N., 08° 04′ W. 27 June 1955		47° 30′ N., 08° 00′ W. 28 May 1956	
Depth	Iron	Depth	Iron	Depth	Iron	Depth	Iron
0	46	10	17	0	23	90	21
10	13	100	154	10	7	170	6
100	45	200	290	50	11	260	7
600	10	265	22	100	7	350	9
745	10	275	7	200	146	490	4
885	13	355	17	300	15	660	4
1025	11	435	29	400	13	860	5
1280	7	600	27	500	21	1100	9
1670	11	720	22	585	8	1500	6
2060	8	810	50	655	26	1890	7
2650	1	910	39	780	10	2180	11
2950	21	1050	34	930	27	2580	9
3250	58	1190	77	1080	9	3190	4
3540	37			1150	9	3700	7
				1320	15	4000	8
				1520	9	4570	5
				1720	16		
				1945	5		
				2245	7		
				2540	6		
				2840	10		
				3140	13		
				3440	12		
				3700	5		
				3990	18		
				4270	9		
				4460	4		

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SUMMARY

A method, suitable for routine use, of determining total iron in sea water is described. The water is acidified to about 0·13 N with hydrochloric acid and is heated for 5 h in an autoclave at 140° C. Iron is determined absorptiometrically with 1:1 phenanthroline after reduction with hydroxylamine hydrochloride.

Tests of the method, collection and storage of samples and the variability of results are described.

Iron contents of water samples from the English Channel and the Bay of Biscay are reported.

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MARINE ALGAL ZONATION AND SUBSTRATUM IN BEER BAY, SOUTH-EAST DEVON

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(Text-figs. 1–4)

A preliminary examination of the marine algal zonation of Beer Bay, south-east Devon, indicated that there might be some divergences from the basic zonation on the south coast of England as described by Grubb (1936) and Evans (1947). Moreover, it appeared that the divergences might be due to an effect of the substratum being superimposed upon the normal intertidal zonation. To investigate this further a survey of the marine algal vegetation and the substratum of the intertidal regions of Beer Bay was carried out.

Beer is situated approximately at the centre of Lyme Bay (National Grid 30/2389). The Bay is shown in detail in Fig. 1, with the areas surveyed stippled. The Bay is exposed from the south-east to the south. Although the south-east gales can be severe at Beer, they are less frequent than gales from the south-west, which seem to produce the most severe wave-action in the Bay. In these gales, the waves, which are travelling in a north-easterly direction outside the headland, seem to alter their direction, and travelling due north, sweep right into the Bay and cause considerable wave-action, even along the cliffs on the west side. The exposed nature of the Bay is reflected in the absence of *Pelvetia canaliculata* Dcne. & Thur. and *Ascophyllum nodosum* Le Jol., the almost complete absence of *Fucus spiralis* L., and the occurrence of *Alaria esculenta* Grev. at Beer Head and The Hall (Fig. 1).

Throughout this survey the marine algae were identified from the *Handbook of the British Seaweeds* (Newton, 1931), and the names used are those given in Parke's (1953) Check List.

SUBSTRATUM

The most westerly outcrop of the Chalk on the south coast of England occurs at Beer, and as a result the cliffs have been described by several authors (Meyer, 1874; Rowe & Sherborne, 1903; Jukes-Browne, 1904). The cliffs surrounding the Bay consist almost entirely of the Upper, Middle and Lower Chalks, but there is a zone of 2·5–3 m at the base of the cliffs where the chalk passes into the Upper Greensand. Directly beneath the clearly defined Lower Chalk there is a 1 m bed of harder rock, which Rowe & Sherborne (1903)

described as a transition bed between the Lower Chalk and Upper Greensand. They called this the Cenomanian Limestone. Jukes-Browne (1904), Dewey (1948), and Woodward & Ussher (1911) all include this bed in the Lower Chalk and apply the term Cenomanian to all the Lower Chalk at Beer. Below this zone occurs the siliceous rock shown as the Upper Greensand and it is the harder parts of this Greensand that form most of the flat expanse of rock which is exposed on each side of the Bay at low tide. However, in a few places, particularly on the east side of the Bay, the Cenomanian Limestone persists on top of the Greensand and takes the form of large flat-topped rocks

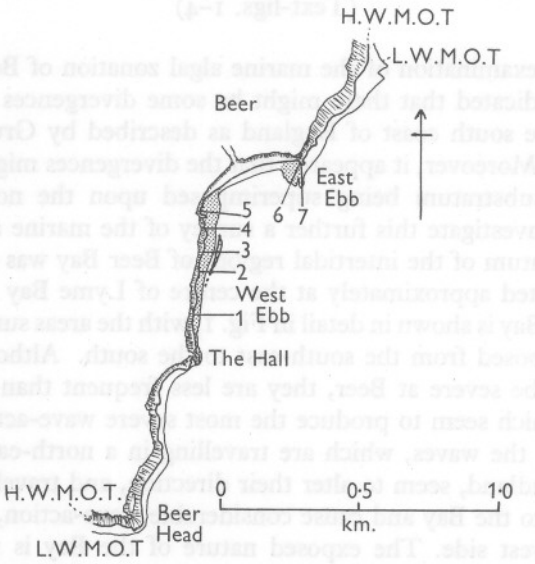

Fig. 1. Map of Beer Bay. Areas which were investigated are stippled. Numbered lines indicate positions of transects.

projecting well above the general level of the surrounding Greensand. At the base of the cliffs there are areas of chalk boulders which are the remains of extensive falls of cliff. Although these are much softer than fragments of the Greensand or of the Limestone, and tend to be eroded away rather quickly, they are continually being replaced by minor cliff falls. The beach is entirely of pebbles which range in size from stones 10–15 cm in diameter down to a fine shingle. Pebbles also occur in small isolated areas along the foot of the western cliffs where there are no chalk boulders. In the centre of the Bay and below the lowest tides there is a rather coarse sand.

METHODS OF SURVEY

Plane-table maps

Plane-table maps of the two sides of the Bay were prepared on a scale of 30 ft. to 1 in. and various fixed points marked on them to facilitate later work. The rock outcrops on both sides of the Bay were only mapped down as far as extreme low-water spring tides. In August of both 1954 and 1955 the substratum and the zones of the dominant algae were plotted on these maps and they are reproduced on a reduced scale as Figs. 2 and 3.

Transects

In 1955, seven transects, down through the intertidal zone, were investigated. The positions of these transects are shown on Fig. 1. Levelling along these transects was done with a modified form of the levelling apparatus developed by Miss J. M. Kain (in preparation). On a calm day the height of the sea in relation to fixed points on the transects was recorded and with the aid of a tidal curve and the predicted range of the tide for that day, which were kindly supplied by the Hydrographer to the Admiralty, the mean tidal levels, as quoted by the Admiralty, were found for each transect. This was later checked by levelling back to a bench mark.

RESULTS OF THE SURVEY

Substratum maps

Greensand, limestone, chalk boulders and pebbles are plotted on the substratum maps, and the areas colonized by the reef-building worm *Sabellaria alveolata* are also indicated. These worms build up extensive colonies of honeycomb-like structure at certain points between high-water neap tides and low-water spring tides. The colonies are usually quite extensive and vary considerably in depth. In some places they form a uniform cover 2–5 cm deep and in other places they are in the form of tussocks. As will be shown later it is mainly on these colonies that the anomalies in the normal zonation occur.

Species maps

Five main groups are considered in the species maps, these are: *Enteromorpha* spp., *Ulva lactuca*, *Fucus vesiculosus*, *F. serratus* and *Gigartina stellata*. *Enteromorpha* was not divided up into species, but it was known to include *Enteromorpha intestinalis* and *E. compressa* and probably several other species. The *Fucus vesiculosus* was a form without vesicles and was probably the form described in Newton (1931) as *F. vesiculosus* var. *evesiculosus* Cotton. Throughout the area this was the only form of *F. vesiculosus* found, and Knight & Parke (1950) say: 'An almost complete absence of vesicles characterizes the whole *F. vesiculosus* zone on the Devon, Manx and Argyll coast, in very

exposed places such as at the foot of vertical cliffs exposed to full surf action.' At Beer this alga is not growing on vertical cliffs but, as already mentioned, there is considerable wave action in the Bay. *Laminaria* spp. were not plotted as these only became dominant below the level of the mapped areas. It should be recorded that, although in several places the high-tide mark was well up the cliffs, there were none of the zones described by Anand (1937) as being characteristic of the chalk cliffs of Sussex.

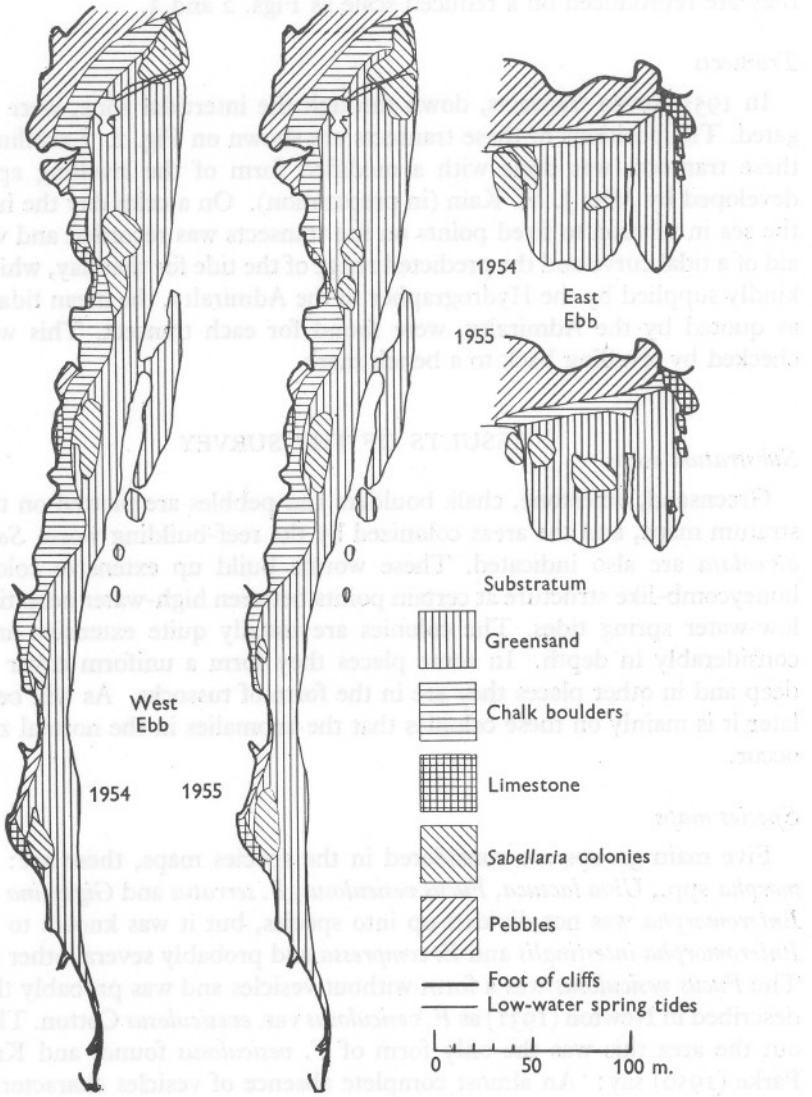

Fig. 2. Substratum maps 1954 and 1955.

Species and substratum

The maps of the west side of the Bay show five areas colonized by the *Sabellaria* worms and the major parts of these colonies were dominated by *Ulva lactuca* or *Gigartina stellata*. On the east side of the Bay the worm colonies were also dominated by either *Ulva* or *Gigartina*. It should, however, be pointed out that *Gigartina* was also dominant on some extensive areas that

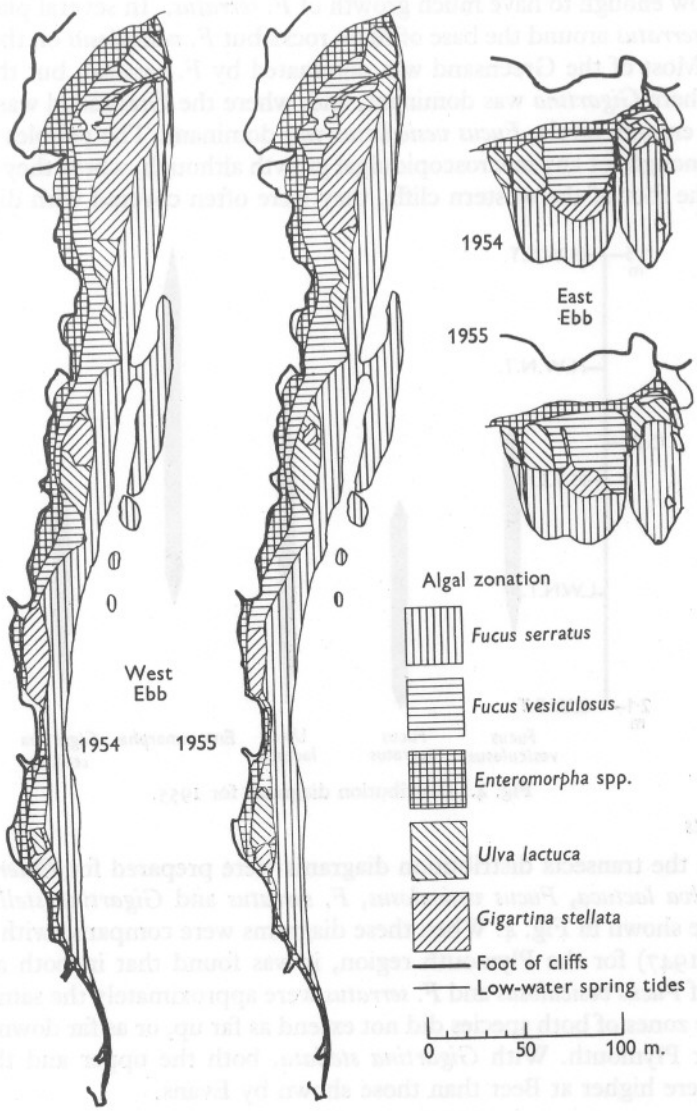

Fig. 3. Algal zonation 1954 and 1955.

were not colonized by the *Sabellaria* worms but, apart from one or two very small areas, *Ulva* was only dominant on areas colonized by the *Sabellaria* worms. The chalk boulders at the base of the cliffs were almost entirely covered with a dense growth of *Enteromorpha*. This growth was correlated with the occurrence of fresh water running out of the Greensand at the base of the cliffs and forming streamlets running between these chalk rocks. *Fucus vesiculosus* dominated most of the rest of the chalk rocks which did not extend down low enough to have much growth of *F. serratus*. In several places there was *F. serratus* around the base of these rocks but *F. vesiculosus* on the top and sides. Most of the Greensand was dominated by *F. serratus*, but there were areas where *Gigartina* was dominant, and, where the Greensand was exposed at high enough levels, *Fucus vesiculosus* was dominant. The pebbles were not stable enough for any macroscopic algal growth although, where they occurred along the foot of the western cliffs, they were often covered with diatoms.

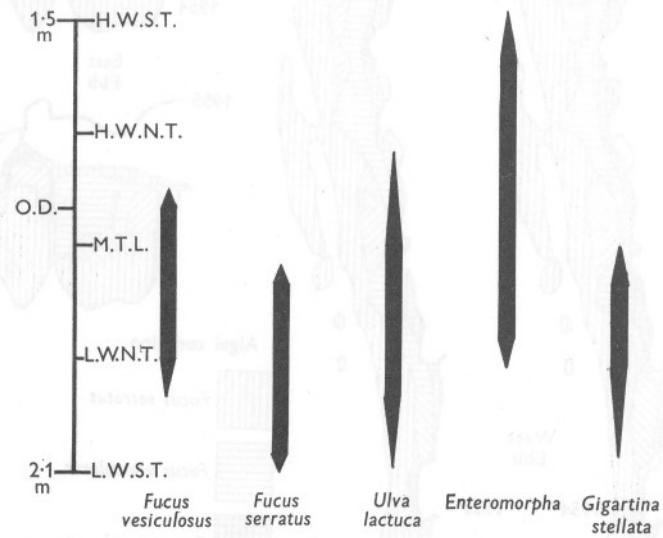

Fig. 4. Distribution diagrams for 1955.

Transects

From the transects distribution diagrams were prepared for *Enteromorpha* spp., *Ulva lactuca*, *Fucus vesiculosus*, *F. serratus* and *Gigartina stellata*, and these are shown in Fig. 4. When these diagrams were compared with those of Evans (1947) for the Plymouth region, it was found that in both areas the means of *Fucus vesiculosus* and *F. serratus* were approximately the same, but at Beer the zones of both species did not extend as far up, or as far down, as they did near Plymouth. With *Gigartina stellata*, both the upper and the lower limits were higher at Beer than those shown by Evans.

NITROGEN ESTIMATIONS ON *ULVA*

In an attempt to determine if the dominance of *Ulva lactuca* on the *Sabellaria* colonies was in any way reflected in a change in the nitrogen-content of the *Ulva*, some estimations of the total nitrogen-content of *Ulva* samples were carried out. The material was collected at Beer in June 1956 and the samples were treated immediately on return to London. *Ulva* was collected from areas of 100 cm^2 and, after a quick washing to remove sand, etc., was dried to constant weight in an oven at 100° C. The percentage nitrogen content of the samples, on a total dry-weight basis, was then determined by means of the micro-Kjeldahl method. Eight samples of *Ulva* growing on *Sabellaria* colonies, and two samples not on colonies, were estimated. The mean of the dry weights of *Ulva* per 100 cm^2 on the colonies was 1·37 g, and off the colonies was 1·01 g. The mean percentage nitrogen on a total dry-weight basis was 0·68% on the colonies, standard deviation 0·21, and off the colonies was 2·64%, standard deviation 0·14. These results show a slightly higher yield per unit area, but a lower nitrogen content per unit dry weight on the colonies. This may indicate a more rapid growth of *Ulva* on the colonies. In both cases the values are considerably less than those quoted by Milner (1953), who gives a value of 4·87% on a dry-weight-less-ash basis, i.e. 3·95% on a total dry-weight basis.

DISCUSSION

It seems clear from the species maps that, at Beer, *Ulva lactuca* dominates large areas only if they are colonized by the *Sabellaria alveolata* worms. On the *Sabellaria* colonies the *Ulva* is different in appearance from that off the colonies, in that the plants on the colonies are smaller in height and much more tufted at the base than the forms growing off the colonies. This dominance of *Ulva lactuca* on the colonies of *Sabellaria* may be related to one or more of three possibilities. (i) The *Sabellaria* colonies form a very unstable substratum and the larger algae such as the fucoids cannot become established on them. (ii) Due to the presence of some factor produced by the *Sabellaria* worms, the growth of *Ulva* on the colonies is very rapid and hence the *Ulva* soon forms a complete cover to the exclusion of other algae. (iii) The colonies produce something that is toxic to most algae but not to *Ulva*.

The first factor does not seem to be likely as *Gigartina* plants reach considerable size where they are the dominant plants on the *Sabellaria* colonies and these probably grow at a comparable rate to the fucoids. Further, in some areas the fucoids do encroach slightly on to the *Sabellaria* colonies and are thus able to grow on the colonies if they get a chance. By the same reasoning, the idea that there may be some toxin released must be excluded. It is, however, difficult to show any definite evidence for the second factor and the nitrogen estimations did not give any explanation here.

Cotton (1910) noted the good growth of *Ulva* in quiet brackish water that

was strongly polluted, he also found that *Ulva* could assimilate high levels of nitrate and ammonia. Arber (1901) asserted that abnormally high levels of nitrates caused inhibition of carbon-assimilation in *Ulva* cultures. Letts & Richards (1911) found the addition of filtered sewage, up to 10%, gave a considerable increase in growth, growth being estimated by the increase in surface area. They also found that the increase was greater than that brought about by the addition of nitrate and phosphate. Foster (1914) found that *Ulva* grew quite well on ammonium nitrate, urea and acetamide. In all this work no attempts were made to prevent, or even reduce, bacterial contamination.

Kylin (1942) found that glucose, ascorbic acid and heteroauxin, at certain concentrations, all increased the rate of division in *Ulva* sporelings. In 1943 he commented on the stimulatory effects of thiamin and of biologically active substances in the surface layers of the sea, especially if the water was collected in regions of dense algal growth. Later (1945) he found that the effects of these biologically active substances and the effects of iron and manganese were additive. Again, however, these cultures were contaminated.

Cotton (1911) commented on the abundance of *Ulva* on mussel beds and pointed out that, under these conditions, sporing tends to be reduced and the main form of reproduction is vegetative. As previously stated, I have noted that the plants on the *Sabellaria* colonies at Beer are small in extent and very tufted at the base. This may indicate the extensive vegetative reproduction mentioned by Cotton.

Gigartina occurs both on the Greensand and on the *Sabellaria* colonies and thus appears not to be in any way affected by the *Sabellaria* worms, although it should be pointed out that the highest level at which *Gigartina* occurred at Beer was on a *Sabellaria* colony. As was previously stated, the two species of *Fucus* do not show any divergences from the normal zonation found on the south coast of England. Both species occur on all types of substratum.

Enteromorpha shows a wide distribution throughout the intertidal zone, but, as this genus is known to be greatly influenced by local conditions such as the presence of fresh water and high nitrogen sources, the wide distribution is not surprising. Although *Enteromorpha* was very abundant on the chalk boulders, it occurred also at the same levels on the Greensand, and, furthermore, its distribution was correlated with that of fresh water which ran from the base of the cliffs, and thus, in this case, there was no correlation of distribution with substratum.

From this investigation it is concluded that the distribution of the main marine algal species in Beer Bay was quite normal for an exposed area on the south coast of England and, with the exception that *Ulva lactuca* was only dominant over large areas where these were colonized by the reef-building worm *Sabellaria alveolata*, there was no effect of substratum on the distribution of the algal species.

I wish to thank Dr G. E. Fogg for his helpful criticism of this work, Mr J. H. Belcher for help with the nitrogen estimations, and Miss J. M. Kain for help in the construction of the level used on the transects.

SUMMARY

The intertidal zonation of the dominant algal species in Beer Bay, south-east Devon, was examined in relation to substratum by means of plane-table maps and transects. The dominance of *Ulva lactuca* on colonies of the reef-building worms *Sabellaria alveolata* was noted, but the distributions of *Fucus vesiculosus*, *F. serratus*, *Gigartina stellata* and *Enteromorpha* spp. showed no correlation with substratum.

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SPECTRAL COMPOSITION OF THE LIGHT OF POLYNOID WORMS

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(Text-figs. 1–14)

The spectral composition of the light of only one marine animal is known, viz. the ostracod *Cypridina hilgendorfii* (see Coblentz & Hughes, 1926; Eymers & van Schouwenburg, 1937). It is desirable to have spectral energy curves for the light of other animals in order to relate these to the spectral sensitivity of photoreceptors, and to calculate total radiant energy in the visible range. To further these ends I have measured the spectral energy distribution of the light of some polynoid worms.

The luminescence of polynoids originates in the elytra or scales covering the dorsal surface. The photocytes form a single epithelial layer on the lower surface of the centre of the elytrum, and the light shines through the elytrum, which is clear and non-pigmented over the luminescent tissue. The light appears emerald-green in colour, and presumably has an emission peak somewhere between 510 and 530 mμ. In the normal response the light is emitted in brief discontinuous flashes, some 0·1 sec. in duration (Nicol, 1953, 1957*a*). Repeated or strong shocks sometimes produce a prolonged glow, in which the luminescence tends to become exhausted. Separate flashes vary greatly in intensity, owing to facilitation and fatigue (Nicol, 1954). The problem, then, is to determine the spectral composition of brief flashes of weak green light, varying greatly in intensity. The procedure adopted is described below.

MATERIAL AND METHODS

Four species of polynoid worms were used, viz. *Lagisca extenuata*, *Gattyana cirrosa*, *Polynoë scolopendrina* and *Harmothoë longisetis*. Elytra were removed from a worm under $MgCl_2$-narcosis, and washed in sea water. An isolated elytrum was mounted in a glass and Perspex moist chamber over a pair of electrodes, and the chamber was sealed with a glass coverslip. This arrangement allowed the light to be detected from above and below the scale. Below the chamber lay an 11-stage photomultiplier (E.M.I. no. 6260), with a 45 mm end-window; above, a 14-stage photomultiplier (E.M.I. no. 6685), with a 9 mm end-window. The two photomultipliers were connected to separate cathode-ray oscilloscopes, and photographic records of the luminescent responses were made on moving paper. The arrangement is illustrated in Fig. 1.

The lower photomultiplier was used to provide an index of flash intensity. A coloured filter was placed between the specimen and the upper photomultiplier, which was used to measure the light transmitted by a certain spectral band. The coloured filters were Ilford's spectrum set, nos. 601 to 608, covering the visible spectrum; curves are given in *Ilford colour filters*, published by Ilford Ltd. In some instances a neutral filter (Chance's neutral glass ON 31 or 32) was placed over the lower photomultiplier to prevent saturation from very bright flashes. This arrangement allowed very bright responses to be recorded by the lower photomultiplier, without altering

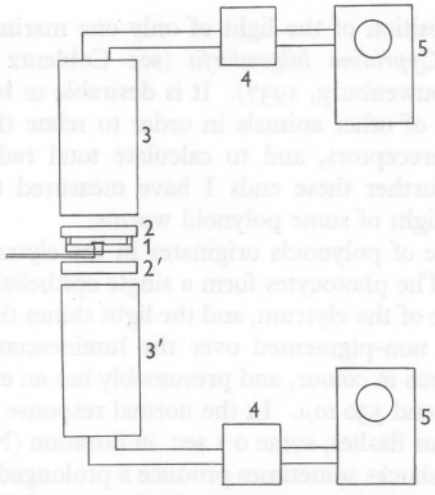


Fig. 1. Diagram of apparatus. 1, moist chamber containing elytrum and electrodes; 2, coloured spectral filter; 2′, neutral filter; 3, photomultiplier 6685; 3′, photomultiplier 6260; 4, d.c. amplifiers; 5, cathode-ray oscilloscopes.

voltage on the tube, in those instances when measurements were being made with coloured filters 606–608 in front of the upper photomultiplier. I determined the transmission of my set of filters with a spectrophotometer (Unicam SP 500).

Both photomultipliers had Cs–Sb photocathodes, with high sensitivity in the violet, and very low sensitivity in the red. The spectral sensitivity of photomultiplier no. 6685 was determined by the National Physical Laboratory. Combined data for photomultiplier no. 6685 and coloured filters are given in Table 1.

The mains voltage was maintained constant for all equipment by a voltage stabilizer. Both photomultipliers were run off the same power-pack, which held steady voltage, as determined by periodic checks.

Repeat determinations, made with a constant light source, showed that measurements could be made on the oscilloscope screen with an accuracy of $\pm 2\%$.

A series of observations was made with the several coloured filters on each elytrum. If the elytrum continued to respond with sufficient intensity, it was possible to do a run with all filters on a single elytrum. From two to eight runs were made with all filters for the elytra of each species. Since the elytra flash repetitively to stimulation, each photographic record reveals a series of flashes (10 or more), a selected number of which was measured. The conclusions are based on about 150 photographic records and an analysis of some 1000 flashes.

Room temperatures during the measurements varied from 18° to 19° C.

TABLE 1. CERTAIN CHARACTERISTICS OF ILFORD SPECTRUM FILTERS AND E.M.I. PHOTOMULTIPLIER NO. 6685

Ilford filters	Filter range (mμ)	Maximal transmission		Representative wavelength (mμ)	Area of curve $S_\lambda T_\lambda$*
		λ	%		
Violet 601	400–485	440	16·8	433	230·0
Blue 602	440–495	465	7·1	465	48·0
Blue-green 603	470–525	490	13·5	490	81·0
Green 604	500–540	515	7·8	514	32·1
Yellow-green 605	525–570	545	6·7	548	24·43
Yellow 606	560–610	575	7	573	11·0
Orange 607	575–700	600	18·2	595	23·26
Red 608	610–700	700	81	661	5·6

* S, sensitivity of photomultiplier. T, transmission of filter.

OBSERVATIONS

ESTIMATION OF ACCURACY, USING A KNOWN LIGHT SOURCE

In order to evaluate the accuracy of the method, light from a known source was measured by means of the Ilford spectrum filters and photomultiplier no. 6685. The light was provided by a substandard lamp (colour temperature 2360° K), and was passed through a yellow-green filter (Chance OGR 2). Measurements of the response were made on the oscilloscope-face for each of the spectral filters nos. 601–608. To reduce intensities, a Chance neutral density glass (no. ON 31) was used in conjunction with Ilford filters nos. 603–607. Relative transmission values of the green filter OGR 2 were determined with a spectrophotometer (Unicam SP 500). The curves in Fig. 2 show the actual transmission of filter OGR 2 (curve A), and the calculated spectral composition ($\mathcal{J}_\lambda T_\lambda$) of the light reaching the photomultiplier (curve B). The circles in Fig. 2 are the first estimations of relative spectral energy, made with spectral filters, photomultiplier and oscilloscope.

Most of the filters have rather broad transmission bands, and the sensitivity of the photomultiplier changes greatly over the visual spectrum. The values for the combination $S_\lambda T_\lambda$ are based on the assumption of an equal energy spectrum. Light having a pronounced spectral peak will differ from an equal energy spectrum in its effects at various wavelengths according to the characteristics of each factor in the combination $E_\lambda S_\lambda T_\lambda$. To predict the results, an

approximate energy curve was drawn from the points in Fig. 2, and energy levels ($E_{\lambda A}$) from this curve were used to calculate a series of values for $\int E_{\lambda A} S_\lambda T_\lambda$. These values were then used to correct the results, in the manner outlined in the next section. The final corrected estimations of relative spectral composition, based on direct measurements, are represented by the circles in Fig. 3, which also gives the calculated spectral composition of artificial light ($\mathcal{J}_\lambda T_\lambda$). Values for $\mathcal{J}_\lambda$ were taken from Skogland (1929). There is reasonably good agreement between predicted and measured values. These measurements, of course, were made under optimal conditions (steady light intensity and absence of background noise).

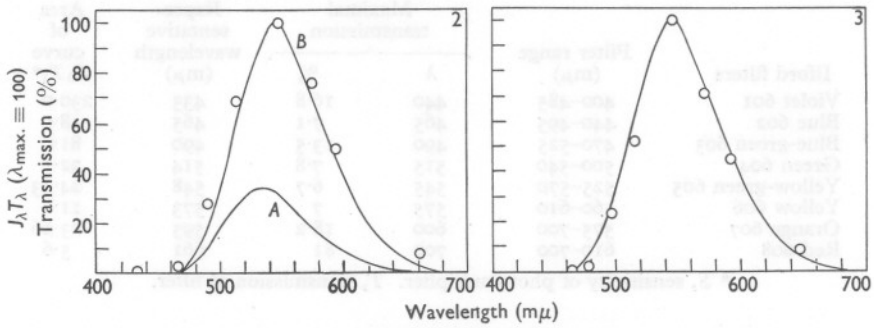


Fig. 2. Curve A: transmission (%) of a green filter. Curve B: calculated relative spectral energy of light from a tungsten lamp (2360° K), transmitted through a green filter (Chance OGR 2) ($\mathcal{J}_\lambda T_\lambda$). Circles are first measurements of relative spectral energy made by means of coloured filters and photomultiplier no. 6685.

Fig. 3. Curve as in Fig. 2B (calculated relative spectral energy of artificial light—source 2360° K plus Chance OGR 2). Circles are corrected measurements of relative spectral energy.

MEASUREMENTS OF THE LIGHT FROM POLYNOID ELYTRA

First approximate results obtained by measuring the light emission of four species of polynoids are given in Table 2, and the data are presented graphically in Figs. 4–7. Some representative photographic records are shown in Fig. 8. The data for an experiment on one animal (*Polynoë*) are given in greater detail in Table 3, to illustrate the calculations involved. Measurements for all four species of polynoids are pooled together to give the emission curve of Fig. 9. The measurements derived from the use of filters 602, 606, 607 and 608 are less reliable than the others, owing to high density of the filters (602, 606) and low sensitivity of the photomultiplier at long wavelengths (orange and red). The electrical response to red light which reached the photocathode was very small, and the results in the red region of the spectrum can be in error by a factor of 2. With the denser filters the transmitted light was equal to, or below, visual threshold. The main source of error lies in evaluating response height through the background noise at high amplification. This was

TABLE 2. FIRST APPROXIMATIONS FOR SPECTRAL ENERGY OF THE LIGHT OF POLYNOIDS

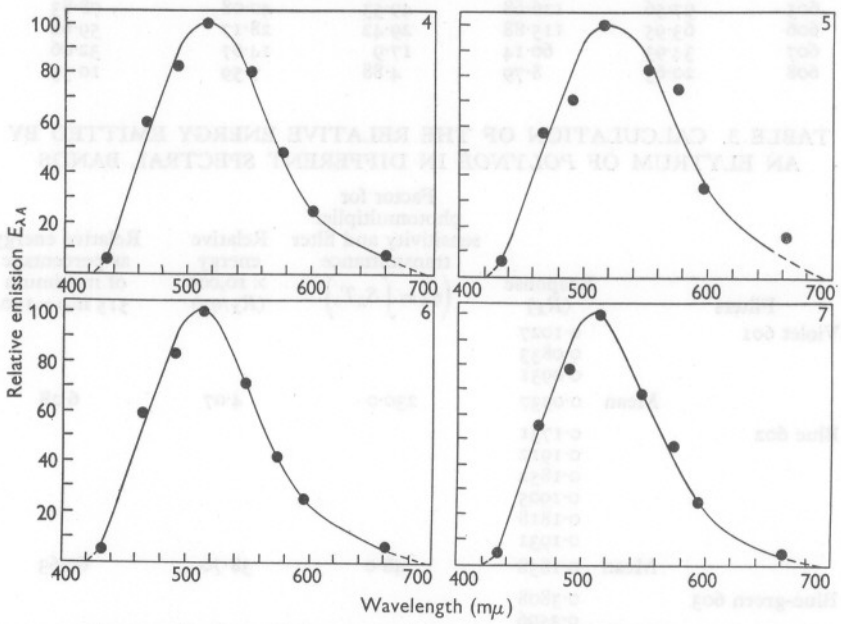
Filters	Averages of readings. *Lagisca*	*Gattyana*	*Harmothoë*	*Polynoë*	Means, four species ($\lambda_{max.}$ as 100)
601	6·63	9·43	3·61	3·62	5·85
602	71·17	87·63	41·37	32·88	58·53
603	98·77	109·96	58·24	45·60	78·50
604	118·91	151·36	69·57	58·32	100
605	97·56	126·68	49·53	40·08	78·83
606	63·95	115·88	29·42	28·17	59·62
607	34·93	60·14	17·9	14·67	32·06
608	20·65	8·79	4·88	7·59	10·53

TABLE 3. CALCULATION OF THE RELATIVE ENERGY EMITTED BY AN ELYTRUM OF *POLYNOË* IN DIFFERENT SPECTRAL BANDS

Filters		Response (R_X)	Factor for photomultiplier sensitivity and filter transmittance $\left(\eta_X = \int S_\lambda T_\lambda\right)$	Relative energy × 10,000 (R_X/η_X)	Relative energy as percentage of maximum 515 mμ = 100
Violet 601		0·1027			
		0·0833			
		0·0951			
	Mean	0·0937	230·0	4·07	6·28
Blue 602		0·1731			
		0·1912			
		0·1852			
		0·1905			
		0·1818			
		0·1931			
	Mean	0·1858	48·0	38·70	60·63
Blue-green 603		0·3808			
		0·3506			
		0·3818			
		0·3759			
		0·4100			
	Mean	0·3798	81·0	46·89	72·33
Green 604		0·2126			
		0·2136			
		0·2217			
		0·2068			
		0·1955			
		0·1982			
	Mean	0·2081	32·1	64·83	100
Yellow-green 605		0·1191			
		0·1040			
		0·1201			
		0·1002			
	Mean	0·1109	24·43	45·41	70·04
Yellow 606		0·0401			
		0·0344			
	Mean	0·0377	11·0	34·27	52·86
Orange 607		0·0367			
		0·0386			
	Mean	0·0376	23·26	16·17	24·94
Red 608		0·0356			
		0·0300			
	Mean	0·0328	5·6	5·86	9·04

particularly difficult in the weak responses obtained with the yellow, orange and red filters. Each point on the curves represents the mean of some thirty measurements.

Because of the broad transmission of the filters, the first approximate results for relative spectral emission were corrected as follows. The mean



Figs. 4–7. Curves showing relative spectral energy of light emitted by four species of polynoids, viz. *Lagisca* (Fig. 4), *Gattyana* (Fig. 5), *Harmothoë* (Fig. 6), and *Polynoë* (Fig. 7).

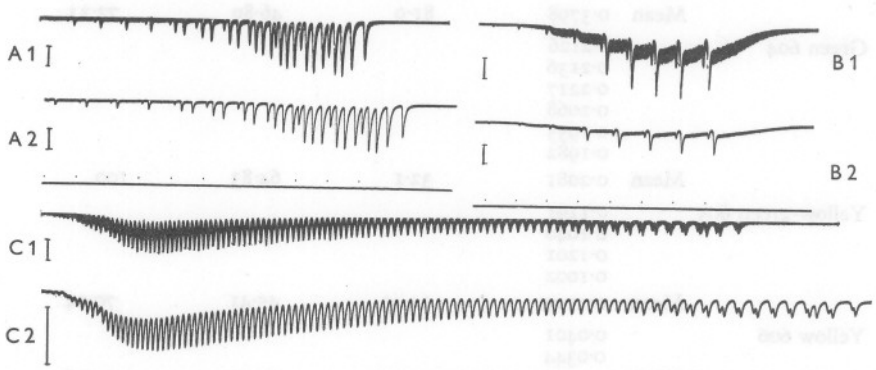


Fig. 8. Oscillograph records of the luminescent responses of *Harmothoë longisetis*, selected as examples. Records as follows: A 1, upper photomultiplier + blue filter 602; A 2, lower photomultiplier; B 1, upper photomultiplier + blue-green filter 603; B 2, lower photomultiplier; C 1, upper photomultiplier + yellow filter 606; C 2, lower photomultiplier. Relative amplifications shown by vertical lines. Electrical stimuli on lower lines of A 2 and B 2.

spectral energy curve of Fig. 9 was used to provide approximate values for radiant flux ($E_{\lambda A}$). With these values, curves were plotted for $E_{\lambda A}S_\lambda T_\lambda$ against λ (Fig. 11). Ratios were then obtained for each filter

$$\rho_1 = \frac{\int E_{\lambda A} S_\lambda T_{\lambda X}}{\int E_{\lambda A} S_\lambda T_{\lambda 604}},$$

which were used to predict the experimental results. Similar ratios were determined for measured responses

$$\rho_2 = \frac{R_X}{R_{604}}.$$

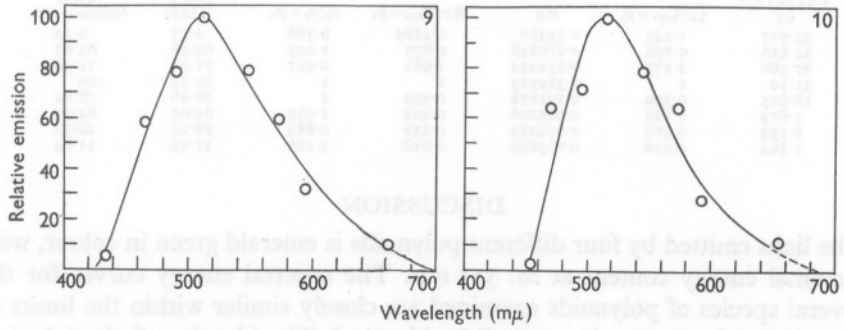


Fig. 9. Composite curve showing relative spectral energy of polynoid light (mean of determinations of four species, viz. *Lagisca*, *Polynoë*, *Harmothoë* and *Gattyana*). First approximate values.

Fig. 10. Composite curve showing relative spectral energy of polynoid light. Corrected results.

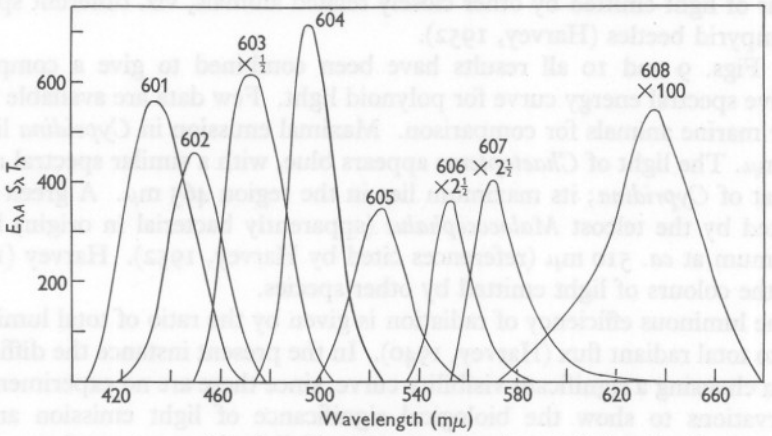


Fig. 11. Curves for combinations $E_{\lambda A}S_\lambda T_\lambda$ plotted against λ. Values for $E_{\lambda A}$ are taken from the curve in Fig. 9.

The ratios $\rho_3 = \rho_2/\rho_1$ were then used to correct the points on the spectral curve. New values for representative mean wavelengths were calculated from the centre of gravity of curves $E_{\lambda A} S_\lambda T_{\lambda X}$. The procedure is illustrated in more detail in another paper dealing with the light of *Chaetopterus* (Nicol, 1957*b*). The calculations are assembled in Table 4, and the corrected results are plotted against λ in Fig. 10.

The relative spectral energy curves (Figs. 4–7, 9, 10) are asymmetrical, with peaks at *ca.* 515 mμ (510–520 mμ). Most of the light emitted is in the blue-green, and there is very little in the violet and red.

TABLE 4. CALCULATION OF RELATIVE SPECTRAL COMPOSITION OF THE LIGHT OF POLYNOIDS

Filter	$E_{\lambda A} S_\lambda T_\lambda = \zeta_X$	$\zeta_X/\zeta_{604} = \rho_1$	RX	$RX/R_{604} = \rho_2$	$\rho_2/\rho_1 = \rho_3$	Corrected values $Qx\rho_3$	$Qx\rho_3$ $\lambda_{515 m\mu} = 100$	Mean λ (from curves $E_{\lambda A} S_\lambda T_\lambda$) (m$\mu$)
601	35·617	1·145	0·13386	0·4189	0·366	2·13	2·14	455
602	24·616	0·792	0·279648	0·875	1·105	64·38	64·67	470
603	67·566	2·173	0·632934	1·981	0·912	71·26	71·59	494
604	31·10	1	0·319523	1	1	99·54	100	515
605	18·625	0·599	0·191678	0·599	1	78·46	78·82	545
606	5·873	0·189	0·065296	0·204	1·079	64·05	64·35	572
607	8·133	0·262	0·074223	0·232	0·885	28·24	28·37	592
608	0·504	0·016	0·005869	0·018	1·125	11·79	11·84	653

DISCUSSION

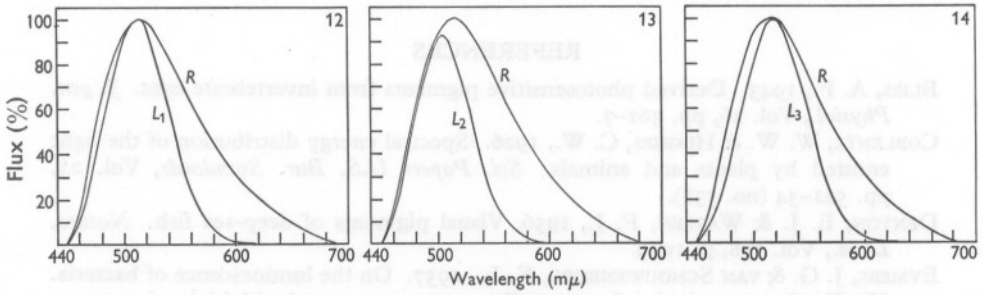
The light emitted by four different polynoids is emerald green in colour, with maximal energy content at *ca.* 515 mμ. The spectral energy curves for the several species of polynoids examined are closely similar within the limits of experimental error, and may well be identical. The identity of physiological mechanisms controlling luminescence in polynoids suggests that the same identity may exist in biochemical mechanisms. However, this argument cannot be pressed very far in view of the known differences existing in the colour of light emitted by other closely related animals, viz. different species of lampyrid beetles (Harvey, 1952).

In Figs. 9 and 10 all results have been combined to give a composite relative spectral energy curve for polynoid light. Few data are available from other marine animals for comparison. Maximal emission in *Cypridina* lies at 480 mμ. The light of *Chaetopterus* appears blue, with a similar spectral range to that of *Cypridina*; its maximum lies in the region 465 mμ. A green light emitted by the teleost *Malacocephalus* (apparently bacterial in origin) has a maximum at *ca.* 510 mμ (references cited by Harvey, 1952). Harvey (1955) lists the colours of light emitted by other species.

The luminous efficiency of radiation is given by the ratio of total luminous flux to total radiant flux (Harvey, 1940). In the present instance the difficulty lies in choosing a significant visibility curve, since there are no experiments or observations to show the biological significance of light emission among polynoids, i.e. what photoreceptors polynoid light is accustomed to excite. As a first attempt I have determined the luminous efficiency for human

scotopic vision (from C.I.E. values for relative efficiency of radiation (scotopic vision)). The relevant curves are given in Fig. 12. Luminous efficiency for polynoid light is 61%. This means that the worms appear 39% less bright than they would be if all the energy were concentrated at that wavelength (505 mμ) for which the dark-adapted human eye is most sensitive.

Visibility curves for various invertebrates and lower vertebrates have maxima ranging from about 490 to 540 mμ (e.g. *Eledone*, 490 mμ; *Limulus*, 520 mμ; *Lepomis*, 540 mμ) (Graham & Hartline, 1935; Grundfest, 1932; Bliss, 1943). Vertebrate rhodopsins, occurring in marine coastal and surface



Figs. 12–14. Luminous efficiency of light emitted by polynoids. Curves for radiant flux (R) of polynoid light, and luminous flux based on human scotopic vision, $\lambda_{max.}$ at 505 mμ (L_1) (Fig. 12); luminous flux based on a theoretical visual curve with maximum at 490 mμ (L_2) (Fig. 13); and luminous flux based on a theoretical visual curve with maximum at 520 mμ (L_3) (Fig. 14).

fish, show absorption maxima around 500 mμ; porphyropsins, found in wrasse, trout, etc., have maxima around 520 mμ; deep-sea teleosts have visual pigments with absorption maxima around 480 mμ (Wald, 1952, 1953; Granit, 1955; Denton & Warren, 1956). The emission spectrum of polynoid light is fairly broad. Calculations based upon two generalized visibility curves, similar in shape to those for human scotopic vision, but having maxima at 490 and 520 mμ, give luminous efficiencies of 51 and 66% respectively (Figs. 13, 14). A narrow spectral emission curve, like that for *Cypridina* with its maximum at 480 mμ, will show much lower luminous efficiencies for visibility curves having maxima at longer wavelengths.

I wish to thank Mr F. A. J. Armstrong for help in technique, and Dr E. J. Denton for advice concerning measurements and calculations of light intensity. Part of the apparatus used in this investigation was purchased with a grant from the Royal Society.

SUMMARY

The spectral composition of the light of four species of polynoid worms has been measured, viz. *Harmothoë longisetis*, *Gattyana cirrosa*, *Polynoë scolopendrina* and *Lagisca extenuata*. The method involved the use of coloured spectral filters and two multiplier phototubes. The spectral emission curves of the four species are similar. They are asymmetrical in shape, prolonged towards longer wavelengths, with maxima at about 515 mμ (510–520 mμ). Values for luminous efficiency are calculated (ratio of luminous flux to radiant flux); for human scotopic vision ($\lambda_{max.}$ at 505 mμ), efficiency is 61%.

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THE FEEDING AND CONDITION OF PLAICE LARVAE IN GOOD AND BAD PLANKTON PATCHES

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(Plate I and Text-figs. 1–3)

In spite of the high fecundity of many food-fish species, only a minute proportion of the total eggs spawned enter the fishery later on, as marketable adults. This principle is not in dispute. There is, however, a considerable division of opinion among fisheries biologists on the general shape of the mortality curve. Hjort (1914, 1926) suggested that the final size of a year-class of cod and herring is determined shortly after hatching, and is related to the larval food supply and drift. Sund (1924) supported this view. Johansen (1927) investigated yearly fluctuations in the abundance of fish larvae in Danish waters, and came to the conclusion '. . . that in cold winters, when there is a relatively marked outflow of comparatively fresh water from the Baltic, through the Belts and Southern Kattegat, the tiny plaice larvae fail to obtain sufficient nourishment and die of starvation *en masse*'. Rollefsen (1930) demonstrated the lethal effect of agitation on the vulnerable stages of the cod egg, and thought that wave action during incubation might strongly influence the early slope of the mortality curve. The observations of Soleim (1940, 1942) on herring larvae off the coast of Norway, and in the laboratory, led him to infer a critical starvation period following yolk resorption.

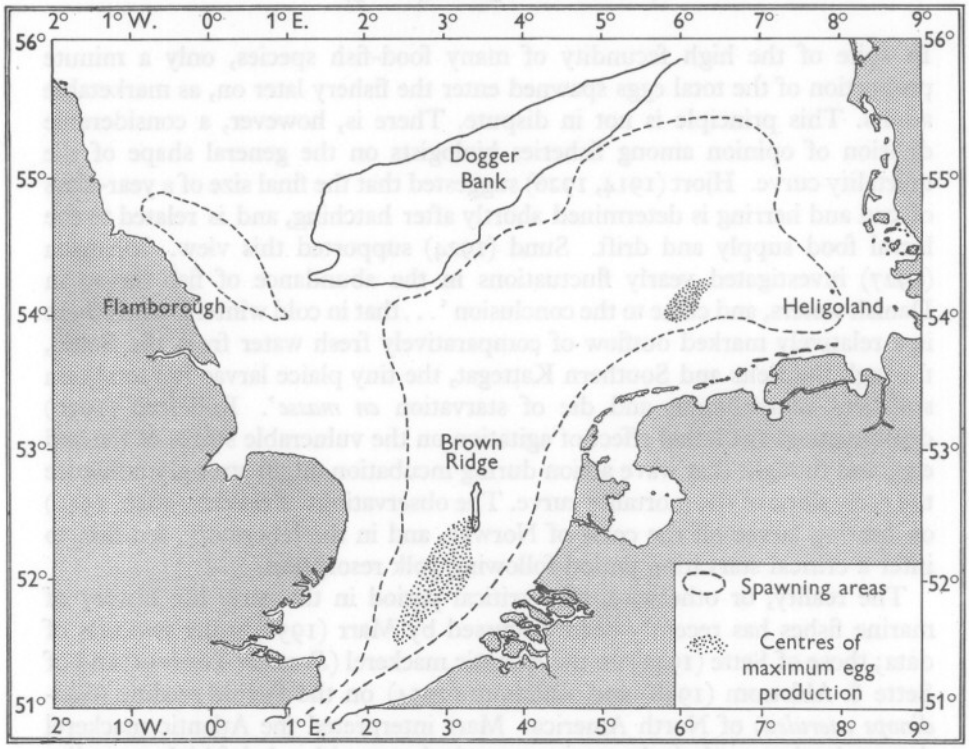
The reality, or otherwise, of a critical period in the early life history of marine fishes has recently been discussed by Marr (1956) using two sets of data; those of Sette (1943) on the Atlantic mackerel (*Scomber scombrus*) and of Sette & Ahlstrom (1948) and Ahlstrom (1954) on the Pacific sardine (*Sardinops caerulea*) of North America. Marr interpreted the Atlantic mackerel data as having a relatively constant survival rate with a brief high mortality at the age of 30–40 days, but no critical period at the time of yolk resorption. Although the Pacific sardine records show an apparent critical phase, Marr contested the reality of this result on the basis of inadequate sampling of the very young larval population.

As a complement to the studies of Simpson (1951) on the fecundity of North Sea plaice (*Pleuronectes platessa*) and the distribution of its eggs and larvae (in press), preliminary attempts were made during the 1955 spawning season, to follow the fate of plaice egg broods during their early life history. Bad

weather limited activities, but some significant observations were made on the condition of plaice larvae in good and bad feeding conditions, relevant to the unsolved problem of early mortalities.

SAMPLING TECHNIQUE

The spawning season of the North Sea plaice lasts from late December until late March, with the peak of egg production occurring round about the end of January. The spawning area extends from the Straits of Dover to the south-east edge of the Dogger Bank and round into the Heligoland Bight (Text-fig. 1). There are two centres of maximum production: in the south, over the



Text-fig. 1. Plaice spawning grounds in the southern North Sea.

Brown Ridge, and in the north-east, off Heligoland. The Southern Bight spawning ground covers an area of some 8000 square miles; the Heligoland ground, some 2500 square miles. In addition, there is a minor spawning ground off Flamborough Head.

Marr (1956) has already stressed the importance of adequate coverage, in time and space, of spawning areas during mortality surveys, and criticizes the inference of Soleim (1942) regarding a critical phase, on these grounds. Plaice

larvae from the Southern Bight drift in towards the Dutch and German coasts, parts of which are still mined. As winter weather interferes with plans for frequent surveys over such a large area of sea from a single research vessel, it was decided to attempt an intensive mortality study of the egg and larval population around a point marked by a floating radio buoy, rather than to assess the death-rate for the whole spawning area. The limitations of such a scheme were fully realized; in particular, the fact that the resultant mortality curve would not necessarily be typical for the whole area, even during the same period in time. Furthermore, it was not known whether a floating buoy, equipped with a 'tail' of sea drogues would continue to mark a pelagic plaice population in all weathers.

In late January 1955, a Heligoland larva net of 1·5 m diameter, with 60 meshes per inch silk, was used from R.V. *Sir Lancelot* south-west of the Brown Ridge, in search of an extensive patch of evenly scattered young plaice eggs. Such a patch was found, and a buoy, fitted with a short-range radio transmitter and a set of sea drogues, planted in the middle of it. By intensively sampling a close grid around the buoy in the middle of a big patch, it was hoped to overcome the problem set by differential water movement during gales, on the assumption that eggs and larvae moving out of grid range would be equally replaced.

Fair weather continued for a period of 12 days, during which time six grids of thirteen equally spaced stations per grid, were completed. Each grid covered an area of 1 square mile with the buoy as its centre. Two plankton hauls were made at each station, sampling after dusk to limit larval avoidance (Silliman, 1943; Bridger, 1956). Representative salinity samples and temperature records remained consistent throughout the 12-day period. Thereafter, strong south-westerly winds and a heavy swell shifted the buoy some 40 miles to the north-east in a week, and it was clear from the rapidly changing plaice egg population, supported by temperature and salinity records, that the buoy had moved off the original patch.

A second attempt was made in early March, and once again we were fortunate enough to have a 12-day period of tolerable weather. Another extensive patch of evenly distributed eggs and larvae was found south-west of the Brown Ridge, the buoy planted and a total of six grids completed before gales interfered with operations. In this case the grid had an extra station and covered an area of 5 square miles to give the ship plenty of room to manoeuvre into sampling positions during rough weather.

I do not intend to dwell at length on the difficulties attending this method of deriving a mortality curve. It is sufficient to say that in a shallow sea area, the chances of maintaining contact with the same fish brood throughout incubation and early larval development are not good. Differential water movements due to currents, tide and strong winds must have a profound effect on brood dispersion, rendering the study of diminishing numbers within a small body

of water, an uncertain method of assessing mortality. A reasonable period of moderate weather is necessary for success.

Although these surveys failed to produce a mortality curve, they did focus attention on an anomalous situation very relevant to the death-rate of larval fish in the sea. There was a noticeable scarcity of plankton during the first series of grids in late January, coupled with generally poor larval condition and no indication of growth beyond the yolked stage. Plankton was abundant during the March grids; a good proportion of the larvae was robust and apparently advancing beyond the stage of final yolk loss. These differences made themselves felt during the cursory examination of plankton samples at sea. A more detailed study of formalin-preserved material was made in the laboratory.

DEVELOPMENT STAGES OF THE PLAICE

A plaice egg is provided with food, and its development rate during yolk utilization is, in normal circumstances, controlled by temperature (Apstein, 1909). Larval fish, on the other hand, may start taking food before the yolk is completely resorbed (Table 2). Experience in the laboratory suggests that the larval feeding rate affects the development rate at a given temperature. Thus, consistently successful feeders will reach metamorphosis long before their less voracious brethren in the same tank. Any attempt to assess the development rate of sea larvae without fore-knowledge of their feeding rates, must be very approximate. If the development rate varies from place to place in sea areas with patchy plankton, then it follows that over-all estimates of the early mortality rates must be similarly approximate.

Aurich (1941) produced a series of developmental stages for the plaice larva, based on the investigations of Dannevig (1897), Reibisch (1902) and Apstein (1909), which take into account the principal morphological changes between hatching and metamorphosis. Mr A. C. Simpson of this laboratory has amended Aurich's staging to give the following categories (Pl. I, figs. 1–5):

Stage 1. Yolk still present.
2. Yolk resorbed but notochord still straight.
3. Eyes still symmetrically placed. Notochord bent.
4. Eye started to move, but not yet reached edge of head.
5. Eye on or over the edge of the head.

I have further subdivided stages 1 and 2 as follows:

Stage 1. Yolk-sac stage.
(*a–c*) Divided into three categories according to the amount of yolk in the sac (indicated +) and also to the degree of curling of the gut and extent of ventral mesectodermal fusion (Shelbourne, 1956).

(*d*) A yolk spherule stage when the yolk has been reduced to a small sphere, usually located in the arch of the intestine.

2. (*a*) Early. The yolk completely resorbed but the distinctive cushion of tissue below the caudal axis not yet fully developed.

(*b*) Late. Caudal cushion distinct.

If food is scarce, the yolk spherule stage is succeeded by early stage 2 (*a*) when all the yolk has disappeared. In good food conditions, however, larvae may start heavy feeding whilst yolk is still present. The drain on the yolk is then interrupted and a yolk spherule may be carried over to stage 2 (*b*) when the caudal cushion is complete. For the purposes of this investigation, I prefer to regard stages 1 (*d*) and 2 (*a*) as a transitional group, lying between the 'yolked' and 'non-yolked' larvae of previous development studies. If a truly 'critical period' does occur in the life history of a brood of fish, it is surely at this point, when yolk reserves are exhausted and the larvae have to rely on external food sources.

COMPARATIVE ABUNDANCE OF PLANKTON

After removal of the plaice fraction, the net hauls at five representative stations per grid were analysed for zoo- and phytoplankton, using the Stempel pipette technique. The results are presented in Table 1. The estimates are to the nearest thousand after adjustment to an arbitrary total flowmeter reading of 200 revolutions per grid (40 rev./station). The species dealt with were

TABLE 1. THE COMPARATIVE ABUNDANCE OF PLANKTON IN THE JANUARY AND MARCH SAMPLES

		Zooplankton (thousands)				Phytoplankton (thousands)				
Date	Grid no.	Total copepods	Copepod nauplii	*Oikopleura* sp.	*Fritillaria* sp.	*Biddulphia* sp.	*Paralia*	*Bacillaria*	*Bellarochia*	*Navicula*
20. i. 55	1	30	–	–	–	–	–	–	5	–
21. i. 55	2	43	–	–	–	+	1	–	4	+
22. i. 55	3	36	–	–	–	–	11	–	–	–
24. i. 55	4	63	–	–	–	–	1	1	–	–
26. i. 55	5	36	–	–	–	1	4	–	–	+
1. ii. 55	6	21	–	+	+	1	+	–	–	–
8. iii. 55	7	66	2	6	1	49	4	7	–	5
10. iii. 55	8	94	2	7	1	358	5	73	7	23
16. iii. 55	9	193	4	10	4	1539	48	182	24	297
18. iii. 55	10	112	+	6	29	774	–	31	–	603
20. iii. 55	11	121	+	3	+	1070	–	57	–	255
22. iii. 55	12	174	2	5	+	1678	2	15	–	174

The numbers (to nearest thousand) are the total plankton counts for five representative stations on each grid, adjusted to a total flowmeter reading of 200 revs. + = present in small numbers.

common to both patches, but other diatoms were present in large numbers during the March cruises. The Heligoland larva net is not a quantitative sampling instrument for the smaller animals, e.g. copepod nauplii and very young appendicularians, nor for diatoms, but these organisms are caught in rough proportions to their abundance.

It is clear from Table 1 that over-wintering conditions prevailed in the first plankton patch. Adult copepods, too large to be used as food by plaice larvae, were fairly abundant, but copepod nauplii were not in evidence. A few *Oikopleura* made their appearance on the last grid in early February. Phytoplankton was generally scarce. By early March, the spring outburst was well under way; the plankton samples were characterized by the abundance and variety of both animal and plant species.

DIET OF PLAICE LARVAE

The quantity and nature of larval gut contents were recorded as part of the staging analysis. The results for both sets of grids are displayed in Table 2. In the absence of vulnerable animal food in January, the larvae ate plants only. The stomachs were never full nor the partly digested 'green food remains' (Lebour, 1919) identifiable, although fragments of diatom tests could be recognized. The value of plant food for larval growth is a debatable point. If sufficiently abundant, the large thin-walled diatoms, e.g. *Biddulphia* and *Coscinodiscus*, may help sustain larvae in the transition stage; when scarce, as in January, the energy expended during foraging activity may not be balanced by the calorific value of the plants eaten.

The spring diatom outburst is closely followed by a marked increase in the zooplankton, particularly the appendicularian fraction. The important part *Oikopleura* plays in the diet of plaice larvae from the southern North Sea, has already been discussed by Shelbourne (1953). When the pelagic larval phase and the appendicularian outburst coincide, these small, soft-bodied, vulnerable creatures are eaten to the exclusion of other zooplankton species. In the March plankton patch, they were present in numbers sufficient to support a considerable population of larval plaice, and, as will be seen later, to have a measurable effect on physical condition in the transition stage.

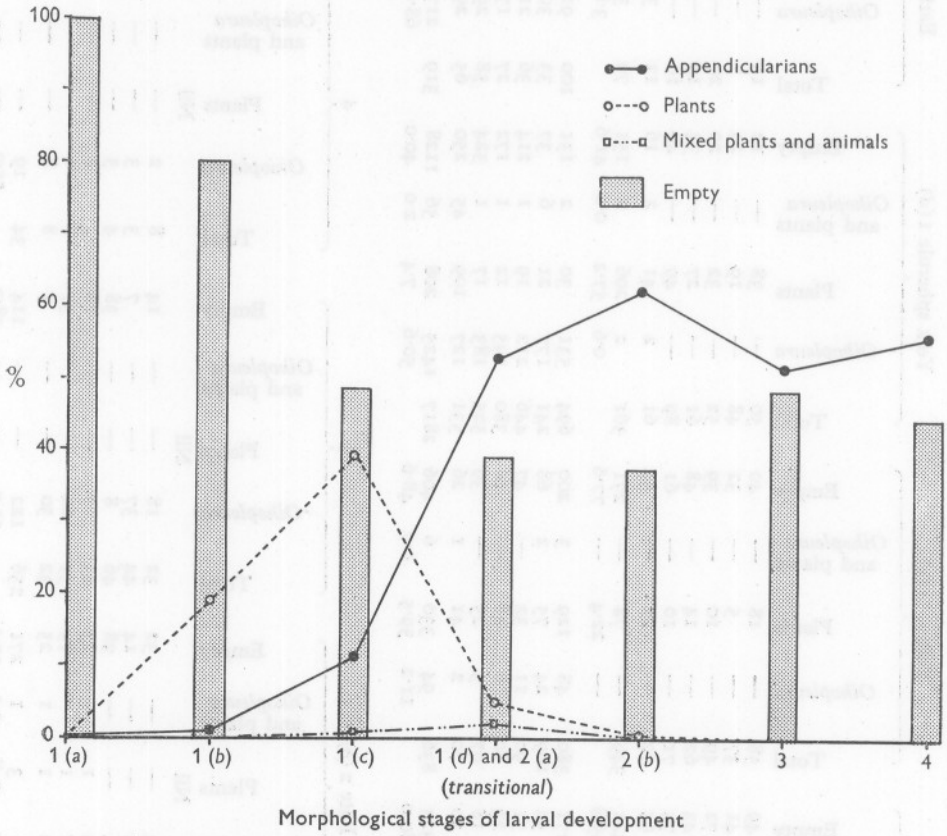
The feeding analysis for March is expressed graphically in Text-fig. 2. Larval feeding can start as early as the mid-yolk period, with diatoms the main food item until the end of the yolked stage, when appendicularians become important. The average larval mouth is probably too small to accept juvenile appendicularians before the transition stage is reached, even though the prey may be attacked during the yolk phase of the predator. Exclusive feeding on *Oikopleura* and *Fritillaria* continued throughout the subsequent pelagic life of the larva. The small proportion of stomachs containing mixed diatoms and appendicularians suggests that the change-over from plant to animal food is comparatively abrupt.

TABLE 2. THE GUT CONTENTS OF PLAICE LARVAE FROM BOTH PLANKTON PATCHES

Stage ...	Yolk + + 1 (*b*)					Yolk + 1 (*c*)					Yolk spherule 1 (*d*)					Early 2 (*a*)				
	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty
Grid 1	53	—	4	—	49	58	—	18	—	40	50	—	38	—	12	15	—	7	—	8
2	42	—	1	—	41	37	—	5	—	32	48	—	19	—	29	7	—	2	—	5
3	72	—	—	—	72	49	—	10	—	39	52	—	32	—	20	20	—	8	—	12
4	43	—	—	—	43	62	—	14	—	48	61	—	27	—	34	14	—	1	—	13
5	81	—	6	—	75	71	—	10	—	61	89	—	49	—	40	10	—	4	—	6
6	69	—	4	—	65	72	—	21	—	51	61	2	41	2	16	13	3	3	—	7
Totals	360	—	15	—	345	349	—	78	—	271	361	2	206	2	151	79	3	25	—	52
%		—	4·2	—	95·8		—	22·4	—	77·6		0·6	57·2	0·6	41·6		3·8	31·6	—	64·6
Grid 7	215	2	42	—	171	380	48	129	3	200	694	531	30	2	131	100	91	—	—	9
8	68	—	16	—	52	169	24	75	2	68	241	177	21	6	37	33	30	—	—	3
9	35	1	3	—	31	90	11	32	—	47	446	212	19	1	214	36	21	1	—	14
10	28	—	5	—	23	60	6	28	—	26	380	195	12	1	172	27	17	—	—	10
11	23	1	4	—	18	67	3	25	—	39	525	183	17	1	324	58	29	1	—	28
12	37	—	7	—	30	70	2	41	1	26	531	127	109	45	250	65	29	3	4	29
Totals	406	4	77	—	325	836	94	330	6	406	2817	1425	208	56	1128	319	217	5	4	93
%		1·0	19·0	—	80·0		11·2	39·5	0·7	48·6		50·6	7·4	2·0	40·0		68·0	1·6	1·2	29·2

Stage ...	Late 2 (*b*)					3					4				
	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty	Total	*Oikopleura*	Plants	*Oikopleura* and plants	Empty
Grid 1–6	Nil					Nil					Nil				
Grid 7	146	114	—	—	32	32	18	—	—	14	8	2	—	—	6
8	89	75	—	—	14	44	37	—	—	7	3	3	—	—	—
9	142	44	—	—	98	46	8	—	—	38	4	3	—	—	1
10	63	39	1	—	23	23	7	—	—	16	3	2	—	—	1
11	157	77	1	—	79	59	22	—	—	37	8	1	—	—	7
12	129	102	1	1	25	32	30	—	—	2	8	8	—	—	—
Totals	726	451	3	1	271	236	122	—	—	114	34	19	—	—	15
%		62·1	0·5	0·1	37·3		51·7	—	—	48·3		55·9	—	—	44·1

The superimposed histograms represent the proportion of empty stomachs found at each development stage. With the onset of feeding activity, the 'empty' proportion drops, to reach a steady level, about 40%, for the post-yolk stages. The samples used in this analysis were caught between 18.00 h and midnight. In an earlier paper on larval feeding habits (Shelbourne, 1953),



Text-fig. 2. Gut contents of plaice larvae from a good plankton patch.

I followed the normal decline in feeding activity during the same period of darkness, and from these earlier records have calculated the mean proportion of empty stomachs as 34%. The fairly consistent level of emptiness during the post-yolk stages in March 1955 can therefore be explained by diurnal changes in the feeding rate, under the influence of light, rather than by scarcity of suitable food.

THE CONDITION OF TRANSITION STAGE LARVAE

There was an association between food supply and the condition of the transition-stage plaice larvae. The problem of measuring larval condition was tackled by clearing and photographing five selected larvae (Pl. I, figs. 6–10), ranging from very thin to very robust, enlarging the prints to microscope image size, and using these prints as visual standards in the subsequent catch analysis.

The guiding principle in assessing robustness was the relationship of the soft parts (gut and muscular axis) to the cartilaginous head structure. A thin larva thus appeared ill-proportioned, with a prominent head and a reduced trunk. A robust larva, on the other hand, had balanced proportions, with a heavily muscled trunk, conspicuous gut and a far less prominent head.

Although the standards were somewhat subjective, the difference between larval condition during the January and March grids, is obvious enough (Table 3). The figures for each grid are the adjusted totals from two hauls taken at each station on the grid. The adjustment factor (for volume of water filtered) was reached by dividing the mean flowmeter revolutions per grid by the actual flowmeter reading. In this way one can compare the larval numbers from each grid on a particular patch, and the adjusted total of larvae examined per patch does not differ markedly from the actual total. The mean flowmeter reading for patch 1 differed from that of patch 2. The patch totals are not therefore adjusted to one another, but the condition compositions, dealing with proportions, are comparable. These proportions are expressed graphically in Text-fig. 3.

Plaice larvae were not very abundant in January. Half those at the beginning of the transition stage (end of yolk stage) were in medium condition, the other half thin. There were no robust or very robust individuals. Larvae caught at the end of the transition stage showed a distinct trend towards thinness; yolk reserves had been exhausted and soft structures reduced during continued foraging activity.

In contrast, about half the early transitional larvae from the good plankton patch were robust or very robust, indicating profitable feeding before complete yolk loss. In the same good food supply, 90% of the larvae leaving the transition stage were robust or very robust; fatter than their slightly younger contemporaries, not thinner as in January. There were no late stage 2 larvae in the poor plankton patch. In reasonable conditions for survival, one would expect this group to have appeared in the plankton by early February, accompanied by definite signs of increasing robustness in the late transitional stage, a necessary prelude to the formation of the characteristic caudal cushion. In the absence of these signs I am tempted to conclude that starvation conditions prevailed in the January patch and that survival was low. Roughly one-third of the late stage 2 larvae caught in the second plankton

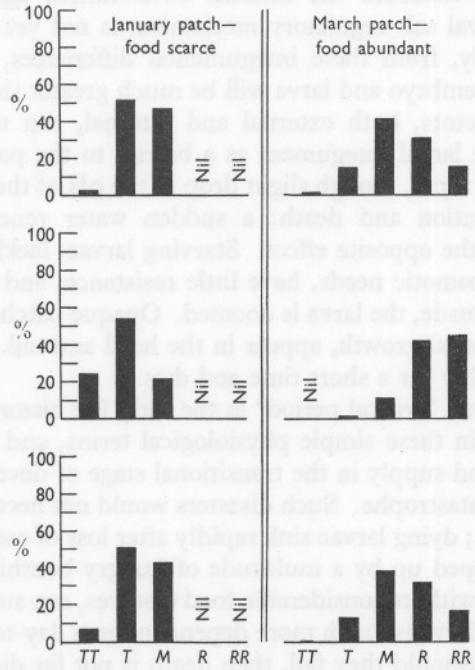
TABLE 3. ADJUSTED NUMBERS PER DEVELOPMENT STAGE OF PLAICE LARVAE, WITH A CONDITION ANALYSIS OF THE TRANSITIONAL STAGES

Date 1955	Grid no.	Yolk + + + 1 (*a*)	Yolk + + 1 (*b*)	Yolk + 1 (*c*)	Yolk spherule 1 (*d*)	Condition of larvae with yolk spherule: Very thin	Thin	Medium	Robust	Very robust	Early stage 2 (*a*)	Condition of early stage 2 (*a*) larvae: Very thin	Thin	Medium	Robust	Very robust	Late stage 2 (*b*)	Stage 3	Stage 4	Stage 5
Plankton patch 1. Mean temp. 6·8° C. Mean salinity 35·2 %																				
20. i.	1	45	45	49	43	3	16	24	—	—	13	6	7	—	—	—	—	—	—	—
21. i.	2	27	41	36	44	1	31	12	—	—	7	3	4	—	—	—	—	—	—	—
22. i.	3	63	61	42	45	2	17	26	—	—	16	4	9	3	—	—	—	—	—	—
24. i.	4	36	56	81	80	—	51	29	—	—	18	1	10	7	—	—	—	—	—	—
26. i.	5	94	96	84	104	2	48	54	—	—	11	2	8	1	—	—	—	—	—	—
1. ii.	6	62	66	68	58	—	29	29	—	—	13	3	4	6	—	—	—	—	—	—
Totals		327	365	360	374	8	192	174	—	—	78	19	42	17	—	—	—	—	—	—
Condition composition of transitional larvae (%)						2·1	51·4	46·5	—	—		24·4	53·8	21·8	—	—				
Plankton Patch 2. Mean temp. 4·1° C. Mean salinity 35·0 %																				
8. iii.	7	200	226	399	729	2	143	303	202	79	105	—	2	13	42	48	153 (45)	34	8	—
10. iii.	8	56	73	181	258	2	56	119	48	33	35	—	—	1	15	19	95 (33)	47	3	—
16. iii.	9	36	39	99	490	1	89	211	134	55	40	—	—	10	20	10	156 (54)	51	4	—
18. iii.	10	30	27	57	361	—	25	143	131	62	26	—	1	2	13	10	60 (30)	22	3	—
20. iii.	11	25	19	56	436	1	46	155	159	75	48	—	2	4	17	25	130 (47)	49	7	—
22. iii.	12	45	39	74	557	—	47	236	198	76	68	—	—	6	29	33	135 (49)	34	8	—
Totals		392	423	866	2831	6	406	1167	872	380	322	—	5	36	136	145	729 (258)	237	33	—
Condition composition of transitional larvae (%)						0·2	14·4	41·2	30·8	13·4		—	1·6	11·2	42·2	45·0				

The bracketed numbers in the late stage 2 (*b*) column represent larvae with a vestige of yolk still remaining in the body cavity.

patch had a vestige of yolk in the body cavity, a sure sign of better conditions for larval growth and survival.

There can be no doubt that a strong correlation must exist between larval condition and food supply, when other environmental factors lie within the limits of tolerance. During sampling the only hydrographic observations made were of temperature and salinity. The mean sea temperature was



Text-fig. 3. Condition of transitional plaice larvae from good and bad plankton patches: *TT*, very thin; *T*, thin; *M*, medium; *R*, robust; *RR*, very robust. *Upper*, end of yolk stage, 1 (*d*). *Middle*, beginning of post-yolk stage, 2 (*a*). *Lower*, total transition stages, 1 (*d*)+2 (*a*).

probably more favourable in January (6·8° C), than in March (4·1° C), and there is no evidence from previous work that the small salinity difference between patches (35·2‰ : 35·0‰), could have such a profound effect on larval condition. However, there are growing indications of variable condition among developing plaice eggs caught at sea, and it is therefore unwise to assume that the January and March larvae of this investigation started life as embryos with uniform viabilities.

DISCUSSION

Many dangers beset the newly emerged marine fish larvae, not the least of which is osmosis. The mechanism of water and salt regulation is well known for the adult teleost, where its efficiency depends on the development of gills

and chloride secreting cells, a completed circulatory system and a virtually water and salt proof skin (Krogh, 1939). Only the gill and oral membranes are permeable. Cod and plaice larvae (representing the pelagic marine group) lack these essential structures up to the stage of complete yolk loss (Shelbourne, 1956). The integument is extremely thin over the whole of its surface, and a considerable amount of energy must be expended, in the form of osmotic work, to maintain the internal environment against the osmotic gradient. The larval salt regulatory mechanism is not yet fully understood, but it seems likely, from these integumental differences, that the osmotic hazard facing the embryo and larva will be much greater than that facing the adult. Several factors, both external and internal, can upset the efficient functioning of the larval integument as a barrier to the passage of salts and water. In tanks, a rapid, though slight drop in the pH of the water is followed by coma, dehydration and death; a sudden water renewal, intended to benefit, can have the opposite effect. Starving larvae, lacking sufficient food reserves to meet osmotic needs, have little resistance, and once an 'osmotic breach' has been made, the larva is doomed. Opaque patches, often mistaken for fungal or bacterial growth, appear in the head and tail regions; the larva sinks, vibrates feebly for a short time and dies.

The problematical 'critical period' in the early life history of marine fishes can be explained in these simple physiological terms, and in natural conditions, a critical food supply in the transitional stage of development, is likely to produce local catastrophe. Such disasters would not necessarily be evident from spot samples; dying larvae sink rapidly after loss of osmotic control, and are probably snapped up by a multitude of hungry benthic scavengers. An adult marine fish, with its considerable food reserves, can survive lengthy lean periods. Its early larva is much more dependent on a day-to-day supply from external sources. Should they fail, then death is not far distant.

Throughout a spawning period, in seas characterized by very uneven plankton distribution in time and space, it is reasonable to suppose that the fates of larval populations vary considerably, from local catastrophe in food conditions below subsistence level, to local prosperity where plankton is rich. These variations would inevitably be masked in the mean mortality curve for a large area. Given moderate weather, plankton patches would seem to be better suited to investigations on the 'critical period' in the life history of fish larvae, than vast spawning areas.

SUMMARY

In January and March, during the 1955 plaice spawning season, plankton samples were collected with a Heligoland larva net at stations on a grid around a floating radio buoy in the southern North Sea. There was a decided scarcity of suitable food for plaice larvae in the January patch, and this famine was

reflected in the deteriorating physical condition of those larvae caught at the transition stage of development, when yolk reserves were becoming exhausted and an adequate external food supply essential. By March, the spring plankton outburst was in full swing. The condition of transitional larvae improved in this good food patch. Feeding started about the mid-yolk phase, mainly on plants. By the time most of the yolk had been resorbed, the appendicularians *Oikopleura* and *Fritillaria* had become the principal food items, and remained so throughout pelagic larval life.

Accurate mortality estimates during transient phases of development, depend largely on an understanding of the way in which the feeding rate affects the progress of larval development at a given temperature. Without this knowledge, the present data cannot be used to calculate mortality rates in the two plankton patches, but there are indications that in January, food was too scarce to support the growth and continued survival of the larval population, whereas in March, sufficient food was available for growth in the transitional stage, thus increasing the prospects of post-yolk survival.

There is reason to suppose that in local starvation conditions, larval control over their own internal salt balance would be greatly reduced, by lack of energy reserves for osmotic work at the thin integument. Failing a rapid improvement in the food situation, death must inevitably follow, and such local catastrophes would be hidden in the mortality curves derived from surveys over vast spawning areas.

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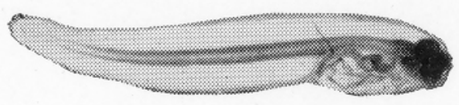
EXPLANATION OF PLATE I

Development stages of plaice larvae, after Simpson (left). Fig. 1. Stage 1 (6·0 mm). Fig. 2. Stage 2 (7·6 mm). Fig. 3. Stage 3 (9·2 mm). Fig. 4. Stage 4 (12·6 mm). Fig. 5. Stage 5 (12·2 mm). Condition standards of transitional plaice larvae (right). Fig. 6. Very thin (6·1 mm). Fig. 7. Thin (6·3 mm). Fig. 8. Medium (6·9 mm). Fig. 9. Robust (6·8 mm). Fig. 10. Very robust (7·5 mm).



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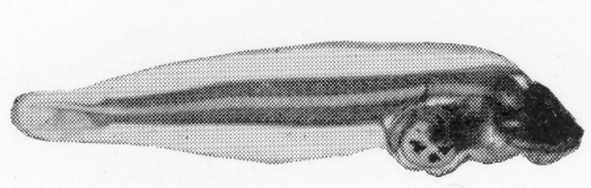

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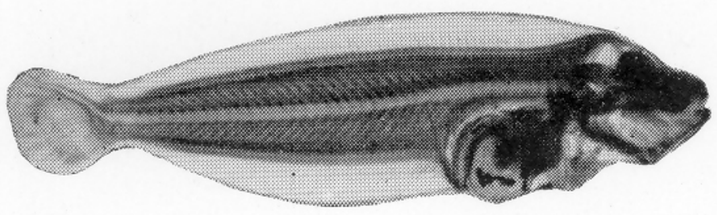

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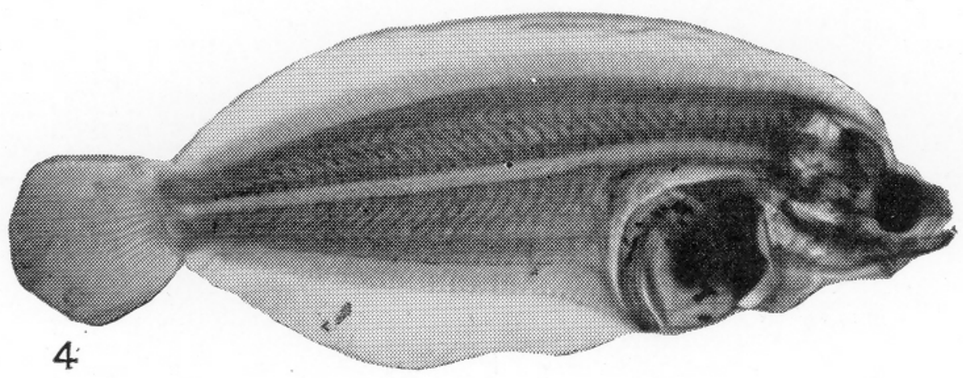

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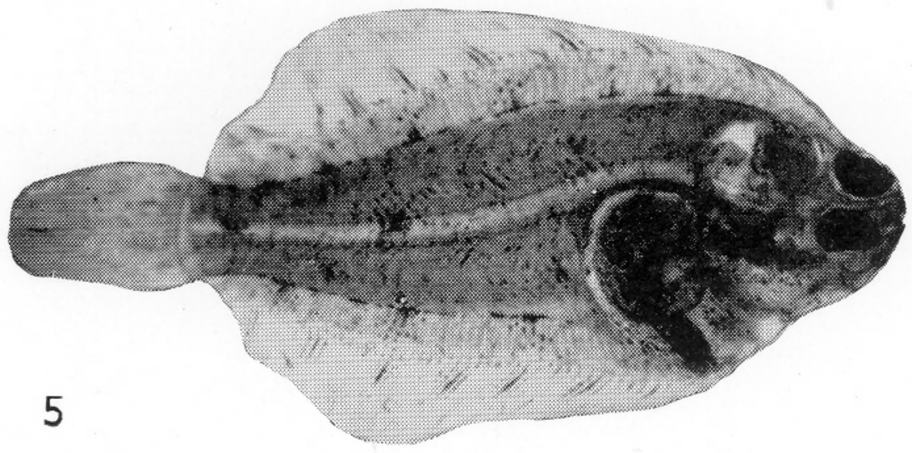

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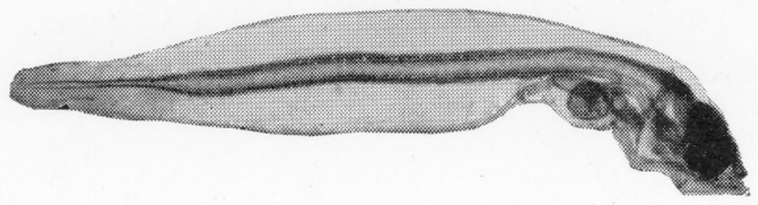

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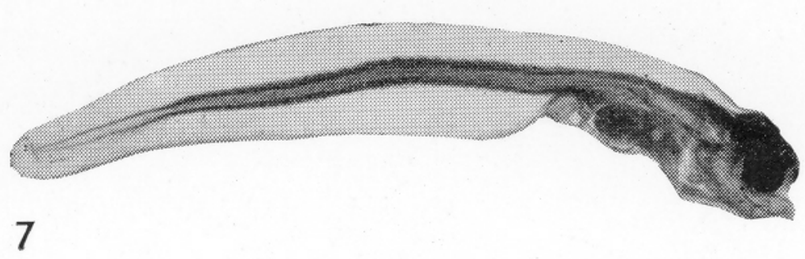

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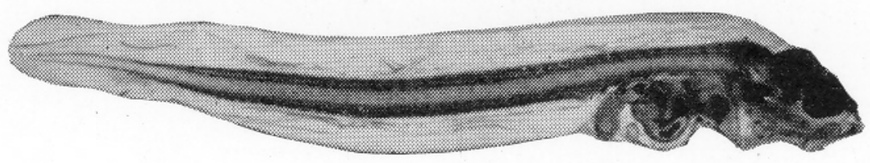

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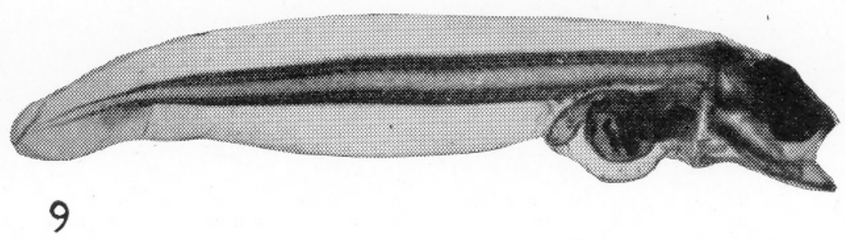

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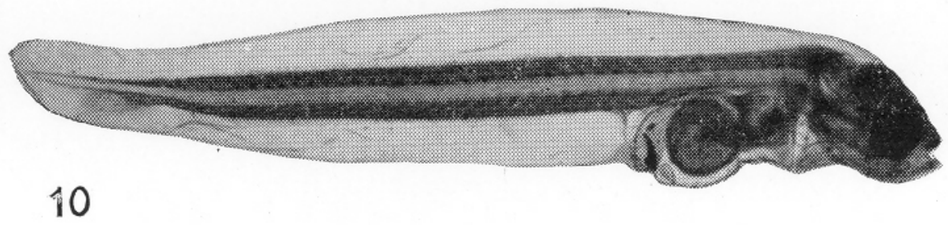

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THE RESPONSES OF *SCROBICULARIA PLANA* (DA COSTA) TO OSMOTIC PRESSURE CHANGES

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(Text-figs. 1–5)

Scrobicularia plana is an estuarine lamellibranch often numerous in intertidal, brackish muds. The animal normally lies in a burrow, 6–10 in. below the surface of the mud, and possesses long, extensible siphons through which it makes contact with the overlying water. Therefore it is probable that, as far as the salinity relations of the animal are concerned, the external medium is represented by the water above the mud.

From studies of its distribution *S. plana* is evidently tolerant of wide salinity variations in the external medium. In the Tamar estuary the species is distributed mainly in the upper half of the tidal zone down to just below mid-tide level (Spooner & Moore, 1940), and at Whitstable it is most common at mid-tide level along seaward parts of the 'bound shingle zone' (Newell, 1954). Similarly, in the extensive mud flats of the Thames estuary at Chalkwell in Essex it occurs most abundantly at mid-tide level and is completely absent from the more sandy deposits lower down the shore. This concentration of the population near mid-tide level means that the animals are not exposed to the great changes in salinity during each tidal cycle experienced by those animals living near low-water mark (Milne, 1938). However, Green (1957) in a study of a population of *S. plana* in the Gwendraeth estuary in South Wales has shown that here they are subjected to a salinity as low as two parts per thousand for a short period before being uncovered by the retreating tide.

In the Tamar, Spooner & Moore record the species along the estuary from St John's Lake, where there are 'almost marine conditions in drier parts of summer', to North Hooe, with a salinity of 20·2‰ at high water during a dry summer (Percival, 1929). In the Thames estuary the variation in salinity during that part of the tidal cycle to which an animal living near mid-tide level would be subjected is not very great. There are, however, considerable seasonal variations depending on the extent of dilution of the river by fresh water from land sources, and at Chalkwell the mid-tide salinity ranges from 25·2‰ in a wet winter to 32·4‰ in a dry summer.[1] At Whitstable the salinity does not differ greatly from that of the Channel and southern North Sea, the

[1] All information concerning salinities at Chalkwell has been obtained from the Water Pollution Research Laboratory, and we are grateful to the Director for permission to quote unpublished figures.

maximum variation at high water recorded during the years 1953–4 being from 29·58 to 34·52‰ (El-Maghraby, London Ph.D. Thesis, 1955).

These considerations make it clear that *S. plana* can tolerate almost marine conditions, salinities of about 20‰, and, for short periods at least, salinities as low as two parts per thousand.

Since *S. plana* normally experiences variations in external salinity, and since observations made during a study of rhythmic activities of this animal (Freeman, unpublished) showed that they were affected by dilution of the external medium, a study has been made of the effect of changes of external salinity on the concentration of the blood and on some aspects of the behaviour of *S. plana*.

MATERIALS AND METHODS

Animals used in these experiments were collected from the mud flats at Chalkwell in Essex. They were allowed to burrow in mud from the same situation and kept under sea-water circulation at the Plymouth Laboratory.

Blood samples were obtained from the heart, which was exposed by cutting each valve of the shell along a line between the insertions of the anterior and posterior adductor muscles, and removing that part of the shell which, freed from the restraint of the adductor muscles, was raised by the elasticity of the hinge ligament. Samples of 4–6 mg of blood for measurements of depression of the freezing-point were taken directly into capillary tubes which were immediately sealed at both ends by injection of silicone stopcock grease from a hypodermic syringe. These operations were carried out in a moist chamber saturated with respect to sea water. Depression of the freezing-point was estimated by a method similar to that of Jones (1941) and Gross (1954). The blood samples and a series of NaCl standards of appropriate concentrations, similarly sealed in uniform capillary tubes, were fastened to a glass frame with silicone stopcock grease and frozen by immersion in alcohol cooled to the temperature of solid carbon dioxide. They were immersed in a vessel of cold, 5 M-NaCl, which was kept continuously stirred, and allowed to warm slowly in a lagged box. A rate of warming of 1° C in 45 min was obtained by keeping the box in a constant temperature room at 2° C. The time taken for the complete disappearance of the crystals was noted, this being facilitated by viewing the crystals through crossed polaroids. The depression of the freezing-point of the blood samples was calculated from the curve relating melting time to the freezing-point of the standards.

Specimens used for measurement of opening rates were removed from the mud or acclimation vessel and left in air for 5 min. At the end of this time they exhibited what may be termed the normal degree of closure. In this state the shell valves are sufficiently apposed to prevent the animal protruding its foot or siphons, but the free edges of the mantle lobes are still visible between the lower edges of the shell. Here the lobes of the two sides are closely applied

to form a pallial curtain that, in the absence of complete fusion, probably functionally simulates that condition. Twenty animals were placed in each experimental vessel, in which they were covered to a depth of about 2 in, and spaced widely so that the activity of any specimen would be unlikely to disturb those adjacent to it. They were observed at 5 or 10 min intervals and recorded as open if the inhalant siphon was clearly visible beyond the margin of the shell. If the foot alone was protruded or just the closed tip of the siphon was visible the animal was recorded as half open. Chapman & Newell (1956) observed that the inhalant siphon was protruded soon after an initial gaping of the shell valves and that the siphon was open at its tip during extension. The protrusion of the inhalant siphon therefore provided a convenient indication that the animal was open, in the sense of being exposed to the external medium.

Diluted sea water for all experiments was made by adding distilled water to Plymouth circulation water, which is referred to throughout as 100% sea water.

EXPERIMENTS AND RESULTS

THE RELATION BETWEEN OSMOTIC PRESSURE OF THE BLOOD AND THAT OF THE EXTERNAL MEDIUM

Although the estuarine and marine lamellibranchs that have been studied exhibit little or no osmoregulatory ability (Prosser, 1950), experiments were first carried out to determine whether *S. plana* conformed to this general picture. Animals were equilibrated at 15° C for 48 h in 100% sea water and in sea water diluted to 80, 70 and 60%. Others were equilibrated in 50% sea water for 48 h when some of them were transferred to 30% for a further 60 h, the rest remaining for the same length of time in 50%. Measurements of freezing-point depression of the blood and of the external medium are shown in Table 1.

These results show that the osmotic pressure of the blood agrees closely with that of the external medium down to dilutions of 50%, but in 30% sea water the osmotic pressure of the blood is significantly higher than that of the external medium.

The agreement of the osmotic pressure of the blood with that of the external medium means that, if, as suggested above, the external medium of the animal in its natural habitat is represented by the water above the mud, the osmotic pressure of the blood of animals taken from the mud should agree with that of the overlying water rather than that of water contained in the mud. To examine this the following experiment was carried out. Blood samples were taken from animals collected from the upper limit of their distribution at Chalkwell immediately after being uncovered by the tide, on a day (13 September 1956) when there had been a sudden decrease in flow of fresh water over Teddington weir. In Table 2 the depression of the freezing-point

of the blood is compared with that of samples of water taken from above the mud 15 min before the tide receded.

These figures show that there was no significant difference between the osmotic pressure of the blood and that of the overlying water. In his study of the salinity of intertidal muds, Smith (1956) comments that although the quantitative relationship between salinity of water contained in the mud and the varying salinity of the overlying water is not known, the interstitial

TABLE 1. RELATION BETWEEN DEPRESSION OF THE FREEZING-POINT OF THE EXTERNAL MEDIUM AND OF THE BLOOD OF *SCROBICULARIA PLANA*.

The figures in the right-hand column are calculated values of Student's *t*, applying Bessel's correction for small samples.

	No. of observations	Mean freezing-point depression (° C)	Standard deviation	*t*
100 % sea water	13	1·90	0·048	0·291
Blood	11	1·89	0·011	
80 % sea water	6	1·55	0·009	1·06
Blood	9	1·60	0·073	
70 % sea water	7	1·37	0·077	0·572
Blood	10	1·35	0·059	
60 % sea water	6	1·12	0·079	1·49
Blood	9	1·17	0·041	
50 % sea water	5	1·052	0·016	0·316
Blood	5	1·054	0·012	
30 % sea water	7	0·592	0·0104	13·6
Blood	5	0·745	0·0382	

TABLE 2. DEPRESSION OF THE FREEZING-POINT OF THE BLOOD OF *SCROBICULARIA PLANA* AT CHALKWELL

	No. of observations	Mean freezing-point depression (° C)	Standard deviation	*t*
Overlying water	9	1·756	0·025	0·51
Blood	16	1·762	0·028	

salinities give a picture of changes within past weeks. The immediate past history of the Chalkwell muds was of exposure to lower salinities than that given in Table 2. The records of the Thames Conservancy show that the dilution of the river by fresh water flowing over Teddington weir was less on the day when the samples were taken than on any of the preceding 10 days, and the survey of the Water Pollution Research Laboratory, which correlates freshwater flow at Teddington with chlorinity of the water along the Thames estuary, indicates that the average chlorinity at high water at Chalkwell over these preceding 10 days was about 16·5‰, and the average over the preceding 2 weeks was only 16·8‰. On the day the samples were taken the flow at Teddington was 656·2 million gallons, corresponding to a chlorinity at high

water at Chalkwell of about 17·5‰. This agrees fairly well with a calculated chlorinity of 17·85‰ for sea water with the depression of the freezing-point given in Table 2 (Robinson, 1954). The blood of the animals, therefore, agreed with the overlying water rather than with any average picture of changes within the preceding 2 weeks. Moreover, the normal situation of this deposit-feeding lamellibranch is with its siphons protruded into the overlying water, and experiments reported later in this paper show that the blood of specimens that do not protrude their siphons is almost unaffected by the salinity of the water that surrounds the shell and mantle margin. This lends support to the view stated earlier that the salinity with which the animal comes into equilibrium is that of the overlying water rather than water contained in the mud.

RATE OF EQUILIBRATION TO DILUTED SEA WATER

Although it has been shown that, except when *S. plana* is subjected to very low external salinities, its blood attains the same osmotic pressure as the external medium, no indication has been given of the time necessary for equilibration. In order to study the rate of equilibration several animals were transferred from the mud under sea-water circulation to 80 and 60% sea water at 15° C. At intervals specimens were taken at random from those in the experimental vessels and measurements made of the depression of the freezing-point of their blood. The results are shown in Fig. 1.

The time taken for equilibration was approximately 8 h in 80% sea water and 25 h in 60% sea water. Within the limits imposed by small sample size these figures give a picture of the effect on a population of *S. plana* of a sudden change in the salinity of the external medium. Most noticeable is the considerable scatter of the freezing-point of the blood of animals in 80% sea water up to 4 h, and of animals in 60% sea water up to 14 h. This scatter was interpreted as indicating that, when transferred to the dilute medium, some animals had remained closed longer than others and therefore the estimation of the freezing-point of their blood did not represent the result of a maximal exposure of their tissues to the lowered external salinity over the time stated. These readings would therefore be higher than those of animals that opened almost immediately. Furthermore, the mean of the readings for 1 and 2 h was higher for the specimens in 60% than in 80% sea water, and only very slightly lower after 4 h. The greater concentration difference to which the animals in 60% sea water were exposed should result in a much faster decrease in the tonicity of the blood. The time taken for complete equilibration should not in fact be appreciably longer than in 80% sea water (Jacobs, 1935).

In order to compare the rates of equilibration of open and closed specimens the previous experiment was repeated, but the equilibrating specimens were observed throughout the experiment and only those which had been open or closed continuously were selected for measurement of the freezing-point depression of their blood. The results are presented in Figs. 2 and 3.

These results show that the rate of equilibration of open animals is much more rapid than suggested by the previous experiment. Open animals equilibrate to 80% sea water in 4–5 h and to 60% sea water in 5–6 h. The very rapid rate of dilution of the blood over the first 15 min is particularly noticeable. In contrast the blood of closed animals changed very slowly. Those in 60% sea water, where the concentration gradient is greatest, show an average drop in their blood osmotic pressure of only 1·5% per hour, whereas those in 80% sea water show a drop of about 4% per hour.

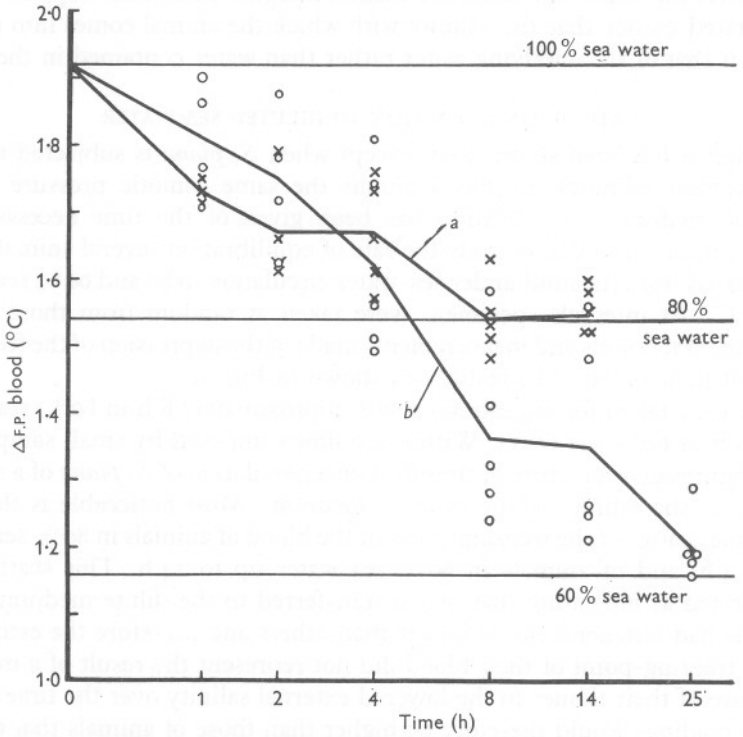

Fig. 1. Depression of the freezing-point of the blood of randomly chosen specimens of *Scrobicularia plana* after varying times of exposure to 80% (×) and 60% (○) sea water. The time scale is abbreviated by being expressed geometrically. *a*, line joining the means of the 80% readings; *b*, the same for the 60% readings.

EFFECT OF DILUTION OF THE EXTERNAL MEDIUM ON RATE OF OPENING

In the previous section it was shown that the average drop in blood osmotic pressure of a population of *S. plana* exposed to 60% sea water was slower over the first few hours than that of a population exposed to 80% sea water, whereas animals selected as having been continuously open showed a more rapid decrease in their blood osmotic pressure over this period in 60% than in 80% sea water. In view of the very small change in osmotic pressure of the

blood of animals that remained closed, it seemed possible therefore that animals suddenly exposed to 60% sea water opened less rapidly than those exposed to the lesser dilution. It was indeed observed when selecting specimens that had been open or closed continuously that very few of the animals in 60% sea water opened soon after being transferred to this medium, whereas very few of those in 80% sea water remained closed throughout the experiment. The results given in the previous section also showed that specimens

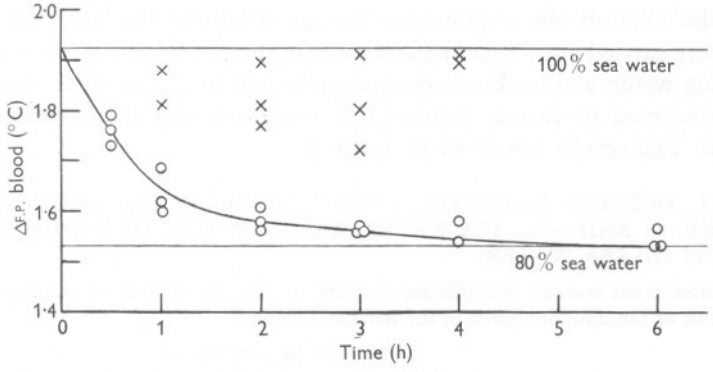

Fig. 2. Depression of the freezing-point of the blood of open and closed specimens of *Scrobicularia plana* after varying times of exposure to 80% sea water. ○, open animals; ×, closed animals.

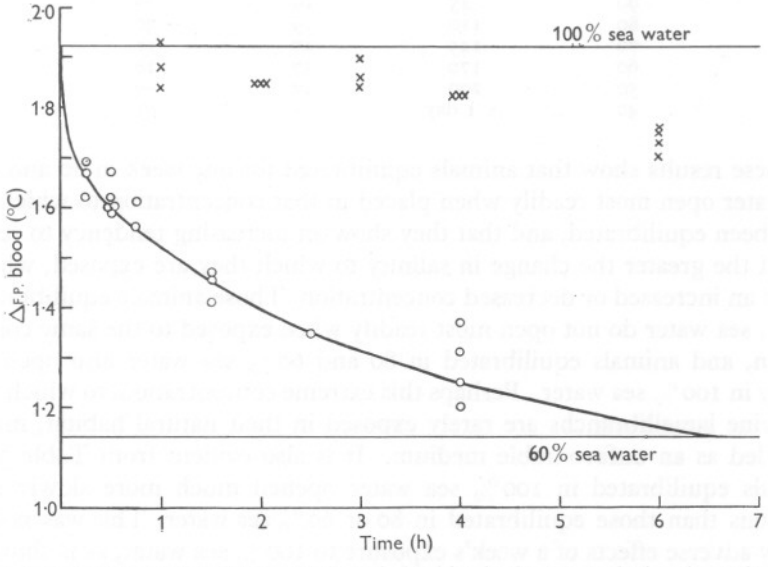

Fig. 3. Depression of the freezing-point of the blood of open and closed specimens of *Scrobicularia plana* after varying times of exposure to 60% sea water. ○, open animals; ×, closed animals.

that were selected as being closed in 60% sea water showed less change in their blood osmotic pressure than those in 80% sea water. This indication that closed animals in 60% sea water were more completely insulated from changes in external osmotic pressure than those in 80% sea water suggested that specimens remained more tightly closed in the more dilute medium. These differences might mean that 80% sea water could be regarded as a more favourable medium for *S. plana*, or that this species responds to the sudden large change in salinity from 100 to 60% sea water by remaining closed.

In order to study the response to changes in salinity the following experiments were carried out. Specimens were equilibrated for one week in running circulation water, and in vessels containing 80 and 60% sea water. They were then transferred to various dilutions of sea water and their opening rates recorded. The results are given in Table 3.

TABLE 3. OPENING RATES OF *SCROBICULARIA PLANA* EQUILIBRATED IN 100, 80 AND 60% SEA WATER, AND EXPOSED TO VARIOUS DILUTIONS OF SEA WATER.

The figures in the body of the table are the time in minutes for half of the specimens to open in each of the dilutions given in the left-hand column.

Experimental concentration, % sea water	Time of 50% opening: Equilibrated in 100% sea water	Equilibrated in 80% sea water	Equilibrated in 60% sea water
100	110	27	57
90	45	19	—
80	110	9	30
70	145	17	18
60	170	17	18
50	290	12	—
40	> 1 day	—	65

These results show that animals equilibrated for one week in 80 and 60% sea water open most readily when placed in that concentration to which they have been equilibrated, and that they show an increasing tendency to remain closed the greater the change in salinity to which they are exposed, whether this is an increased or decreased concentration. Those animals equilibrated in 100% sea water do not open most readily when exposed to the same concentration, and animals equilibrated in 80 and 60% sea water also open very slowly in 100% sea water. Perhaps this extreme concentration, to which these estuarine lamellibranchs are rarely exposed in their natural habitat, may be regarded as an unfavourable medium. It is also evident from Table 3 that animals equilibrated in 100% sea water opened much more slowly in all dilutions than those equilibrated in 80 or 60% sea water. This was not due to any adverse effects of a week's exposure to 100% sea water, as is shown by the following experiment. Some specimens were equilibrated in an open bowl under splashing circulation water, others were allowed to burrow in mud

which was kept under circulation, and others were placed in a vessel of still 100% sea water. They were allowed to open in 100% sea water and the time for 50% of them to open was recorded. Those equilibrated in still water opened in 27 min, those under mud in 46 min, and those under splashing circulation in 120 min. It appears therefore that the very slow opening rate was not due to any difference in salinity of the water in which the animals were equilibrated, but rather to some other condition of pre-treatment. Those equilibrated in an open bowl under splashing circulation had necessarily been subjected to slight, constant vibration not experienced by those in still water or burrowed under mud, and therefore the effect of vibration was investigated in the following experiment. Specimens were equilibrated under splashing circulation and in still water and their opening rates measured in 100% sea

TABLE 4. THE EFFECT OF VIBRATION AND EQUILIBRATION CONDITIONS ON THE OPENING OF *SCROBICULARIA PLANA*

All specimens equilibrated in 100% sea water. Opening rates expressed as time in minutes for 50% opening.

	Equilibrated under splashing circulation		Equilibrated in still water.
	Experimental concentration 100%	Experimental concentration 50%	Experimental concentration 100%
Control	175	250	53
Vibrated	55	129	17

water under conditions where some of them were exposed to constant vibration and others allowed to open under control conditions. Also, in order to determine the interaction between the effects of vibration and those of exposure to diluted sea water, the opening rate was measured in 50% sea water.

Table 4 shows that all the vibrated animals opened more rapidly than those not vibrated. It also shows that the animals equilibrated in still water opened more rapidly than those equilibrated under splashing circulation under both control and vibrated conditions. The vibration acts as a stimulus to open which is superimposed on the control opening rates. Of the animals equilibrated under splashing circulation, those exposed to 100% sea water opened more rapidly than those in 50% sea water, emphasizing the effect of concentration of the medium in influencing opening rate, but those vibrated in 50% sea water opened more rapidly than those not vibrated in 100% sea water. Thus, under these conditions, the effect of concentration of the medium can be completely over-ridden by the effect of vibration.

EFFECT OF DILUTION OF THE EXTERNAL MEDIUM ON OPEN ANIMALS

In previous experiments the effect of changing the concentration of the external medium has been studied only on closed animals, but it is probable that, when burrowed in the mud in its natural habitat, *S. plana* would be

exposed to a changed salinity only when its siphons were protruding into the overlying water. To determine the response of animals with extended siphons to changed salinity, two groups of animals were allowed to open in 100% sea water and when a convenient number were open the water was siphoned out and replaced by 50% sea water in one bowl and by 100% sea water in the other. The effect of this change on the number of animals open is shown in Fig. 4.

This shows that the process of replacing the water did not in itself affect the number of animals open, but the sudden change from 100 to 50% sea water caused more than half of the animals to close.

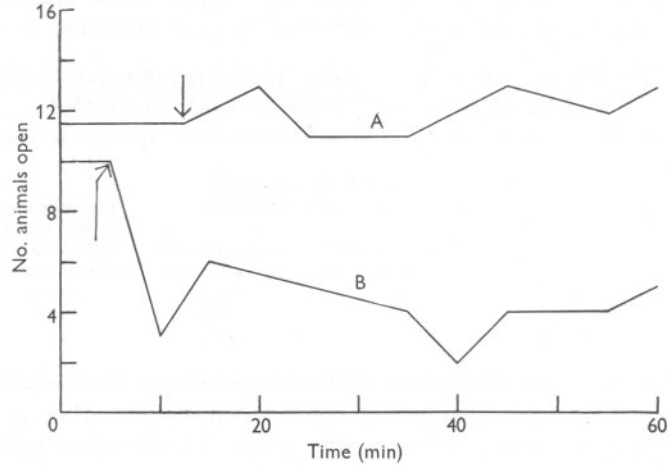

Fig. 4. Effect of dilution of the medium on numbers of open *Scrobicularia plana*. 100% sea water replaced by (A) 100% sea water, (B) 50% sea water, at points marked by arrows.

In this, as in previous experiments where the effect of changed concentration of the external medium has been studied, the medium has differed from that to which the animal was equilibrated both in concentration of individual ions and also in total osmotic pressure. To test which of these factors was significant in influencing the behaviour of *S. plana*, closed specimens were exposed to 100% sea water, 50% sea water, and sea water to which was added an equal volume of 0·9M sucrose solution. This latter medium is equivalent to 50% sea water in ionic concentration and to 100% sea water in total osmotic pressure. The opening rates are compared in Fig. 5.

These results show that animals in the 50% sea water containing 0·45M sucrose behave almost identically with those in 100% sea water and very differently from those in 50% sea water. The factor that tends to keep *S. plana* closed when suddenly exposed to media of different concentration is evidently an alteration in total osmotic pressure.

Some measurements were also made of the depression of the freezing-point

of the blood of animals that had been exposed to the 50% sea water containing 0·45M sucrose. Those that had opened showed signs of very considerable dehydration and with many it was found impossible to obtain enough blood for estimation. Samples from three animals each gave a depression of the freezing-point of 1·83° C, as compared with 1·91 and 1·92 for the blood of the only two specimens that did not open at all during the experiment. Presumably under these conditions the initial tendency is for the blood to lose ions to

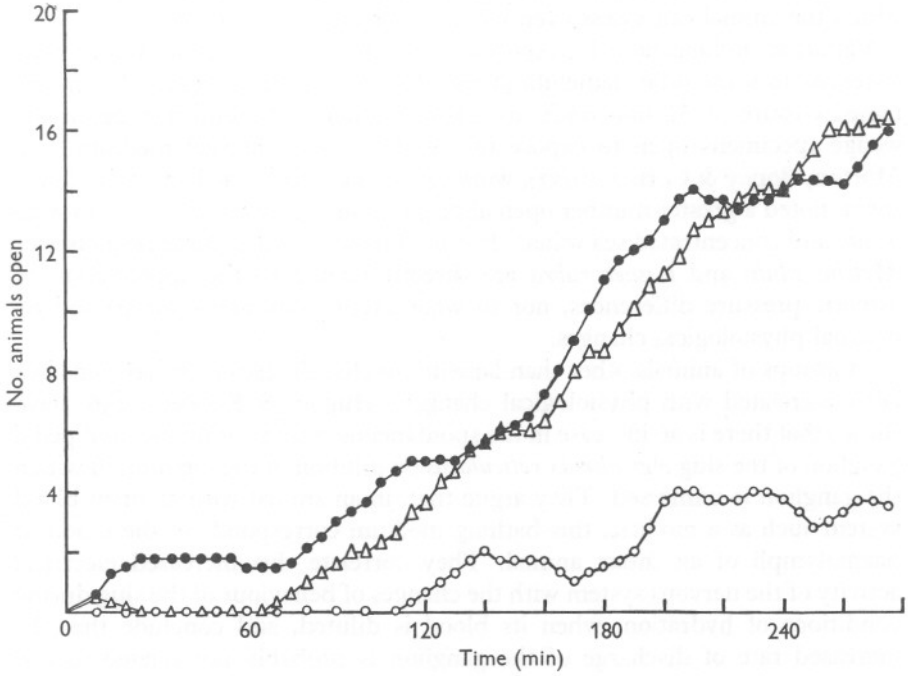

Fig. 5. The opening rates of *Scrobicularia plana* in sea water, 50% sea water, and 50% sea water made isotonic with an equal volume of 0·9M sucrose solution. ●—●, 100% sea water; △—△, 50% sea water containing 0·45M sucrose; ○—○, 50% sea water. (The numbers plotted are the moving average of three readings.)

the medium, resulting in a decreased internal osmotic pressure, with a consequent outward movement of water. The blood might therefore be expected at any one time to show a slightly lower osmotic pressure than the external medium. It was noted that severely dehydrated specimens returned to sea water recovered to an apparently normal condition, although there would be no osmotic gradient tending to bring about a re-entry of water.

DISCUSSION

Scrobicularia plana is similar to other estuarine and marine lamellibranchs that have been studied in showing no osmo-regulatory ability, except at very low external salinities. However, it reacts to extreme changes in external salinity by remaining closed, or, if open, by retracting its siphons, and thus protects its blood from extreme changes in concentration. These responses are to the stimulus of an alteration in total osmotic pressure of the external medium, which the animal can assess even while in the closed condition.

Variations in behaviour in response to varying external salinities have been observed in some other lamellibranchs. Maloeuf (1938) observed the maintained closure of *Mytilus edulis* in distilled water and found it necessary to wedge specimens open to expose the tissues to the external medium, and Morton, Boney & Corner (1957), working on the small lamellibranch *Lasaea rubra*, noted a greater number open after 5 min in sea water as compared with dilute and concentrated sea water. It is not known whether these responses of *Mytilus edulis* and *Lasaea rubra* are directly related to the appreciation of osmotic pressure differences, nor to what extent they are accompanied by internal physiological changes.

In groups of animals other than lamellibranchs, changes in behaviour have been correlated with physiological changes. Hughes & Kerkut (1956) have shown that there is an increase in the spontaneous activity of the isolated pedal ganglion of the slug *Agriolimax reticulatus* on dilution of the medium in which the ganglion is immersed. They argue that, in an animal with an open blood system such as a mollusc, this bathing medium corresponds to the blood or haemolymph of an intact animal. They correlate this increased electrical activity of the nervous system with the changes of behaviour of the slug during conditions of hydration, when its blood is diluted, and conclude that the increased rate of discharge of the ganglion is probably not related to any particular change in behaviour but represents a difference in the 'tonus' or 'vigilance' of the central nervous system against which reflex activity will be expressed. In an extension of this work, Kerkut & Taylor (1956) have shown that the effective change to which the ganglion responds is one of osmotic pressure, and that the limiting rate producing an increase in ganglionic activity is a change of 1% in 4 min. They discuss these results in the light of other osmoreceptors known, particularly in mammals where there is a similar phenomenon of part of the central nervous system being sensitive to osmotic pressure changes in the blood.

The situation in *Scrobicularia plana* differs in one important respect from that in the slug. On exposure to external media of lowered osmotic pressure *S. plana* shows a greater reluctance to open than in sea water, there being a greater tendency to remain closed the greater the decrease in osmotic pressure. These changes in behaviour are accompanied by a much smaller rate of change

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LERNAEOCERA OBTUSA N.SP., A HITHERTO UNDESCRIBED PARASITE OF THE HADDOCK (*GADUS AEGLEFINUS* L.)

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(Text-figs. 1–6)

The present genus *Lernaeocera* comprises seven species. Four of them are known to occur on the western European seaboard. They are: *L. branchialis* (Linnaeus, 1767) *L. lusci* Basset-Smith, 1896, *L. minuta* T. Scott, 1900, and *L. brevicollis* Schuurmans Stekhoven, 1935. The three non-European species have been based on isolated specimens from Chile (*L. rigida* Krøyer, 1863), New Zealand (*L. lotellae* Thomson, 1889) and Antarctica (*L. godfroyi* Quidor, 1912). All are parasitic on fish.

The final hosts infested by the members of this genus can be divided into two groups: the 'inshore' group, comprising those fishes which visit the coastal waters at some stage of their lives and which are exposed to infestation by a parasite reproducing in that zone only; and the 'offshore' group, comprising those which do not visit the coastal waters at any stage and which can be infested only by a parasite with a totally offshore life cycle. One of the common hosts, the Haddock, *Gadus aeglefinus* L., can be included in both groups, as its small coastal populations can be treated, for our purposes, separately from its main offshore stocks. Out of 31 recorded hosts of the European species 27 belong to the inshore group. All the common final hosts, with the exception of the offshore haddock, and all the known intermediate hosts also belong to this group. The present genus *Lernaeocera* might be regarded, therefore, as essentially coastal in character.

L. branchialis, as it has been presented in the previous literature, stands out as conspicuously unusual, when considered against the background of its own genus. It appears to be the only species with the common hosts both in the inshore and the offshore group. In the former it is known to infect commonly such hosts as the Cod (*Gadus callarias* L.) and the Whiting (*G. merlangus* L.), and in the latter—where no intermediate host has been recorded—the haddock. Of all the other species of the genus only one, *Lernaeocera lusci*, has been recorded from offshore hosts but none of these can be regarded as common. Both *L. lusci* and *Lernaeocera* found on haddock resemble each other in the shape of the body, although the latter attains larger sizes. Both also differ in shape from the *L. branchialis* found on the hosts of the inshore group.

In his study of *L. branchialis* the attention of the present author was drawn to this difference between this species and the remaining members of the genus, and also to the differences within the species itself. It seemed that these differences could be explained if it could be proved that the name *L. branchialis* has been used hitherto to cover two distinct species, one from the whiting and the cod and the other from the haddock. Closer investigation has shown that this, indeed, is so. In this paper the existence of the new species is demonstrated. The evidence is to be found in the geographical distribution, specificity and morphology of the adult male and female and in the mode of attachment to the final host.

DISTRIBUTION

Parasites of the genus *Lernaeocera* can become endemic only in the areas inhabited by a suitable intermediate host and their distribution cannot be considered without reference to their intermediate hosts. These are known only for *L. branchialis*, the common intermediate host of which appears to be the Flounder, *Platichthys flesus* (L.) (A. Scott, 1901; Sproston, 1941). Gouillart (1937) and Stekhoven (1936) also list Plaice, *Pleuronectes platessa* L., Gouillart (1937) lists Turbot, *Scophthalmus maximus* (L.), while Oorde de Lint & Stekhoven (1936) mention 'other pleuronectids' without naming any. Shulman & Shulman-Albova (1953) found that the Arctic Flounder, *Liopsetta glacialis* (Pallas) and the Lumpsucker, *Cyclopterus lumpus* L., were—beside the flounder—common intermediate hosts of *L. branchialis* in the White Sea, and they reached the conclusion that the reproductive cycle of this parasite is exclusively coastal in character. Gouillart (1937) also mentions *C. lumpus*, but regards the larvae found on it as being specifically distinct from *L. branchialis*.

The distribution of the fish infested exclusively in the coastal area can be expected to present a gradient with the incidence decreasing as the distance from the shore increases. Such a gradient has been found by Sproston & Hartley (1941) for Whiting and Pollack, *Gadus pollachius* L., infested with *L. branchialis*, and by Templeman (1953) for the cod of the north-west Atlantic infested with the same parasite. The present author studied the distribution of the infested whiting and haddock by examining the commercial catches landed in the Aberdeen Fish Market and the catches made by the research vessels of the Marine Laboratory, Aberdeen. Over 2000 whiting and 30,000 haddock were examined. It became apparent that the two species differ remarkably in the distribution of their infested individuals. The incidence of *Lernaeocera* in whiting fully conformed with the expected pattern. Table 1 shows the results of the examination of 407 whiting in August 1956. The incidence of infestation decreased with the distance from the shore and also markedly with the size of the fish. Examination of 474 whiting in the

Firth of Forth in November 1956 showed that the incidence of *Lernaeocera* tended to decrease eastwards, i.e. towards the mouth of the Firth, and to cease in the waters within the area 10 miles west of May Island. Of the 1300 whiting caught commercially only three were found to be infested. All three were taken a considerable distance from the shore, but constituted such an insignificant proportion of the fish examined that they can be disregarded in any consideration of the distribution.

Infested cod can be found over the entire area of the northern North Sea, but only in small numbers. Of 832 cod examined during the second half of 1955 only 31, or 3·7% were found to be infested. No distinct pattern of distribution has emerged, but it seemed possible that the fishes were infested inshore and migrated outwards. Of the 31 infested individuals only four carried parasites which were not fully mature and all of these were caught no farther than 18 miles from the shore.

The distribution of the infested haddock bore no relation to the distance from the shore at all; neither did the state of the maturity of the parasites. All stages of development, including the youngest post-larval stage, the 'penella', were found at varying distances; the duration of the latter stage is estimated by Capart (1948) to be about 10–15 days. It is difficult to imagine that haddock could frequently be infested near the coast and cover a distance of 100 miles or more in the period of time during which the parasite will remain in this stage of development. The 'penella' stage was found on haddock of all sizes and ages and was not restricted to the younger and smaller individuals which one associates with the inshore waters.

These facts suggested that an intermediate host must exist in the offshore zone and that only a parasite with the reproductive cycle independent of the inshore region can be responsible for the distribution shown by the *Lernaeocera*-infested haddock. For this reason, in the spring of 1956, a search was made for an intermediate host which could account for the completion of the life cycle of the *Lernaeocera* affecting offshore haddock. Six common species of flatfishes were investigated, from numerous localities both in- and offshore (Fig. 1). The results are summarized in Table 2. Over 95% of the investigated Lemon Sole, *Microstomus kitt* (Walbaum), were infested with larval *Lernaeocera*. No other species was found to be infested. Especially noteworthy is the absence of the larvae from plaice, which is regarded by Stekhoven (1936) as one of the common intermediate hosts of *L. branchialis*. No locality shown in Fig. 1 was found to be free of *Lernaeocera*. There is no previous record of the occurrence of *Lernaeocera* in the lemon sole.

As a further check, the distribution of infested haddock was compared with that of lemon sole in the North Sea as determined by Rae (1939). The comparison made it clear that the incidence of the infestation of haddock was fairly closely related to the abundance of the lemon sole in this region.

The problem emerged: why is the offshore haddock infested with

TABLE 1. DISTRIBUTION OF INFESTED WHITING, AS SHOWN BY THE FISH EXAMINED IN AUGUST 1956 BY F.R.S. *EXPLORER*

Date	Locality	Position	Distance from shore (miles)	Depth (fm.)	Size (cm.)	Examined	Infested	Percentage infested
12. viii.	Off Cruden Scaurs	57° 20½′ N., 1° 48′ W.	*ca.* 4	35	21–23	70	6	8·6
12. viii.	Edge of Buchan Deeps	57° 24′ N., 1° 28′ W.	*ca.* 14	42	<25	115	5	4·3
					>25	222	1	0·4
					Total	337	6	1·8

TABLE 2. LIST OF FLATFISHES EXAMINED FOR THE INCIDENCE OF LARVAL *LERNAEOCERA*

Species	Examined	Infested	Percentage infested
Lemon sole, *Microstomus kitt* (Walbaum)	222	211	95·0
Plaice, *Pleuronectes platessa* L.	59	—	—
Witch, *Glyptocephalus cynoglossus* (L.)	60	—	—
Megrim, *Lepidorhombus whiff-iagonis* (Walbaum)	96	—	—
Dab, *Limanda limanda* (L.)	219	—	—
Long rough dab, *Drepanopsetta platessoides* Gill	289	—	—

Lernaeocera, while the offshore whiting is free from infestation? The differences in behaviour and the habitat between the two species provide no answer. While they could explain lower incidence of infestation of whiting, they cannot account for its total absence in this fish. It is apparent therefore that there is only one other possible explanation—the parasite which infests haddock in the open sea is specifically distinct from the one which lives inshore and infests other gadoid species.

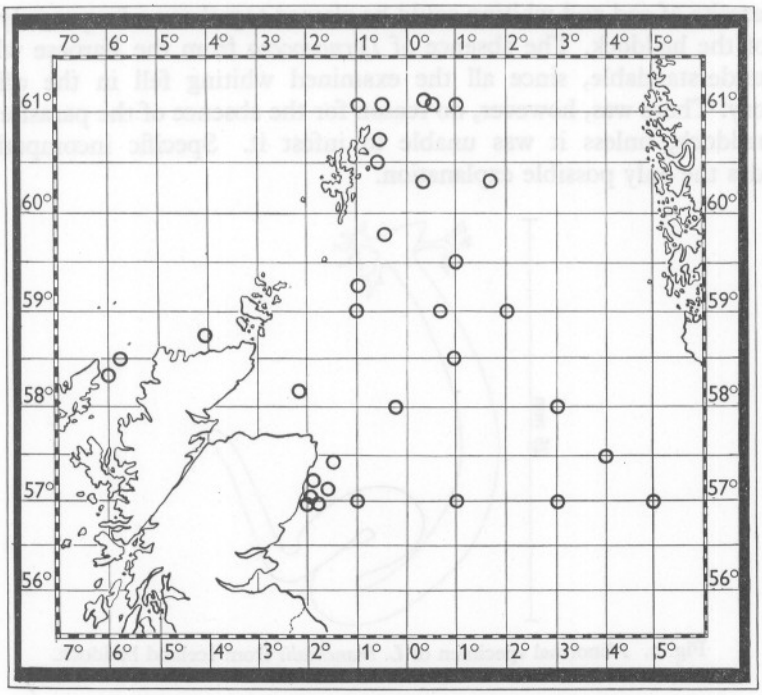

Fig. 1. Localities in which lemon sole infested with *Lernaeocera* have been found.

Investigations in Faröe waters in October 1955 showed, quite surprisingly, the complete absence of *Lernaeocera* from the haddock of that area. The numbers of fish examined on that occasion were 2450 haddock, 477 whiting and 155 cod.

Only the cod was found to be infested by *Lernaeocera* (6 individuals, 5% of the total examined). One of the infested cod carried a 'penella' stage of the parasite. Three were too young to have been migrants from elsewhere. Similar results have been obtained in October 1956, when there were examined 1434 haddock, 123 whiting and 174 cod.

This time 8% of the cod examined were found to be infested, and some of

the 15 infested individuals were again too young to be anything but local fish. Only one haddock was infested with a 15 mm long 'penella' stage.

These results show that *Lernaeocera* is endemic in the Faröe waters. It has presumably spread into that area from the south, possibly carried by cod, and has become established there in presence of an intermediate host. Haddock, on the other hand, do not migrate to Faröe from the North Sea. Both flounder and lemon sole are endemic in Faröe.

The patterns of the distribution of *Lernaeocera* in the North Sea showed that the parasite of cod and whiting could be classed together and separately from that of the haddock. The absence of *Lernaeocera* from the Faröese whiting was understandable, since all the examined whiting fell in the offshore category. There was, however, no reason for the absence of the parasite from the haddock, unless it was unable to infest it. Specific incompatibility provides the only possible explanation.

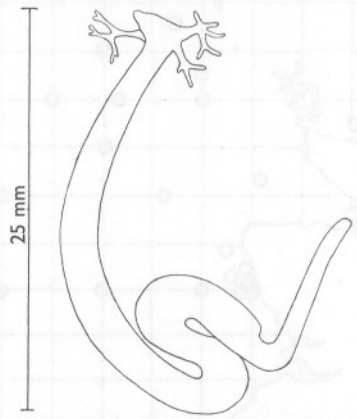

Fig. 2. Abnormal specimen of *L. branchialis* from Iceland haddock.

Investigations were also carried out in Iceland waters. No whiting were caught, but a sample of 250 cod and 299 haddock was examined for *Lernaeocera*. Of these, 23 cod of widely separated areas were infested, but only one haddock carried *Lernaeocera*. The parasite on the haddock was not normally developed (Fig. 2). It was implanted in the branchial arch, all three antlers were present and the length of the body, from the head to the genital flexure, was 25 mm. The widest diameter of the body was no more than $1\frac{1}{2}$ times that of the neck. No egg-strings were present. The general impression was of the retention of juvenile characteristics with simultaneous increase in size, a feature not uncommon in parasites attached to a 'wrong' host.

The geographic distribution of *Lernaeocera* of the cod and the whiting on the one hand and of the haddock on the other suggests that the existence of two species covered until now by the specific name *branchialis* is at least possible.

It should also be mentioned that no records of the infestation of haddock with *Lernaeocera* in either Faröe or Iceland were found by the author in literature.

MORPHOLOGY OF THE ADULT FEMALE

The variations and irregularities of the body shape of *L. branchialis* have prompted some workers (Stekhoven, 1936; Dollfus, 1953) to regard it as a rather unreliable specific feature. It has been felt that the shape of the body might be largely determined by the species and the size of the host. The volume and the shape of the subopercular space, depending on the species of the host, and the abundance of food, depending on its size, were regarded as the main factors determining the shape and the size of the parasite's body.

A logical chain of causes and effects is, smaller host—less food for the parasite—poorer growth—smaller parasite. When, however, it is followed a step further, a conclusion will be reached that the very fact of the parasite being smaller must restore the balance between the size of the parasite and the space available for it. Also, the subopercular spaces of related hosts of equal sizes do not differ sufficiently to produce any marked differences in the shape of the body of the parasite. Consideration of hosts of the same species shows, for example, that although the parasites of small and of large whiting differ in size, and usually also in age, no differences can be observed between the shapes of their bodies.

It must be remembered that the parasite growing in the subopercular space is not enclosed by rigid and immovable walls. The opercula perform constant movements, the effect of which can be compared rather to a series of pushes than a steady pressure. The body bends in the neck region as the result of these pushes and assumes the direction of growth parallel to the longitudinal axis of the body of the host, i.e. in the direction in which the maximum of the available space can be found. Very often a perfectly developed and not at all misshapen parasite is found protruding from under the operculum of the host. The obviously cramped conditions of growth do not seem to have affected the shape of its body. The occurrence of abnormalities must be expected, but they can be taken into account and do not affect the main argument. The existence of the genetical range of variability in shape must also be considered.

The following details of the body shape have been used as specific characters in *Lernaeocera* by the earlier workers. (i) The shape of the antlers (cross-section: T. & A. Scott, 1913; the mode of branching: Stekhoven, 1936). (ii) The structure of the cephalothoracic appendages (2nd antennae, 2nd maxillae: Stekhoven, 1936). (iii) The shape of the trunk (various authors).

The shape of the antlers is a very unreliable character and has been regarded as such even by those who applied it as an auxiliary feature in the diagnosis of

the species. Hardly any two parasites can be found with the identical environmental conditions for the growth of the antlers. The difference in the cross-section of the antlers can be used only to distinguish between *L. lusci* (cross-section oval) and all the other species of the genus (cross-section round).

The structure of cephalothoracic appendages, although it has been suggested as a possible distinguishing characteristic, must be used very cautiously in diagnosis of the species, since the existence of two or more species with the identical structure of these appendages is not impossible.

The shape of the antlers was not helpful in distinguishing *Lernaeocera* found on whiting and on haddock. The structure of the cephalic appendages in the parasites found on these species showed no appreciable differences. Attention was then focused on the shape of the main trunk of the body, which has never been a subject of careful and detailed study. Most of the existing descriptions of the shape of the trunk can be applied to more than one species of *Lernaeocera*. It must be remembered also that most of the descriptive work on the structure of *L. branchialis* is based on specimens found on cod and whiting. Very few, if any, *Lernaeocera* from haddock were thoroughly examined. Of 32 specimens examined by Wilson (1917) none was from haddock, while Stekhoven (1936) had only two parasites from that host from the total of 143 specimens at his disposal.

In the course of this work more than 4000 fully developed specimens of *Lernaeocera* from haddock have been examined. It has not been possible to examine them all thoroughly, but observations have been made on the average shape of the parasite's body. It became obvious that a definite difference existed between the average shapes of *Lernaeocera* from whiting and from haddock. With one exception (Blainville, 1822) the whiting *Lernaeocera* corresponds with all the illustrations made by earlier workers, but the haddock *Lernaeocera* differs from them in a number of easily observable points. When the study of distribution suggested the possibility of the existence of two species, these apparent morphological differences were investigated more closely on the samples of over 60 specimens of mature *Lernaeocera* from both whiting and haddock. The following details of structure were examined: (i) the differences between the angle of flexure of genital segments; (ii) the relations between the thickness of the neck and the main trunk; (ii) the differences of the body shape in the neck and trunk junction area.

Genital flexure. The angles of flexure of the genital segment were measured with a Starret protractor. The results obtained are graphically presented in Fig. 3, which shows a definite difference between the two parasites. More details are given in Table 3. The parasite found on whiting had usually a sharply flexed abdomen. Out of 63 individuals examined only three had the angle of flexure wider than 90° and the average value was 66°. The angle of flexure in the haddock parasite was decidedly more obtuse and averaged 99°,

with values up to 140° being found. The ranges overlapped to the extent of 18·8%.

A sample of *Lernaeocera* collected from Iceland cod in September 1956 was also examined. Although there were somewhat more specimens over 90° than in the parasite of whiting, the cod *Lernaeocera* certainly resembled that

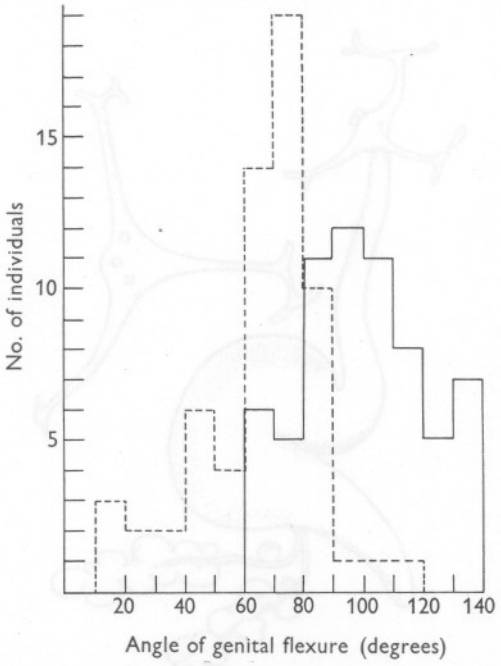

Fig. 3. Distribution of values for angle of genital flexure of *Lernaeocera*. Solid line, parasite of haddock; interrupted line, parasite of whiting.

TABLE 3. THE ANGLES OF GENITAL FLEXURES OF *LERNAEOCERA* FROM DIFFERENT HOSTS

Host species	No. of parasites examined	Range	Mean	More than 90°	Less than 90°
Haddock	65	61° 30′–139° 45′	99°	44	21
Whiting	63	17° 45′–110° 40′	66°	3	60
Cod (Iceland)	25	21° 10′–125° 10′	70°	6	19

from the whiting more strongly than it did that from haddock. Its mean value for the genital flexure was only 4° larger than that of the whiting's parasite, whereas in the haddock *Lernaeocera* it was as much as 33° larger. This feature, as the patterns of distribution and the mode of infestation, tends to draw the dividing line between the parasites of cod and whiting on one side and that of the haddock on the other.

The main trunk of the average haddock *Lernaeocera* bears very close resemblance to that of *L. lusci*, and it would not be surprising if at least some of the records of the latter species from haddock and other hosts of the offshore group proved attributable to the smaller individuals of normal haddock *Lernaeocera*. This surmise removes the difficulty of assuming an 'open sea' reproductive cycle for *L. lusci* which is otherwise a coastal species.

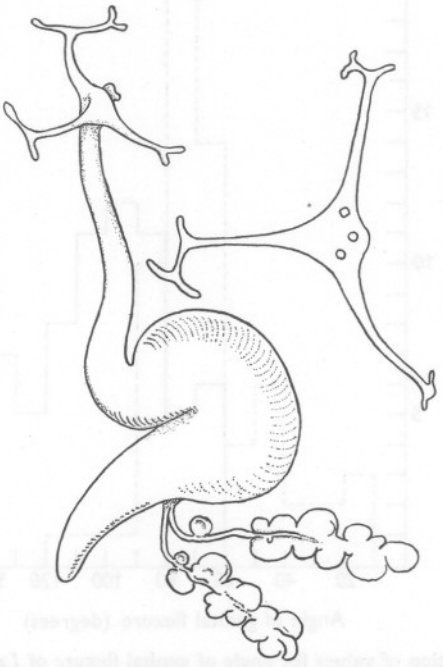

Fig. 4. (Redrawn from Blainville.) *Lernaeocera* showing typical features of the haddock parasite.

It is interesting to note that Blainville (1822), who states in his paper that *L. branchialis* occurs on *Gadus aeglefinus* and *G. barbatus*,[1] illustrated in his drawing of that parasite a body of such typically 'haddock type' that no doubt can be held as to which species was the host of that particular specimen (Fig. 4).

Relation of neck and trunk diameters. Another pronounced difference between the parasites is the relation between the diameters of the neck and trunk. There can be little doubt as to the validity of this feature in the specific diagnosis. The length of the neck may well be dependent on environmental influences, but these can in no way account for marked differences in its thickness and its relationship to the thickness of the main trunk.

[1] According the Günther (1862) the name *Gadus barbatus* is applied to (*a*) younger stage of European Cod, (*b*) Greenland species, *G. ogac*, (*c*) *G. luscus*.

A quantitative check of these differences has been made on 40 individuals from both whiting and haddock and the results are summarized below:

	Range	Mean
Haddock	0·35–0·72	0·50
Whiting	0·23–0·44	0·31

The measurements show that the neck of the haddock parasite is relatively much thicker than that of the whiting, although here again the ratios exhibit a range of variation and some overlap.

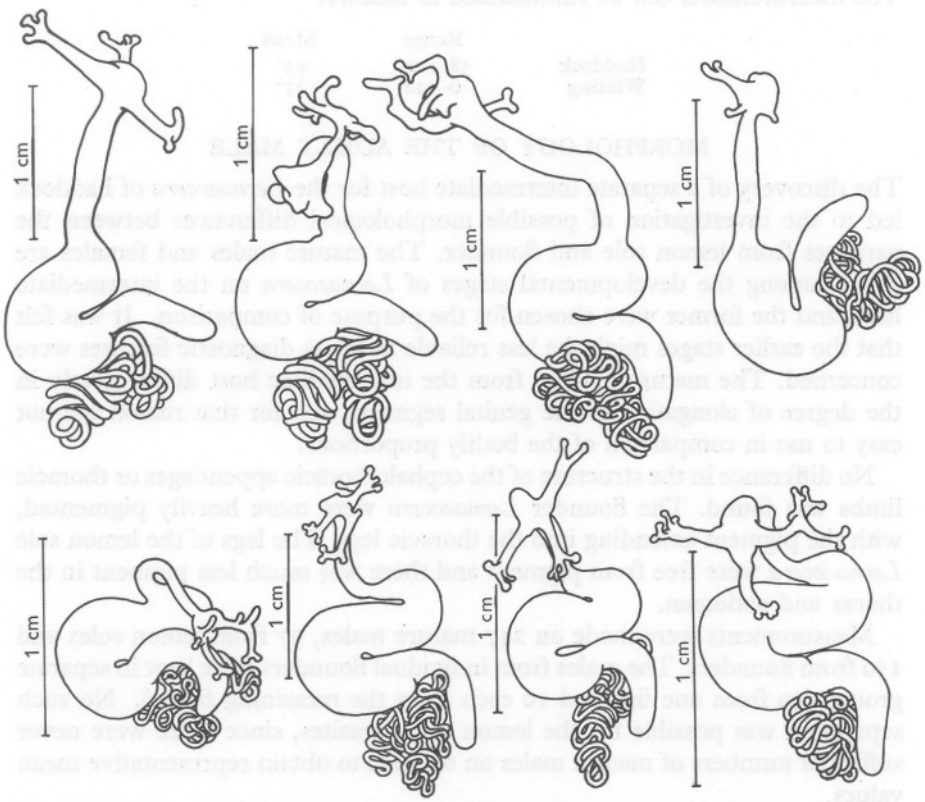

Fig. 5. Morphological differences between *L. branchialis* and *L. obtusa*. Upper, *L. obtusa* from haddock; lower, *L. branchialis* from whiting. Not to scale, but a line indicating 1 cm is drawn beside each specimen.

Shape of neck and trunk junction. Fig. 5 illustrates the third feature distinguishing between the *Lernaeocera* of whiting and haddock. It will be observed that the way in which the neck merges into the trunk is different in both animals. In the parasite of whiting the transition is sudden and well marked. The thin neck abruptly dilates into the trunk with the formation of a prominent bulge at the point of junction of the two parts. The prominence

of the bulge is accentuated by the thinness of the neck. In the parasite of haddock the transition from the neck into the trunk is more gradual and there is usually no bulge present, or only a slight one. The formation of the bulge in the parasite of whiting might be caused by, and is usually associated with, the sharp flexure in that area. The angle between the neck and the anterior part of the trunk is very acute in *Lernaeocera* of whiting and far less acute in that of the haddock. To check this difference quantitatively the angles of flexure were measured in over 40 parasites of haddock and over 50 of whiting. The measurements can be summarized as follows:

	Range	Mean
Haddock	58–142°	93°
Whiting	0–120°	27°

MORPHOLOGY OF THE ADULT MALE

The discovery of a separate intermediate host for the *Lernaeocera* of haddock led to the investigation of possible morphological differences between the parasites from lemon sole and flounder. The mature males and females are found among the developmental stages of *Lernaeocera* on the intermediate host, and the former were chosen for the purpose of comparison. It was felt that the earlier stages might be less reliable as far as diagnostic features were concerned. The mature females from the intermediate host differ greatly in the degree of elongation of the genital segment, and for that reason are not easy to use in comparison of the bodily proportions.

No difference in the structure of the cephalothoracic appendages or thoracic limbs was found. The flounder *Lernaeocera* were more heavily pigmented, with the pigment extending into the thoracic legs. The legs of the lemon sole *Lernaeocera* were free from pigment and there was much less pigment in the thorax and abdomen.

Measurements were made on 247 mature males, 97 from lemon soles and 150 from flounders. The males from individual flounders were kept in separate groups (50 from one fish and 10 each from the remaining fishes). No such separation was possible for the lemon sole parasites, since there were never sufficient numbers of mature males on one fish to obtain representative mean values.

Two separate series of measurements were made. The first series contained measurements of 47 males from lemon soles and 100 from flounders. For this series the following measurements were taken on each individual: (i) total length, (ii) cephalothorax length, (iii) total length minus cephalothorax, (iv) cephalothorax width, (v) abdomen width.

The second set comprised 50 individuals from lemon soles and 50 from flounders. For this series the following measurements were made on each individual: (i) total length, (ii) cephalothorax length, (iii) free thorax length, (iv) abdomen length, (v) cephalothorax width, (vi) abdomen width.

The mean values and the standard errors for these measurements are given in Tables 4 and 5. These tables show that the means for all the characters are higher for the flounder parasites than for those of the lemon soles in both series. In most, though not all, cases the differences between means for the same character differ significantly for the two types of male. The first quantitative observations had suggested the existence of marked differences between the length and width of cephalothorax and between the length of the latter and the remainder of the body in the two types. Ratios were calculated for both pairs in each series and the values, together with the standard errors, are given in Tables 6 and 7. For lemon sole parasites the mean values of both ratios are significantly higher than for any of the flounder parasites.

The major object in taking these measurements was to ascertain whether the parasites from the two host species were distinct and then to ascertain whether such a distinction, if it existed, was confined to one or shown by several characters. In particular, it was important to find out whether the parasites from different flounders resembled one another more closely than they did parasites from lemon soles.

In Tables 8 and 9 are shown the maximum differences between the mean values of the various characters for lemon sole and flounder parasites. The differences for the various measurements have been standardized to allow direct comparisons between them.

These tables show that the separation between the two parasite populations is greatest in the case of abdomen width. Cephalothorax width is also a good discriminating character in series 1, although not so good in series 2 because of the presence in it of one flounder group providing an exceptionally low mean value for this character (0·410 mm). Good discrimination is also provided by the total length minus cephalothorax in series 1, and Table 9 shows that this difference is confined to the length of the free thorax. On the other hand, cephalothorax length does not discriminate well between the two types of parasites. It follows that good discrimination will be provided by any ratio involving abdomen width.

A useful and efficient measure of the differences between the groups of observations has been proposed by Mahalanobis (1930) and called by him the generalized distance. Not only does this quantity take into account any desired number of characters at the same time, but it also gives appropriate weight to different biological characters and takes into account the possible correlations between them (which is not done by a ratio).

If any one character is considered, the mean values for different groups may be arranged as points along a line, the distance of a point from the origin being equal to the mean for that group. The distance between two groups is then the distance between the points representing their mean values. To allow the comparison of distances for different characters all scales of measurement are equalized by dividing measurements by their standard deviations. When

TABLE 4. ADULT MALES, SERIES 1. MEAN VALUES AND STANDARD ERRORS (MM) FOR THE DIFFERENT CHARACTERS

Character		Lemon sole (47)	Flounder (50)	Flounder (10)	Flounder (10)	Flounder (10)	Flounder (10)	Flounder (10)
Total length	Mean	1·298	1·478	1·484	1·490	1·488	1·446	1·430
	S.E.	±0·0060	±0·0058			±0·0130		
Abdomen width	Mean	0·172	0·208	0·212	0·208	0·210	0·204	0·208
	S.E.	±0·0011	±0·0010			±0·0023		
Cephalothorax width	Mean	0·376	0·440	0·442	0·423	0·426	0·426	0·441
	S.E.	±0·0025	±0·0024			±0·0054		
Total length minus cephalothorax	Mean	0·657	0·801	0·812	0·820	0·819	0·800	0·788
	S.E.	±0·0041	±0·0040			±0·0089		
Cephalothorax length	Mean	0·622	0·674	0·672	0·670	0·669	0·646	0·642
	S.E.	±0·0040	±0·0038			±0·0086		

two or more characters are used this method of representation may be extended to two or more dimensions.

For the present data there are seven groups in series 1 and six in series 2. In order to give a measure of distance between lemon sole groups the data in

TABLE 5. ADULT MALES, SERIES 2. MEAN VALUES AND STANDARD ERRORS (MM) FOR DIFFERENT CHARACTERS

Character		Lemon sole (50)	Flounder (10)	Flounder (10)	Flounder (10)	Flounder (10)	Flounder (10)
Total length	Mean	1·302	1·503	1·494	1·468	1·440	1·390
	S.E.	±0·0055			±0·0122		
Abdomen width	Mean	0·168	0·220	0·210	0·210	0·204	0·198
	S.E.	±0·0011			±0·0024		
Cephalothorax width	Mean	0·372	0·440	0·438	0·432	0·435	0·410
	S.E.	±0·0018			±0·0041		
Free thorax length	Mean	0·322	0·357	0·376	0·375	0·368	0·366
	S.E.	±0·0024			±0·0054		
Abdomen length	Mean	0·352	0·458	0·456	0·444	0·434	0·396
	S.E.	±0·0027			±0·0059		
Cephalothorax length	Mean	0·627	0·688	0·662	0·650	0·639	0·628
	S.E.	±0·0040			±0·0090		

TABLE 6. SERIES 1. MEAN RATIOS AND STANDARD ERRORS

Host	Sample size	Cephalothorax length / Cephalothorax width	Cephalothorax length / Total length minus cephalothorax
Lemon sole	47	1·65±0·011	0·92±0·007
Flounder (1)	50	1·54±0·011	0·84±0·006
Flounder (2)	10	1·52±0·022	0·83±0·020
Flounder (3)	10	1·59±0·040	0·82±0·016
Flounder (4)	10	1·57±0·011	0·82±0·005
Flounder (5)	10	1·52±0·020	0·81±0·010
Flounder (6)	10	1·46±0·018	0·82±0·011

TABLE 7. SERIES 2. MEAN RATIOS AND STANDARD ERRORS

Host	Sample size	Cephalothorax length / Cephalothorax width	Cephalothorax length / Total length minus cephalothorax
Lemon sole	50	1·68±0·012	0·93±0·007
Flounder (1)	10	1·57±0·028	0·85±0·023
Flounder (2)	10	1·51±0·023	0·80±0·012
Flounder (3)	10	1·50±0·014	0·79±0·007
Flounder (4)	10	1·47±0·013	0·80±0·011
Flounder (5)	10	1·54±0·029	0·82±0·011

TABLE 8. SERIES 1. DIFFERENCES BETWEEN STANDARDIZED MEAN VALUES FOR DIFFERENT CHARACTERS

Character	Maximum difference between flounder parasites	Minimum difference between flounder and lemon sole parasites
Abdomen width	1·08	4·33
Cephalothorax width	1·12	2·76
Total length minus cephalothorax	1·15	4·03
Cephalothorax length	1·18	0·73

TABLE 9. SERIES 2. DIFFERENCES BETWEEN STANDARDIZED MEAN VALUES FOR DIFFERENT CHARACTERS

Character	Maximum difference between flounder parasites	Minimum difference between flounder and lemon sole parasites
Abdomen width	2·90	3·94
Cephalothorax width	2·31	2·92
Free thorax length	1·11	2·05
Abdomen length	3·30	2·34
Cephalothorax length	2·12	0·03

TABLE 10. DISTANCES BETWEEN GROUPS BASED ON CEPHALOTHORAX LENGTH, LENGTH OF REST OF BODY AND CEPHALOTHORAX WIDTH

(In arbitrary units)

(LS)1		(LS)2		F11		F12		F13		F14		F15	
(LS)2	0·7	(LS)1	0·7	(LS)1	5·3	(LS)1	5·8	(LS)1	5·0	(LS)1	5·2	(LS)1	4·5
F11	5·3	F11	5·9	(LS)2	5·9	(LS)2	6·2	(LS)2	5·5	(LS)2	5·7	(LS)2	5·1
F12	5·8	F12	6·2	F12	0·4	F11	0·4	F11	1·2	F11	1·1	F11	1·2
F13	5·0	F13	5·5	F13	1·2	F13	1·3	F12	1·3	F12	1·1	F12	1·4
F14	5·2	F14	5·7	F14	1·1	F14	1·1	F14	0·3	F13	0·3	F13	1·2
F15	4·5	F15	5·1	F15	1·2	F15	1·4	F15	1·2	F15	1·2	F14	1·2
F16	5·4	F16	6·0	F16	1·2	F16	1·1	F16	1·8	F16	1·7	F16	0·9
F21	6·6	F21	7·2	F21	1·8	F21	1·5	F21	1·7	F21	1·5	F21	2·5
F22	5·4	F22	6·0	F22	0·5	F22	0·4	F22	1·1	F22	1·0	F22	1·0
F23	5·3	F23	5·9	F23	1·0	F23	1·0	F23	1·1	F23	0·9	F23	0·8
F24	4·8	F24	4·8	F24	1·3	F24	1·4	F24	1·4	F24	1·7	F24	0·8
F25	3·5	F25	3·5	F25	2·3	F25	2·6	F25	1·9	F25	2·0	F25	1·2

F16		F21		F22		F23		F24		F25	
(LS)1	5·4	(LS)1	6·6	(LS)1	5·4	(LS)1	5·3	(LS)1	4·8	(LS)1	3·5
(LS)2	6·0	(LS)2	7·2	(LS)2	6·0	(LS)2	5·9	(LS)2	5·4	(LS)2	4·2
F11	1·2	F11	1·8	F11	0·5	F11	1·0	F11	1·3	F11	2·3
F12	1·1	F12	1·5	F12	0·4	F12	1·0	F12	1·4	F12	2·6
F13	1·8	F13	1·7	F13	1·1	F13	1·1	F13	1·8	F13	1·9
F14	1·7	F14	1·5	F14	1·0	F14	0·9	F14	1·7	F14	2·0
F15	0·9	F15	2·5	F15	1·0	F15	0·8	F15	0·8	F15	1·2
F21	2·4	F16	2·4	F16	1·8	F16	0·8	F16	0·6	F16	2·1
F22	0·8	F22	1·7	F21	1·7	F21	1·9	F21	2·8	F21	3·5
F23	0·8	F23	1·9	F23	0·6	F22	0·6	F22	1·1	F22	2·2
F24	0·6	F24	2·8	F24	1·1	F24	1·0	F23	1·0	F23	1·8
F25	2·1	F25	3·5	F25	2·2	F25	1·8	F25	1·8	F24	1·8

LS, lemon sole; F, flounder; 12, denotes the second flounder of the first series, etc.

series 1 and 2 were combined in respect of cephalothorax length, cephalothorax width and the length of the rest of the body and the generalized distances (shown in Table 10) were calculated.

Clearly the points for the parasites of the lemon soles lie very close together and relatively quite far away from the nearest point of the flounder parasites. The shortest distance between the lemon sole parasites and those of the flounder is 3·5, equal to the distance between the two flounder parasite populations farthest apart. The average distance between flounder groups is 1·4.

Having shown that it is quite reasonable to consider the parasites of the flounders as being distinct from those of the lemon sole, it is of interest to find the character or combination of characters which most clearly brings out the difference between the two groups of parasites. To do this, the data from series 2 only were used and the measurements from the parasites of individual flounders combined into a single set. Analysis showed that all characters are useful for the purpose of discrimination, but the additional information in this respect given by cephalothorax length was relatively small. Using all characters, the combination which most clearly brings out the differences between the two groups was found to be

$$(\text{A.W.}) + 0{\cdot}400\,(\text{C.W.}) + 0{\cdot}376\,(\text{F.T.L.}) + 0{\cdot}177\,(\text{A.L.}) - 0{\cdot}145\,(\text{C.L.}),$$

where A.L. is abdomen length, A.W. abdomen width, F.T.L. free thorax length, C.L. cephalothorax length and C.W. cephalothorax width.

This combination is known as a discriminant function (Fisher, 1936). The mean value of this quantity for the lemon sole parasites of series 2 is 27·358 and for the flounder parasites is 33·468. The difference 6·110 has a standard error of $\pm 0{\cdot}221$ and is therefore highly significant. In fact, using this function of the characters to classify an individual parasite of unknown origin, the probability of misclassification is about three in a thousand.

MODE OF ATTACHMENT

The specific name of *L. branchialis* refers to the mode of attachment of this parasite. It is described by Linnaeus (1767) as being located 'ad branchias'. Stekhoven (1936) doubts the fitness of the name and regards the species as a heart rather than a gill parasite. His histological examinations have revealed that the bulbus arteriosus is the main region of penetration by this parasite. In his later work (Stekhoven & Punt, 1937), however, he modifies his opinion and states that the parasite is very often found in other localities. This applies, according to him, primarily to the older hosts. The distance from the point of attachment to the bulbus becomes too great and the parasite is no longer capable of reaching it.

The following observations were made during the present investigations:

(1) Small whiting had the parasite implanted in the bulbus in the majority

of cases (over 75 %). One parasite penetrated the ventricle, the walls of which were pushed out by the antlers.

(2) Out of 295 of the mature female parasites from haddock only 19 were attached to the bulbus arteriosus (6·4 %), while the remaining ones penetrated mainly the ventral aorta and some were attached to the branchial arteries.

(3) In Icelandic cod 8 out of 25 parasites were found in the bulbus arteriosus (33·3 %). Here also one parasite was embedded in the ventricle.

When the above facts are considered, two things become clear:

(*a*) The percentage of parasites in the bulbus is far larger both for whiting and cod than for haddock.

(*b*) This difference is not due to environmental conditions. Both whiting and cod are infested at an early age, while haddock continues to be infested throughout its life.

Parasites which infest a larger host might be unable to penetrate the bulbus due to the distances involved. But it must be remembered that at least a half of the infested haddock become infested during the first two years of their lives. Even some of the old haddock bear mature parasites, with the necks almost as long as the rest of their bodies and fully capable of reaching into the bulbus area. Sometimes a parasite penetrates from one subopercular cavity into the other, so that its neck is twice the length necessary to reach the bulbus.

Reference to Fig. 6 shows that there is no great difference in the spatial relations between the main area of attachment of *Lernaeocera* and the cardiac region of whiting and haddock. It would appear that in whiting the parasite may even have to reach farther back to enter the bulbus than in the haddock; and, indeed, *Lernaeocera* infesting whiting are very often found in the bulbus even when it does not represent the most accessible spot. Fig. 5 shows that in whiting the neck of *Lernaeocera* is often bent at a right angle to the main axis of the body. Being attached at the same level as the heart it has to make a sharp bend in order to reach it. This phenomenon is almost suggestive of a tropism and, in fact, the term 'arterotropism' has been coined for it by Capart (1948).

The haddock *Lernaeocera*, generally with the same possibilities of reaching the heart, is usually implanted more anteriorly in the ventral aorta, although this frequently means that the neck has to travel a longer way. This results in a striking difference between the two parasites. The whiting parasite has a short neck bent at a right angle to the longitudinal axis of the body, and that of the haddock has a relatively longer neck which deviates only slightly from that axis.

THE SEPARATION OF THE SPECIES

In the preceding sections of this paper several definite and consistent differences between *Lernaeocera* infesting whiting and cod and *Lernaeocera* found on haddock were discussed. The differences were of such character and extent

that they could only be explained by the existence of specific distinctions between these two parasites.

We have seen that the geographic distribution of the incidence of *Lernaeocera* in haddock differs greatly from that of cod and whiting. First, haddock is infested throughout the northern North Sea, while the other two hosts are are free from infestation in the open sea. Secondly, no infested haddock is found outside the European continental shelf, while cod of, for example,

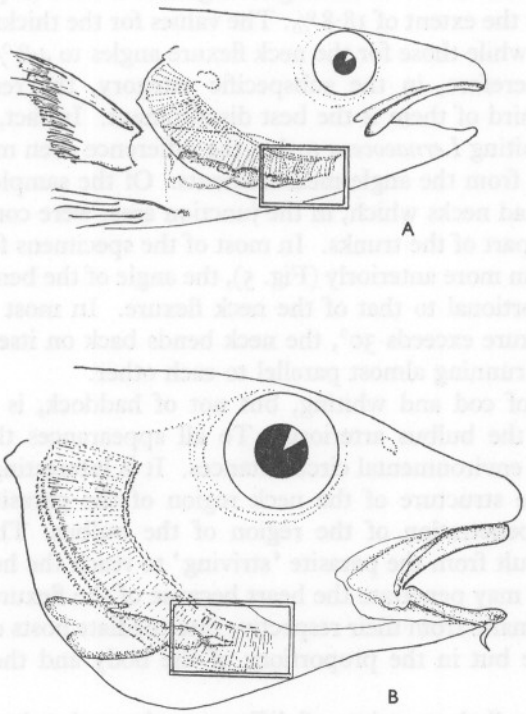

Fig. 6. Heads of (A) whiting and (B) haddock, showing the main attachment area of *Lernaeocera* and its relation to the position of the heart.

Faröe and Iceland are infested to the same, or larger, extent than in the North Sea. One can visualize the spread of *Lernaeocera* from the North Sea northwards. Infested cod carry over the mature parasites to Faröe, the eggs deposited there hatch and, in the presence of a suitable intermediate host (both lemon sole and flounder are present in that area), the parasite becomes established. Haddock, presumably owing to its inability to negotiate the deep water barriers, does not spread its own *Lernaeocera*. Only the specific distinctness of the parasite of whiting and cod can explain the absence of infestation in haddock outside the European continental shelf.

The three most important differences in the morphology of the two types

of *Lernaeocera* were (i) the angles of the genital flexure, (ii) the relation between the ratios of thickness of the neck to that of the trunk, and (iii) the structural differences of the neck and trunk junction area.

Ginsburg (1938), proposing his definition of the arithmetical concept of species, subspecies and race, gives certain values for 'intergradation' of a particular character under comparison. These values are: 10% or less for specific difference, 15–25% for a subspecific one and 30–40% for a racial one. Comparison of the values for the angles of genital flexure (Fig. 3) shows them to intergrade to the extent of 18·8%. The values for the thickness ratios intergrade to 10%, while those for the neck flexure angles to 4·8% only. The first of them is, therefore, in the subspecific category, the remaining two in specific. The third of them is the best discriminant. In fact, the presence of the bulge in whiting *Lernaeocera* makes the difference even more pronounced than it appears from the angle measurements. Of the sample of 58 parasites of whiting 13 had necks which, in the junction area, were completely parallel to the anterior part of the trunks. In most of the specimens from whiting the neck bends again more anteriorly (Fig. 5), the angle of the bend being roughly inversely proportional to that of the neck flexure. In most of the parasites whose neck flexure exceeds 30°, the neck bends back on itself, its distal and proximal parts running almost parallel to each other.

Lernaeocera of cod and whiting, but not of haddock, is embedded predominantly in the bulbus arteriosus. To all appearances this difference is independent of environmental circumstances. It is interesting to speculate to what extent the structure of the neck region of the parasite of whiting is related to its penetration of the region of the bulbus. The characteristic flexure may result from the parasite 'striving' to reach the heart of the host; alternatively, it may penetrate the heart because of the flexure of the neck.

The mature males from their respective intermediate hosts differed not only in absolute size but in the proportions of the body and the extent of pigmentation.

Summing up all these points of difference, the author became convinced that the two parasites are specifically distinct. The existence of some distinguishing features between the two types of *Lernaeocera* has, however, been observed as early as the eighteenth century. O. Fabricius (1780, p. 336) and O. F. Müller (1789, p. 65) both regarded the parasite of the haddock as 'varietas minor' of *Lernaea gadina* (= *Lernaeocera branchialis*), but it appears that size was the only difference prompting these two authors to regard this parasite as distinct from those of '*Gadi barbati*'. The figure which O. F. Müller gives of his *L. gadina* (pl. CXVIII, fig. 4) is evidently that of the cod and whiting *Lernaeocera*.

The discovery that the name *L. branchialis* is at present used to cover two distinct, if very similar, species brings with it the problem of which of the two species should retain the old name and which should be given a new one.

The solution of this problem depends on the host species from which *L. branchialis* was first described. Linnaeus (1767), who first named the animal in the 12th edition of *Systema Naturae* (p. 1092), describes it as parasitizing: 'Gadis, ad branchias.' Possibly Linnaeus never actually saw the animal and details of it must be sought in Strøm (1762), to whom Linnaeus refers. Strøm is rather vague about the hosts on which the parasite occurs, stating that it is found 'i Fiskenes Tokn' (on gills of fishes). He adds later, however, 'besonderlig i Torskenes om Foraaret' (especially on cod in the spring). In view of this statement, which is the oldest on record concerning the host of *L. branchialis*, it seems proper to retain the old name for the parasite of whiting and cod and rename the parasite of haddock, which the author proposes to name *L. obtusa* n.sp. The name is suggestive of the characteristic wide angle of genital flexure.

Lernaeocera obtusa sp.nov.

Lernaea gadina (in part) Fabricius, 1780. (The reference to 'varietas minor', judging from its context, does not constitute a proposal of 'minor' as a name for *Lernaeocera* found on haddock.)

Lernaea gadina (in part) O. F. Müller, 1789. (The reference to 'varietas minor' as above.)

Lernaeocera branchialis (in part) Blainville, 1822. (A figure of *L. obtusa* is given, but Linnaeus 1767, following Strøm 1762, by not mentioning the haddock has implicitly restricted *L. branchialis* to the parasite of the cod.)

Lernaea branchialis (in part) T. & A. Scott, 1913.

Lernaeocera branchialis (in part) Oorde de Lint & Stekhoven, 1936.

Holotype: mature female deposited in British Museum (B.M. no. 1957.2.21.1). *Paratypes*: six mature males and females deposited in British Museum (N.H.) B.M. no. 1957.2.21.2. Six mature males and females deposited in Royal Scottish Museum, Edinburgh, No. Royal Scottish Museum 1957.24. *Type locality*: Northern North Sea. Collected by Z. Kabata.

Description. Female: size within the range of that of *L. branchialis*. Shape generally similar to that of *L. branchialis*, with the following exceptions: (1) The flexure of the neck and the anterior part of the trunk forms roughly a right angle (average of 58 specimens was 93°, with the range of 58–142°), while that of *L. branchialis* forms an acute angle or no angle at all, both parts running parallel to each other. (2) The neck is considerably thicker in relation to the diameter of the trunk than in *L. branchialis*. (3) The flexure of the genital segment forms usually an obtuse angle (average of 65 specimens was 99°), while that of *L. branchialis* forms an acute one.

Male: generally similar to the male of *L. branchialis*, but mean size 1·30 mm as compared with 1·46 of the latter. Cephalothorax longer in relation to the body length than in *L. branchialis*. Cephalothorax and abdomen narrower than in the latter species.

Intermediate host: lemon sole, *Microstomus kitt* (Walbaum); habitat: gills. Final host (female only): haddock, *Gadus aeglefinus* L.; habitat: branchial chamber or gills.

The author wishes to express his gratitude to the following members of the staff of the Marine Laboratory, Aberdeen: Mr J. A. Pope, who is responsible for the statistical analysis and largely for the form of the section on the morphology of the male, Dr B. B. Rae and Dr J. H. Fraser for their interest, encouragement, useful criticism and corrections of the manuscript.

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SUMMARY

The fishes harbouring parasites of the genus *Lernaeocera* can be divided, according to the presence or absence of contact with the coastal waters, into 'inshore' and 'offshore' groups. According to literature, only *L. branchialis* occurs commonly on hosts in both groups. The difference between this and the remaining species of the genus is explained by the existence of two different species covered by the name *L. branchialis*. One of these species is parasitic on cod and whiting, the other on haddock. The two species have also different intermediate hosts (flounder and lemon sole respectively) and differ in morphology of the adult male and female and in the mode of attachment to the final host.

Lernaeocera of whiting and cod is distributed mainly in the coastal area, while that from haddock extends over the whole of the North Sea. The former, but not the latter, is present outside the European continental shelf. All these differences lead to the conclusion that the two types represent two different species. The old name is retained for the parasite of cod and whiting. The parasite of haddock is the new species, to which the name *Lernaeocera obtusa* is given.

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Note added in proof

Since this paper was written, another interesting fact has been brought to light. Investigations in Faröe waters revealed *Lernaeocera* on the gills of the lemon sole. No other flatfish species has yet been found to carry this parasite in that area. The biometric measurements of the adult males found on the lemon sole in Faröe wateres proved them to resemble those of the lemon soles of the North Sea.

A suggestion has been put forward in this paper (p. 573) as to the possible way in which *L. branchialis* spread northwards from the North Sea. It is only larger and older cod which can be regarded as possible carriers of the parasite across the deep water barrier which confines the host of *L. obtusa* within the limits of the continental shelf. Such cod, crossing to Faröes, are unlikely to enter the littoral zone and come in contact with the flounder. The parasite will therefore deposit its eggs in deeper waters and its copepodids, to survive, must become adapted to a host available in those waters. The lemon sole, as the most common local flatfish species, became an intermediate host. The fact that, in spite of the infestation of the lemon sole, no parasite is found on the haddock, strongly suggests that the larvae on that flatfish belong to *L. branchialis*.

The biometric similarity between the parasites found on the lemon soles in Faröes and the North Sea suggests that the bodily proportions of the male are subject to environmental influences and cannot be used as specific discriminant. The conclusions of the section of this paper dealing with the morphology of the male appear therefore to be incorrect.

While not affecting the main argument of this paper, the discovery focuses attention on the interesting and little-known problems of ecology of marine parasites.

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NOTES ON PRACTICAL METHODS FOR THE STUDY OF MARINE DIATOMS

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In the study of marine diatoms examination of fresh material (or of wet mounts in some suitable preservative such as formalin–sea water) is essential, in addition to 'permanent' mounts of 'cleaned' frustules, because the violent cleaning process destroys many of the more delicate forms (e.g. the genus *Guinardia*). Conversely, it is not possible to see the fine details of skeletal structure, upon which the taxonomy of so many diatoms is based, while the organic contents of the cells are still present.

Scatter-mounts are preferred to arranged slides because the examination of large numbers of individuals is essential if the wide range of variation within species of this group is to be justly appreciated (cf. Hendey, 1938, 1951). Further, they help one to appreciate the relative abundance of species within the sample, provided that wet mounts have previously been examined.

The 'cleaning'—removal of the organic contents of the frustules—may be carried out by direct incineration in a platinum crucible, but some form of wet combustion is usually found better and more convenient. The successive treatments with strong mineral acids and powerful bleaching agents that this involves can be carried out satisfactorily as described by Hendey (1938, 1951) if there is ample material available. Frequently, however, in marine biological work, it is necessary to use very small quantities; for example, the gut contents of a few small invertebrates, or the epiphytes from the shell of a single large barnacle.

It is possible to apply the same schedule of successive washings and treatment with acids that Hendey recommends, to smaller amounts of material, if one's facilities include the use of a small centrifuge and a fume cupboard. The reagents can safely be added (in the very small quantities needed) to material in a 12 ml. centrifuge tube directly with a pipette provided the mouth of the tube is kept pointing away from the face of the operator, towards the far side of the fume cupboard. Much time is saved by concentrating the material centrifugally between each stage instead of waiting for it to settle before decanting off the unwanted fluids. The elimination of sulphuric acid is especially facilitated by the small quantity (*ca.* 4 ml.) of reagent needed. One can dilute it by cautiously pipetting water into it in the tube, allowing it to 'kick' slightly and boil momentarily until the tube is gradually filled. This eliminates most of the possibility of trouble from spurting acid when, after bringing the material down again with the

centrifuge, the acid is finally poured off. With the speeding up of the process that use of the centrifuge permits, extra stages, such as treatment with a fat-solvent or extra washing with distilled water can easily be interpolated at appropriate points in the schedule.

Centrifuge tubes of Pyrex glass, scrupulously cleaned, should be used; and it is important to make sure that their ends are adequately cushioned against direct contact with the bottoms of the buckets. It is essential to use one newly drawn or *very* thoroughly cleaned pipette for all stages in the manipulation of each separate sample.

By these means good cleaned samples of marine diatom frustules ready for mounting have been obtained from material as diverse as plankton samples, epiphytes, scrapings from the skin-film of whales and diatomaceous bottom muds; working with very small quantities of material when necessary.

The material, once cleaned and washed, can conveniently be stored in very small vials, labelled, corked and waxed, in either distilled water or alcohol. Alcohol is preferred because it prevents the growths that may take place if the material is stored in water for a long time.

Before mounting dehydration is necessary and this can be completed by direct heating and use of a desiccator filled with fresh silica gel. Several cleaned cover-glasses are placed on black paper in a small petri dish, one large drop of the material, agitated until the diatom frustules cause a faint milkiness of the fluid, is pipetted on to each, the dish covered and heated at just above 100° C for a time, then removed to the desiccator. The slips are now ready for mounting by placing a small drop of the chosen medium near the centre of each, inverting it on to a cleaned slide and proceeding with the appropriate after-treatment (hardening, usually by gentle heat, and perhaps ringing).

There remains the choice of a suitable mountant, and here we are faced with the old problem resulting from the fact that diatom-silex has a refractive index quoted as around 1·40–1·42, so near to that of the best general mountants (e.g. Euparal 1·46 and Canada balsam 1·52) that the index of visibility of frustules mounted in them is too low. A mountant of much higher refractive index is needed.

Much patient experiment with mixtures of sulphur, phosphorus and alkaloids with other substances, usually resinous, and with fluids such as monobromonaphthalene, has been carried out in the past by such workers as Morris (1885) and Bellido (1897, 1927). The latter's work was translated into English (1927) and is extensively quoted by Gray (1953). Bellido's methods resulted in perhaps the finest diatom mounts ever made, rivalling the famous arranged slides of Müller. They consisted essentially of mounting in monobromonaphthalene sealed in hardened shellac cells. The technique is laborious and time-consuming, however, demanding a manipulative skill that can only be acquired through months of practice. The shellac also needs special purification.

In the meantime 'Styrax', and 'Hyrax', a proprietary resin of high refractive index, became popular with several workers. The use of Styrax is described in the introductory chapters of Hustedt's monograph (1930). We have had some good results with these media; but Styrax is difficult to control in the drying-off stages, when bubbles are frequently drawn in under the cover-glass, and it is inclined to give rather a dark ground colour. Moreover, Hustedt (1952) has since found Hyrax inadequate for some forms.

Ghazzawi (1933) revived an old method that dates back to the time of Morris's experiments, a solid but thermoplastic medium of good keeping qualities, obtained by grinding antimony tribromide with the alkaloid piperine. We found that this demanded very careful control of heating, difficult to apply in practice, and that the post-war price of piperine was prohibitive.

Jelly (1930), working on sections of cellulose nitrate film for Kodak Ltd., got good results by melting Canada balsam with alphabromonaphthalene (15 g to 10 ml.) on the water-bath. He suggested that this mixture, which gave him a refractive index of $N_D = 1{\cdot}591$, might also be useful with diatomaceae and ice crystals. I have had moderate success with it (Hart, 1935), but found that some mounts set poorly and tended to develop globules unless the proportions were modified, using a smaller quantity of a bromonaphthalene in balsam already made up with xylene. Some of the mounts thus obtained have lasted well for over 20 years, but the gain in refractive index is too small to give the best results with delicate frustules.

Latterly, the introduction of synthetic resins has led to the introduction of various mountants mostly known only under proprietary names, at least two of which were evolved expressly for the use of diatomists, by authors who published directions for their small-scale synthesis. These are 'Naphrax' (Flemming, 1943) and 'Pleurax' (Hanna, 1949). Pleurax was used extensively by Dr Cupp in the work leading up to her monograph on the marine diatoms of the Pacific coast of North America (Cupp, 1943), which should be a strong recommendation. A sample of Naphrax obtained commercially was very dark-coloured, which detracted from its otherwise excellent optical qualities. We hope to repeat the syntheses described by Fleming and Hanna eventually, in order to test Naphrax and Pleurax against the media described below.

Another proprietary mountant tried has been 'Clearax'—water white with a refractive index stated to be 1·66 when set. It gave good results, but other media seemed better.

For a long time I had failed to find Hanna's description of the small-scale synthesis of his Pleurax, and it was this that led me to experiment on lines suggested partly by Jelly's work, and partly by that of Kirkpatrick & Lendrum (1939). The latter developed a most useful cheap substitute for balsam (DPX, also 'DePex') for bacteriological and histological mounting by dissolving distrene–80, one of the polystyrenes already available commercially, in xylol, with the addition of a small proportion of tritolyl phosphate as plasticizer.

This medium is especially good for preserving the colour of some delicate stains that tend to fade in balsam; its refractive index, however, is but little higher than that of ordinary Canada balsam in xylol.

It was found that the synthetic resin could be dissolved in *a*-bromonaphthalene, and that the resultant syrup was miscible with xylene. Further, it could also be dissolved in *a*-iodonaphthalene, introducing a darker colour but an even higher refractive index. Finally, a useful medium for diatom mounts was achieved by mixing the three solutions obtained by dissolving distrene-80 to saturation in xylene, *a*-bromonaphthalene and *a*-iodonaphthalene, with the aid of gentle heat, in the proportions: two parts xylene solution, two parts *a*-bromonaphthalene solution, one part *a*-iodonaphthalene solution.

The mounts should be dried off at temperatures not greatly exceeding 100° C for about 1 h, and baked again similarly on the following day. If they are heated too strongly or too long immediately after mounting, bubble trouble may result. The mixed medium seems stable in an ordinary balsam-bottle. It may be thickened slightly by evaporating off some of the xylene, or thinned by adding more xylene as necessary.

The mounts seem good optically and have lasted for several months without being ringed. Ringing with gold-size may increase their keeping properties. Two out of some fifty have shown development of minute globules, such as Morris complained of in fluid mounts made with monobromonaphthalene alone, and which he avoided by incorporating a minute proportion of salicilate of chinoline in the mountant. With these polystyrene mixtures, it is thought that the defect was due rather to inadequate dessication before mounting, than to the quality of the naphthalene derivatives, which are obtainable in a much more pure state than in Morris's day.

The heavy halogen naphthalene derivatives have also been tried again mixed with Canada balsam in high proportions, as suggested by Jelly. This gave quite useful mounts but several developed globules in time, and all showed much more background colour than those made from the synthetic resin mixture. Other promising experiments have been made using venetian turpentine (more soluble than Canada balsam in ethylalcohol) as the resinous base, with the same optically effective liquids. It was hoped that by this means material stored in alcohol might be mounted more readily, since complete dessication would not be such a strict necessity. Some good mounts resulted, but dark background colour was again found to be a considerable disadvantage.

Only time can show the keeping qualities of the successful mixture of distrene-80 with xylene and the heavy halogen derivatives of naphthalene. Our next step must be to complete the small-scale syntheses of 'Naphrax' and Pleurax as so generously described by Drs Fleming and Hanna and see how they compare with our mountant. At worst the distrene-80 mixture

provides a first class examination medium easy to prepare and far superior to temporary fluid mounts, even though they may not prove fully 'permanent'.

Throughout the later experiments Prof. Gray's source reference book has been a great help. I should like to thank the Director of the Plymouth Laboratory of the M.B.A., where the work was begun years ago; and also Dr Cox, chemist on the N.I.O. staff, for advice and encouragement.

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THE OCCURRENCE OF *IDOTEA METALLICA* BOSC IN BRITISH WATERS

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(Text-figs. 1 and 2)

Idotea metallica Bosc occurs occasionally in plankton from waters off the west coast of Britain, but since it does not seem to be a British resident it was excluded from a recent review of the genus *Idotea* (Naylor, 1955*a*). Accounts of the distribution of *I. metallica* seldom distinguish between occasional records and resident breeding localities, and this note attempts to explain its occasional occurrence in Britain.

I am grateful to Dr J. H. Fraser, Dr K. M. Rae and Mr G. M. Spooner for the loan of material, and to Dr I. Gordon for facilities at the British Museum. Prof. E. W. Knight-Jones and Dr R. J. Menzies have kindly criticized the manuscript.

SPECIFIC CHARACTERS (Fig. 1)

Body oblong; length about three times the width, except in females which are relatively much broader. *Cephalon* about $1\frac{3}{4}$ times as broad as long; anterior border concave, posterior border less so; marked transverse sinuous furrow behind the eyes; eyes large. *Antennules* hardly extending beyond the third joint of the antennal peduncle; first and second joints expanded, others fairly robust. *Aesthetascs* in pairs, numbering up to 20 or more in males; fewer in females. *Antenna* robust, flagellum shorter than peduncle and about one-sixth the length of the body; flagellum segments numbering up to about 10 in males and 8 in females; terminal style blunt, one quarter to one-sixth the length of the subterminal segment. *Coxal plates* triangular, extending over the whole length of the segment in segments 2 or 3 and posterior ones, becoming only slightly wider posteriorly; 5–7 sharply produced laterally making an angle of less than 45°. *Legs* robust; second leg of adult males having pads of fine setae. *Abdomen* with straight sides; *telson* with apical border straight, with rounded corners (adults) or widely rounded corners (juveniles). *Appendix-masculinus* reaches just beyond the tip of the second pleopod in larger males.

Length: males recognizable from about 8 mm, ranging to about 30 mm; females from 9 to 19 mm.

Colour: uniformly greyish or brown.

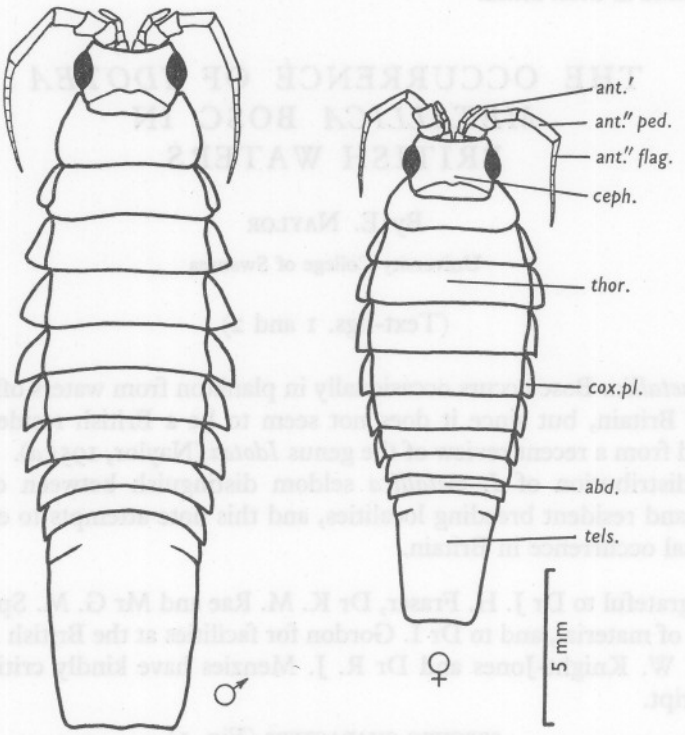

Fig. 1. Adult male and female *Idotea metallica*: *ant.'*, antennule; *ant."ped.*, antennal peduncle; *ant."flag.*, antennal flagellum; *ceph.*, cephalon; *thor.*, thorax; *cox.pl.*, coxal plate; *abd.*, abdomen; *tels.*, telson.

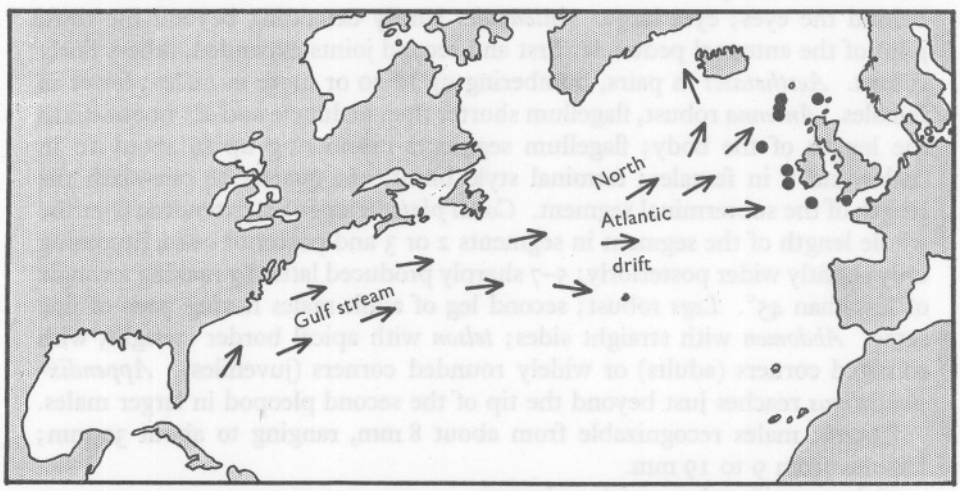

Fig. 2. The occurrence of *Idotea metallica* in British waters. (●, confirmed records of single or 'a few' specimens, from data in Table 1 and in Tattersall, 1906.)

GEOGRAPHICAL DISTRIBUTION

The distribution of *I. metallica* is described by Richardson (1905), Tattersall (1906, 1911), Stephenson (1915), Collinge (1917), Nierstrasz & Stekhoven (1930) and Cărăusu (1955). The species is known to breed in the Black Sea, Adriatic, Mediterranean and along the east coast of North America probably from Florida to Nova Scotia. In the north Atlantic, besides the occasional records from off the west coasts of Britain, there are rare records from off the coasts of Iceland and Greenland. There are also records from the west coast of North America, Patagonia, India and Australia. I have seen specimens from off the west coast of Britain (Table 1), off Plymouth (Marine Biological Association, 1957, p. 200), from the Atlantic, the east coast of North America, the Mediterranean, Montevideo and north-west Australia.

TABLE 1. BRITISH MATERIAL EXAMINED

Material	Location	Date	Source
2♀♀, 3♂♂	55° 49′ N., 16° 44′ W.	1875	British Museum ('Valorous' Expedition)
1 ♂	Near Labadie Bank	2. vii. 50	British Museum (Manihine Collection—as *I. pelagica*)
1 juv.	Bofin Is., C. Galway	1908	British Museum (Norman Collection)
1 juv.	60° 51′ N., 9° 06′ W.	15. vii. 49	Marine Laboratory, Torry, Aberdeen
1 ♂	61° 48′ N., 9° 06′ W.	11. ix. 50	Marine Laboratory, Torry, Aberdeen
1 ♂	59° 45′ N., 3° 00′ W.	7. ix. 54	Marine Laboratory, Torry, Aberdeen
1 ♀	59° 02′ N., 9° 08′ W.	9. vii. 55	Marine Laboratory, Torry, Aberdeen
1 juv.	2 miles E. of Eddystone	7. xi. 49	Marine Biological Laboratory, Plymouth (routine haul with 2 m stramin ring trawl)
1 ♂	49° 14′ N., 5° 11′ W.	2. v. 57	Plymouth Lab., vertical haul with coarse tow-net.

The species is variously recorded from amongst floating weed or timber, amongst floating colonies of *Lepas* (Tattersall, 1906, 1911), or even swimming freely at the surface (Menzies & Dow, 1957); and this surface living habit probably accounts for its wide distribution. Of the other species of *Idotea* in North Atlantic waters *I. baltica* is the only one which seems to live predominantly amongst drift weed (Naylor, 1955*b*), and this species is almost as widespread as *I. metallica* (Cărăusu, 1955). It seems likely that specimens of *I. metallica* reach British waters from the east coast of North America amongst floating debris carried by the North Atlantic Drift (Fig. 2), in rather the same manner as the grapsoid crab *Planes minutus* Leach (Bell, 1853) and several other organisms (Hardy, 1956) are thought to reach these waters. Some of Stebbing's *I. metallica* material in the British Museum is labelled 'Gulf

Stream'. British specimens belong to the form *typica* which is also found on the east coast of North America and in the western Mediterranean; a second form, *elongata*, is restricted to the Black Sea and eastern Mediterranean (Cărăusu, 1955). Though male and ovigerous female *I. metallica* have been occasionally recorded off Britain for the past hundred years or so, the species has not so far established itself.

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RECEPTOR ELEMENTS IN THE COXAL REGION OF DECAPODA CRUSTACEA

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(Plates I and II; Text-figs. 1–8)

Investigation of the proprioceptive organs in the coxal region of crustaceans, the results of which are here recorded, have been to a large extent stimulated by the evidence put forward by physiologists. The probability of the occurrence of such organs across the thoracico-coxal articulations was pointed out by Prof. S. Dijkgraaf in 1955, in a letter to one of the authors (J.S.A.). During systematic study of sensory organs in the legs of crustaceans, made in the autumn of 1956 by the present writers, it was found that in the region of all articulations there are one or two sensory organs consisting of a connective tissue strand and a row of bipolar nerve cells. A paper by Dijkgraaf (1956*a*) on the compensatory eye movements in *Palinurus vulgaris*, in which it is concluded that some proprioceptors in the coxal region must be present, gave us the incentive to persist in examination of this region in spite of considerable technical difficulties. The results obtained fully confirmed Dijkgraaf's view and the presence of receptor organs in several species has now been established. It has been found, moreover, that in the coxal region they are of several kinds differing in their structure and arrangement from any receptor known as yet. The description of them is given below.

The investigations were made chiefly with the lobster, *Homarus vulgaris*, and the crabs *Maia squinado* and *Carcinus maenas*. Some observations were made on *Palinurus vulgaris*, *Astacus astacus*, *Eupagurus bernhardus* and *Cancer pagurus*. Methylene blue was used for staining. Usually the tissues were immersed in a weak solution made by adding 10–15 drops of 0·5% methylene blue in distilled water to 100 ml. of sea water. The nerves of the receptor organs stain in every such preparation provided they are well exposed, but this is a condition not easily fulfilled, as the organs are in a position not at all convenient for observation. Another procedure consisted in injecting a stronger solution of the dye (one part of the 0·5% solution mixed

[1] The continuation of this work at the Plymouth Laboratory has been made possible by a grant from the Royal Society, for which the writer wishes to express his sincere gratitude.

with three to six parts of sea water) directly into the region to be examined, before the animal was dissected. The results were not so consistent as with the immersion method, but sometimes gave better staining of the more deeply situated elements. Some hints on the dissection of the animals are given below (pp. 615 and 622).

After staining the preparations were fixed in ammonium molybdate, washed in water, dehydrated in absolute alcohol and mounted in xylol dammar.

OBSERVATIONS

Homarus vulgaris

In the coxal region of *Homarus* the following nervous organs have been found: (1) receptors of the thoracico-coxal articulation; (2) receptor organ of the coxo-basipodite articulation; (3) a system of innervated elastic strands.

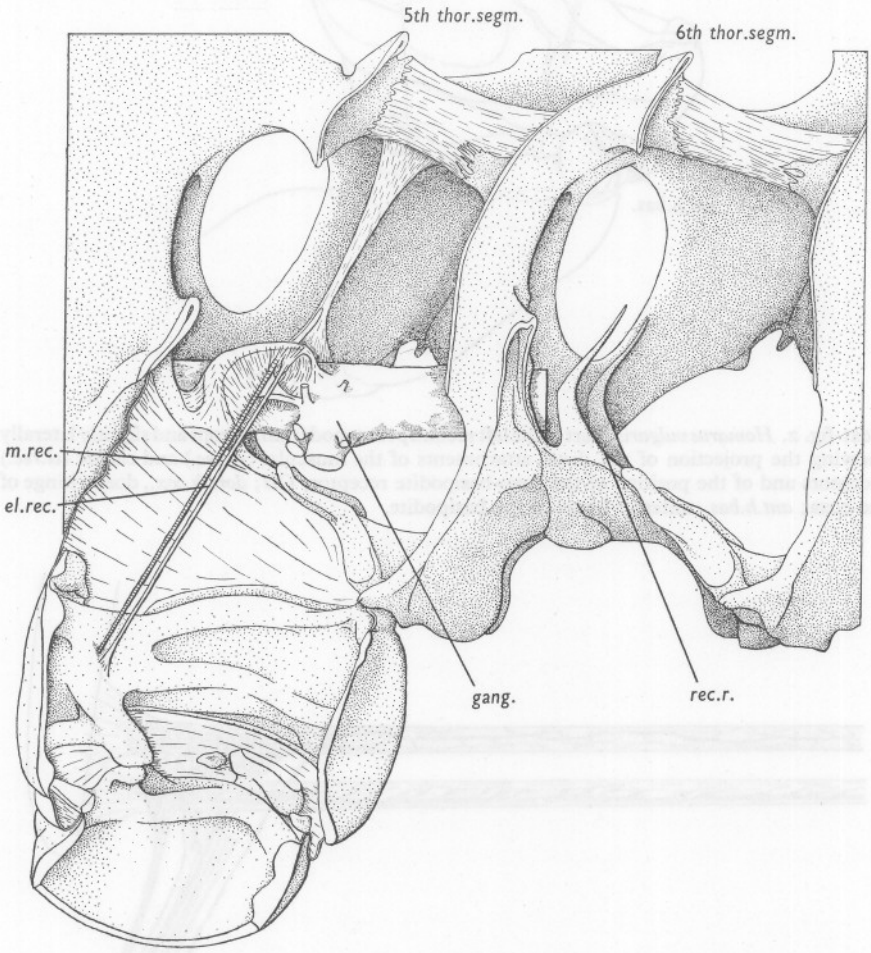
Receptor organs in the thoracico-coxal articulation

These receptors are present in all five peraeopods, in each of which there are two organs, a thin muscle with a special innervation and a strand of connective tissue with a number of sensory nerve cells. In the following description they will be termed the muscular and elastic receptors, respectively. These organs run side by side from their attachment on the endophragmal skeleton in the vicinity of the ganglion of the neural cord, to their insertion on the coxopodite (Text-fig. 1). In the 4th to 7th thoracic segments, that is those of the 1st to 4th peraeopods, the receptors originate on special projections of the endophragmal skeleton for which the term receptor rods is proposed. The rods arise close behind the ascending parts of the endosternites which, with their upper expansions, the mesophragms, form arches over the ganglionic cord and contribute to the walls of the sternal canal.

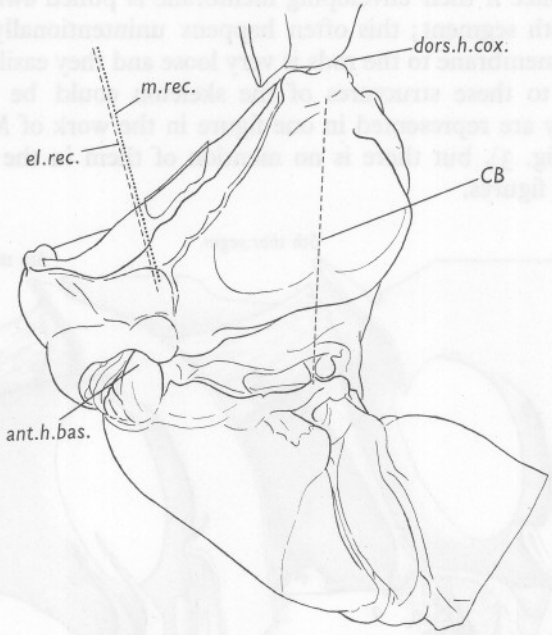
As seen in Text-fig. 1, the receptor rods are curved; their lower parts are directed upwards and forwards but then bend so that their upper parts are directed up with a backward inclination. Starting with a broader base at the border of the endosternites, they diminish in thickness and become slender and flexible. In the 4th thoracic segment the basal rigid portion is short, whereas the upper flexible part is long and has a strong backward inclination. In the following segments the rigid portions become gradually longer and the inclination of the upper parts less pronounced.

The receptor rods are enveloped by a connective tissue membrane which is continuous with the sheath of the neural cord. From the tips of the rods connective tissue strands extend upwards to the roof of the sternal canal where they blend with the membrane lining its walls; they help to keep the flexible parts of the rods straight in the position shown in Text-fig. 1 on the right side of the 5th segment, for when they are severed, as normally happens on dissection aimed at exposing the neural cord from the dorsal side, the rods assume the curved shape shown on the left side of the same segment. They

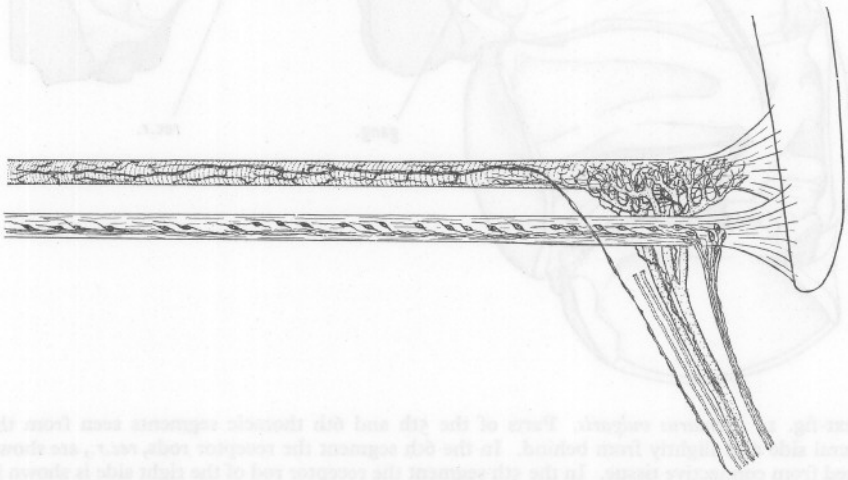
straighten at once if their enveloping membrane is pulled away, as in Text-fig. 1 in the 6th segment; this often happens unintentionally, as the connexion of the membrane to the rods is very loose and they easily slip out of it. No reference to these structures of the skeleton could be found in the literature; they are represented in one figure in the work of Milne Edwards (1851, Pl. 9, fig. 3), but there is no mention of them in the text or in the explanation of figures.



Text-fig. 1. *Homarus vulgaris*. Parts of the 5th and 6th thoracic segments seen from the lateral side and slightly from behind. In the 6th segment the receptor rods, *rec.r.*, are shown freed from connective tissue. In the 5th segment the receptor rod of the right side is shown in its natural position, kept straight by a connective tissue strand; that of the left side is shown curved as it usually looks when exposed from above. *gang.*, ganglion of the neural cord; *m.rec.*, *el.rec.*, muscular and elastic receptors of the second peraeopod.



Text-fig. 2. *Homarus vulgaris*. Part of the left second peraeopod from in front and slightly laterally showing the projection of the distal attachments of the muscular (*m.rec.*) and elastic (*el.rec.*) receptors and of the position of the coxo-basipodite receptor, *CB*; *dors.h.cox.*, dorsal hinge of the coxa; *ant.h.bas.*, anterior hinge of the basipodite.



Text-fig. 3. *Homarus vulgaris*. Semi-diagrammatic drawing showing proximal parts of the muscular receptor (above) and the elastic receptor (below) with associated nerve elements. Nerve fibres of the additional innervated strands are drawn in dotted lines (cf. Text-fig. 5).

The two receptors are attached to the flexible part of the rod, the elastic receptor to its tip, and the muscular one not far from it (Text-fig. 3). Near the attachment of the muscular receptor its myofibrils are replaced by connective tissue fibres which thus serve as a short tendon; these fibres and those of the elastic receptor spread fan-wise in passing into the membrane around the rod. The two receptors run from their origin to their insertion close together without having any connexions with each other. A nerve given off by a neighbouring trunk squeezes its way between the receptors, but otherwise has not any relation with either of them.[1]

The distal attachments of the two receptors are not at the same spot. The point of insertion of the muscle on the coxopodite can best be determined in relation to the anterior hinge of the basipodite. If an imaginary line parallel to the axis of the leg be drawn through this hinge, the point of insertion of the receptor muscle would be found a little laterally to this line, and nearer to the proximal than the distal border of the coxopodite. On the inner surface of the coxa there is often a small depression marking this spot, the position of which, projected on to the outside, is shown in Text-fig. 2. It should be noted that here the muscle tissue of the receptor extends up to the cuticle. The elastic receptor inserts a little farther distally and medially from this point; its fibres pass into the membranous tissue of the dermis and since they diverge and blend with this membrane their exact endings cannot be defined as well as that of the muscle.

In their proximal parts the two receptors are of nearly the same calibre, measuring in middle-sized specimens about 90 μ. The elastic receptor is of about the same thickness all along its length except at the very end, whereas the muscular one becomes gradually thicker distally.

In the 8th thoracic segment, where no special receptor rod is present, the two receptors originate on the pillar of the endosternite. Otherwise they exhibit the same features, a slight difference being that the elastic receptor is comparatively longer, so that its insertion is more distal.

Structure of the muscular receptor

The muscular receptor is composed of bundles of myofibrils with a small amount of connective tissue between them; stronger connective tissue fibres run longitudinally on its periphery. The cross-striation of the myofibrils is

[1] This nerve, which arises from a trunk distributing its branches in the coxopodite, is peculiar in that it consists of bipolar nerve cells and their processes. The cells, which differ in their staining properties from the sensory elements of the receptors, are scattered along the nerve with two accumulations, one near the ganglion and the other at the diaphragm of the fracture plane of the leg. It is on this diaphragm that the distal cell processes, or at least the majority of them, end. Similar ganglionated trunks have been observed in *Palinurus* and in crabs. The occurrence of a nerve of such unusual structure in this part of the body suggests that it might play some role in the regeneration of an autotomized limb. Another interesting feature observed is the presence of a plexus of fine nerve fibres in the sheaths of the main trunks arising from the ganglion.

somewhat finer than in the neighbouring ordinary muscles, being of a similar type to that of one of the muscles (RM 1) of the abdominal receptor organs (Alexandrowicz, 1951).

A broad bundle of nerve trunks extends between the ganglion and the muscular receptor (Text-fig. 3, Pl. I, figs. 1–4). Two sorts of nerve fibres can be distinguished: (1) motor fibres innervating the muscle tissue, and (2) fibres ending at the proximal end of the receptor in its tendinous region. The former run down alongside the muscle giving off branches which penetrate between the myofibril bundles, subdividing to supply the bundles abundantly up to the distal end of the muscle. This innervation has the same characteristic pattern as in all other muscle receptors, which is a great help in locating these organs among ordinary muscles.

The fibres ending in the tendinous region appear to be of two kinds. Most of them are given off by two stout main fibres which as they approach the receptor divide into a variable number of unusually thick branches; each of these breaks up into numerous arborizations which penetrate between the fibres of the tendon. Considering the thickness of the main trunks and the density of their ramifications it appears that the amount of nerve substance is here greater than that of connective tissue (Text-fig. 3; Pl. 1, figs. 3, 4). Some of the nerve branches extend into the region of the connective tissue which accompanies the muscle; one or two branches may be seen running some distance along the muscle, but there is no evidence of any anatomical relation between this sort of nerve and the muscle tissue itself.

The appearance and distribution of the thick trunks in the tendinous region of the muscular receptor is much like that of the dendritic processes of the nerve cells situated near the muscle components of the receptor organs of the extensor muscles of the thorax and abdomen. In the coxal receptors, however, no cells are present near the muscle. Consequently, the cells emitting these trunks must be situated in the ganglion of the neural cord, and, as there can be no reasonable doubt about the sensory nature of the fibres terminating in the tendon, they must be regarded as dendritic processes of receptor neurons.

The exact situation of the cell bodies of these neurons has not been established. The main difficulty is that the cells in the ganglion take a much longer time to stain with methylene blue than the fibres on the receptor, and when the latter are fading out their tracing up to their cells becomes uncertain. This obstacle might perhaps be more easily overcome in some other species.

Among the thick fibres reaching the receptor some others of a much finer calibre have been observed, which are presumably of a different kind. The number of these accessory fibres is uncertain, and as regards their destination it can only be said that they pass into the entanglements of the terminations of the thicker nerves.

Structure of the elastic receptor

The elastic receptor consists of longitudinally directed fibres forming a tube in which a row of nerve cells and their processes are included. The fibres have elastic properties, but must be made of some substance other than the elastin of vertebrate tissues, for they do not show a specific affinity to orcein or to Weigert's resorcin fuchsin. Stained with Azan they appear brilliant red, and so, in sections through their proximal attachments, stand out well against the blue-stained tissue of the membrane enveloping the receptor rods. They can be stained with iron haematoxylin and, more selectively, with Gomori's method. The latter proved useful for obtaining a contrasting coloration of these fibres and the muscle tissue. It should be noted that the fibres on the periphery of the receptor muscle, and in other organs described below, show the same staining reaction.

The nerve cells form a row which extends almost the whole length of the receptor. They are all bipolar in shape but vary in their dimensions. The largest are situated near the proximal end of the receptor, where some may lie outside the strand. The size of the cells diminishes towards the distal end of the strand; finally they become so small that often there is doubt whether a swelling of the nerve fibre is a cell or a bead-like artifact. It is for this reason, and also because not all the cells in the tube stain equally well, that their number is uncertain; it appears to exceed fifty, but may be considerably greater. The distal processes of the cells, which are often of a wavy appearance, are applied to the fibres of the strand and evidently become attached to them, as they all keep the same direction parallel to the axis of the organ. If the axis of a cell body is not in line with its process, the latter, in order to become adjusted to the longitudinal direction of the elastic fibres, turns at an angle which, at the proximal end of the cell row, can even be acute.

The distal processes can be followed for a distance of about two or three lengths of the cell bodies, at which point the methylene-blue coloration usually stops. In some preparations a finer prolongation beyond this point may be noticed, but it is doubtful whether it is to be regarded as consisting of nervous substance. The proximal cell processes, the axons, run as a bundle alongside the cell row, enclosed within the same tube of elastic fibres. As each cell adds its axon to it, this bundle becomes thicker proximally. Coming out of the receptor, the nerve bundle runs towards the ganglion near to that of the muscular receptor (Pl. I, fig. 2).

The receptor of the coxo-basipodite articulation

The receptor of the coxo-basipodite articulation belongs to the system of similar organs occurring in all joints of the peraeopods of decapods, from the coxopodite downwards. It consists, as do all others of this system, of a connective tissue strand and a row of bipolar nerve cells. It is situated on the

triangular plate of the coxopodite, the apex of which is the dorsal hinge articulating with the thoracic skeleton. The connective tissue fibres of the receptor originate near this hinge and run downwards to the rim of the basipodite near the insertion of the m. levator basipoditis, that is, at a point about halfway between the anterior and posterior hinges of the basipodite. The position of this point projected on to the outside of the leg is shown in Text-fig. 2.

The row of nerve cells begins at a certain distance from the proximal end of the organ; numerous nerve cells are accumulated here, many of them lying outside the strand (Pl. I, fig. 6). Farther distally they form a more regular row and become gradually smaller until they are minute. In the proximal accumulation both larger and smaller elements are present, but they are never as small as those at the distal end of the strand. The distal processes of the cells are applied to the fibres of the strand in the same way as in the elastic receptor previously described. In short, the structure of these organs is fundamentally the same, the difference in the appearance of the coxo-basipodite receptor being due only to features of secondary importance such as the less regular arrangement of its fibres and of the nerve cells.

Owing to the shape of the coxopodite its dorsal hinge is situated more proximally than the point of insertion of the two receptors of the thoracico-coxal articulation, which consequently extend distally beyond the point of origin of the coxo-basipodite receptor. This arrangement is shown in Text-figs. 2 and 4.

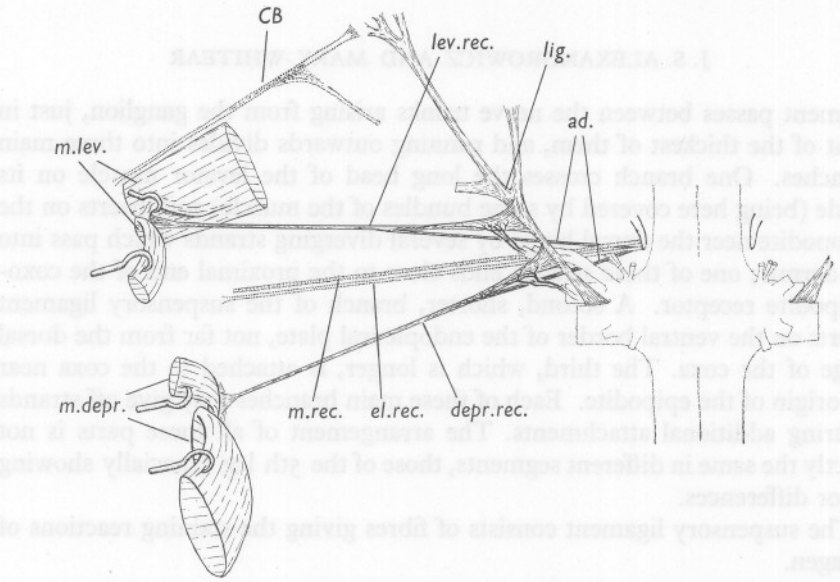
The system of innervated elastic strands

In this system which is regarded as constituting the receptor elements of m. levator basipoditis and m. depressor basipoditis the following parts can be distinguished: (1) a stronger non-innervated strand which will be referred to as suspensory ligament, (2) the main innervated strands, and (3) the additional innervated strands (Text-figs. 4 and 5).

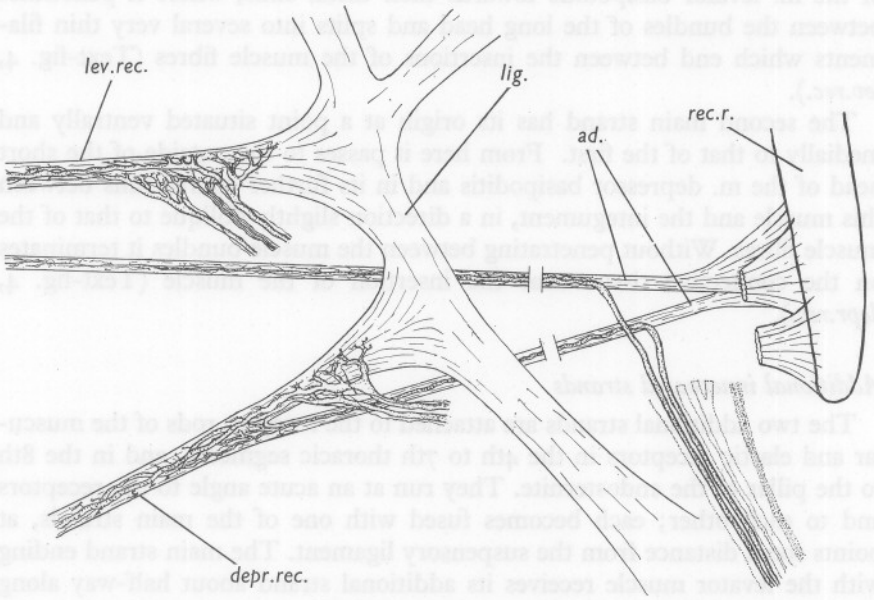
Suspensory ligament

The suspensory ligament is a flat band of connective tissue which extends from underneath the neural cord towards the dorsal hinge of the coxopodite, dividing into branches which insert on several points situated at various distances from the hinge. The mesial part of the ligament is continuous with a membrane lying under the ganglion, which has a firm attachment to the borders of the endosternite, at the place where the short heads of the m. levator and m. depressor basipoditis originate.[1] From this point the suspensory

[1] These portions of the named muscles are situated beneath the main nerve trunks arising from the ganglion. According to Schmidt (1915) they originate, in *Astacus*, at the proximal border of the coxopodite. In *Homarus* their line of attachment has been found more proximally, along the border of the endosternite. The nomenclature of these and other muscles mentioned in this paper is that of Schmidt, which has also been adopted by Cochran (1935) and by Balss (1941).



Text-fig. 4. *Homarus vulgaris*. Topography of the system of innervated elastic strands in relation to other receptors in the coxa. The elements represented as if lying in one plane are in the animal body arranged in a cylindrical fashion, those seen in the upper part of the figure being approximately opposite to those in the lower part; besides, the axis of the coxa is almost perpendicular to the horizontal plane of the neural cord. *lig.*, suspensory ligament; *lev.rec.*, *depr.rec.*, levator and depressor receptors; *m.rec.*, *el.rec.*, muscular and elastic receptors; *CB*, coxo-basipodite receptor; *m.lev.*, *m.depr.*, parts of the levator and depressor muscles; *ad.*, additional innervated strands.



Text-fig. 5. *Homarus vulgaris*. Nerves of the levator and depressor receptors; same lettering as above. Note the difference in the innervation of each strand. The muscular and elastic receptors are cut away near their origin at the receptor rod (*rec.r.*) (cf. Text-fig. 3).

ligament passes between the nerve trunks arising from the ganglion, just in front of the thickest of them, and running outwards divides into three main branches. One branch crosses the long head of the levator muscle on its inside (being here covered by some bundles of the muscle) and inserts on the coxopodite near the dorsal hinge by several diverging strands which pass into the dermis; one of these strands ends close to the proximal end of the coxo-basipodite receptor. A second, shorter, branch of the suspensory ligament inserts on the ventral border of the endopleural plate, not far from the dorsal hinge of the coxa. The third, which is longer, is attached to the coxa near the origin of the epipodite. Each of these main branches may give off strands securing additional attachments. The arrangement of all these parts is not exactly the same in different segments, those of the 5th leg especially showing major differences.

The suspensory ligament consists of fibres giving the staining reactions of collagen.

Main innervated strands

There are two main innervated strands connecting with the suspensory ligament by means of diverging fibres (Text-figs. 4, 5; Pl. II, fig. 7). One of the strands originates at a point on the ligament situated anteriorly to the thickest nerve trunk of the segment and runs between the short and long heads of the m. levator basipoditis towards their distal ends, where it penetrates between the bundles of the long head and splits into several very thin filaments which end between the insertions of the muscle fibres (Text-fig. 4, *lev.rec.*).

The second main strand has its origin at a point situated ventrally and medially to that of the first. From here it passes to the outside of the short head of the m. depressor basipoditis and in its further course runs between this muscle and the integument, in a direction slightly oblique to that of the muscle fibres. Without penetrating between the muscle bundles it terminates on the connective tissue near the insertion of the muscle (Text-fig. 4, *depr.rec.*).

Additional innervated strands

The two additional strands are attached to the receptor rods of the muscular and elastic receptors in the 4th to 7th thoracic segments, and in the 8th to the pillar of the endosternite. They run at an acute angle to the receptors and to each other; each becomes fused with one of the main strands, at points some distance from the suspensory ligament. The main strand ending with the levator muscle receives its additional strand about half-way along its length, but the second additional strand is shorter and reaches the main depressor strand nearer the ligament (Text-fig. 4).

The innervated strands consist of fibres of elastic properties, for they can be stretched to about twice their length and return to the original condition when the extending force is relaxed. Evidently they are made of the same substance as the fibres of the elastic receptor. In sections through the region of their attachment to the ligament, stained with Azan, the passage of the thicker red fibres of the elastic strands into the blue-stained finer elements of the ligament can be well observed.

Nerves of the innervated strands

The arrangement of the nerve fibres in the innervated strands shows particular features in each of them (Text-fig. 5).

The strand inserting at the depressor muscle, which for short is termed the depressor receptor, receives three stout fibres. Two of them come from the nerve trunk arising next in front of the thickest trunk of the leg. Along with these stout fibres run a few others, of extremely fine calibre, the number of which is difficult to determine. A third stout fibre, but not so thick as the two others, travels in the additional strand. It comes out of the ganglion with the bundle of nerves of the muscular receptor, penetrates into the additional strand and reaches the main strand near the other nerves and distally to them. All three fibres break up into numerous branches, their terminations supplying the strand in a good part of its length (Pl. II, fig. 8).

The other main strand, the levator receptor, receives: (1) two stout fibres, associated with very thin ones as in the other strand; (2) a bundle of several fibres, probably six, which are much thinner, but not so thin as those accompanying the two stout ones. All these fibres are given off by the nerve trunk which originates from the ganglion with a common root with that containing the nerves to the depressor strand, but from a more dorsal division of it which carries motor and sensory nerves of the coxopodite.

The additional strand of the levator receptor receives its nerve fibre from the ganglion in the same bundle as that of the other additional strand (Text-fig. 5). Penetrating into the strand, this nerve gives off many ramifications ending on the elastic fibres (Pl. I, fig. 5); distally the nerve elements become gradually finer and less distinguishable. If some of them pass on to the strand they can be only very thin ones.

To sum up: both the depressor and levator receptors have a similar nerve supply of two stout fibres accompanied by very fine ones. They differ in that the depressor receptor gets a third thick fibre brought by its additional strand, whereas the levator receptor receives a bundle of thinner fibres from the same nerve trunk in which its two thick fibres are travelling. As to the additional strands, one appears only to carry a third fibre to the depressor receptor, whilst the second is an organ in its own right with nerve terminations on its elastic components.

As regards the origin of the nerve fibres it has been noticed that the two thick fibres of the depressor strand, when followed in the proximal direction, are found at the ganglion close to the bundle containing the fibres of the muscular receptor and those of the additional strands. It is possible that the nerves of the levator strand have a similar origin, but this could not be observed directly with sufficient certainty.

Although so many nerve elements are mentioned above, the description may not yet be complete. In some cases, for instance, thin fibres have been noticed which possibly enter the additional strands with the thick ones, but they were not distinct enough to be followed.

The relation of the nerve elements to the strands is interesting in several points. One is the calibre of the nerve fibres, which is larger than is ever met with in nerves supplying a muscle bundle of comparable dimensions. Another is the tendency of even the thick nerves to penetrate between the elastic fibres of the strands and to occupy an axial position; this feature can best be observed in transverse sections. In the main strands there is a somewhat irregular intermingling of various elements, but in the additional levator strand it can clearly be seen that the elastic fibres form a tube in which the nerve fibre and its branches are enclosed.

The branches of the nerve fibres in the main strands are of various lengths and thicknesses. In the region where the main fibres enter the strand they give off many thick short branches, the ramifications of which end after a short course (Pl. II, fig. 8). The picture of their terminations in methylene-blue preparations is hazy, but from what can be seen it can be inferred that the area of distribution of each branch is small. As, however, these branches are numerous it looks as if nerve endings were present at every point of the elastic fibres, as far as the nerves reach. The thin short branches of the main trunks behave like the secondary branches of the thick ones. The long branches run down the strand and give off in their turn shorter ramifications ending near their origins and longer ones continuing the distal course. It is not quite clear how far the nerves extend in each of the strands, but it may be assumed that they occupy at least the half of their length. It has not been possible to determine whether or not each of the main fibres sends its branches as far as the others. The best preparations show such an abundance of intermingling nerves that the tracing of individual elements is uncertain.

As there are no cells between the endings of these fibres and the ganglion it is evident that the cell bodies of all these neurons lie within the central nervous system. Since there can hardly be any doubt that the innervated strands having relations with muscles are receptors of some kind, their nerves, at least the majority of them, have to be regarded as afferent fibres, being elongated dendritic processes of sensory nerve cells. The nature of the thin fibres is an open question as other interpretations are possible.

Hints on dissection

All parts of the animal body should be cut away leaving only the ventral part of the thorax with the coxopodites and parts of the basipodites. The sternal canal should be opened from above, beginning at the posterior segments, and the parts of the endophragmal skeleton cut down to a level slightly above the dorsal hinge on the coxa. The receptor rods can now be located more or less easily depending on the size of the specimen; they appear curved as shown in Text-fig. 1 if the membrane enveloping them has not been damaged. To expose the muscular and the elastic receptors in their whole length it is necessary to remove a good part of the chitinous case and of the muscles of the coxa, while it is borne in mind that the receptors run almost vertically from their origin on the rods towards the anterior hinge of the basipodite; the lines of incisions should therefore run down the coxa one a little in front of its dorsal hinge, and the other on the opposite side of the leg. It is better not to try to expose the receptors at once, but to put the preparation into the staining solution, and to continue the dissection after the proximal parts of the receptors become visible. The staining is often impeded by clots of blood adhering to the receptors and other organs; the clots can be removed with a forceps and a fine scalpel, but to do this without spoiling the organs is a delicate operation. Two ways of proceeding further can be followed. The preparations can either be left in the staining solution and then fixed without removing the chitin, which goes off easily later after fixation in ammonium molybdate, or the soft parts can be detached from the chitinous cuticle at this earlier stage. In the latter case the receptor rods must be cut through first, and then all soft parts cautiously separated from the cuticle, while the muscle tendons should be cut through at their bases. Then the preparation can be spread and pinned on to a paraffin plate. This method has the advantage of permitting better observation of the staining, but the tissues are easily damaged.

To obtain preparations with the suspensory ligament and the coxo-basipodite receptor, the lateral line of incision must be made behind the dorsal hinge of the coxa. It is possible thus to get all receptor organs on one slide. For study of innervated strands it is preferable to remove the chitin during the staining because otherwise it is difficult to spot the strands and expose them in the right way.

The only certain way of finding the suspensory ligament is by tracing the innervated strands up to their origin on this ligament, but the strands cannot be practically identified until their nerves have stained. The separation of the ligament from the arteries, nerves, connective tissue strands and blood clots is difficult, and can best be performed after the preparations have been transferred into xylol.

BRACHYURA

Proprioceptors originating at the endophragmal skeleton and ending on the coxopodites have been found in all the crabs investigated, but their arrangement is not the same as in *Homarus*, the important difference being that the elastic receptor appears to be missing. The innervated strands are present in *Cancer* and in *Carcinus*, though forming a simpler system than that of the lobster; in *Maia* they could not be found as separate organs.

Muscular receptor

The muscular receptors are present in all five peraeopod segments, but only in that of the chela is there a special chitinous projection to which the

muscle is attached and for which the term receptor rod may appropriately be used. No mention of this part of the skeleton could be found in the literature, so it will be described here.

The receptor rod is a long thin projection from that plate which limits the 4th thoracic segment anteriorly, and which is called the second endopleurite by Drach (1939).[1] The receptor rod arises from the ventral border of this plate, laterally to the mid-point of the border, and projects at an acute angle inwards and backwards, ending at approximately the same distance from the mid-line of the body as the inner corner of the endopleurite plate (Drach's apophyse interne) (Text-fig. 6, *rec.r.*). The length of the rod in examples of the three species was as follows:

	Length and breadth of carapace (cm)	Length of rod (mm)
Maia	14 × 12	11·5
Cancer	10 × 15	17
Carcinus	5·5 × 7	10

In *Maia* the rod is comparatively shorter; it arises at a less acute angle and its tip is situated more behind and farther away from the corner of the endopleural plate than in the other species. The tip of the receptor rod is attached by feeble connective tissue to the ligament extending from this corner to the next-following arthrophragm. The point of attachment lies about half-way along this ligament (Text-fig. 6).

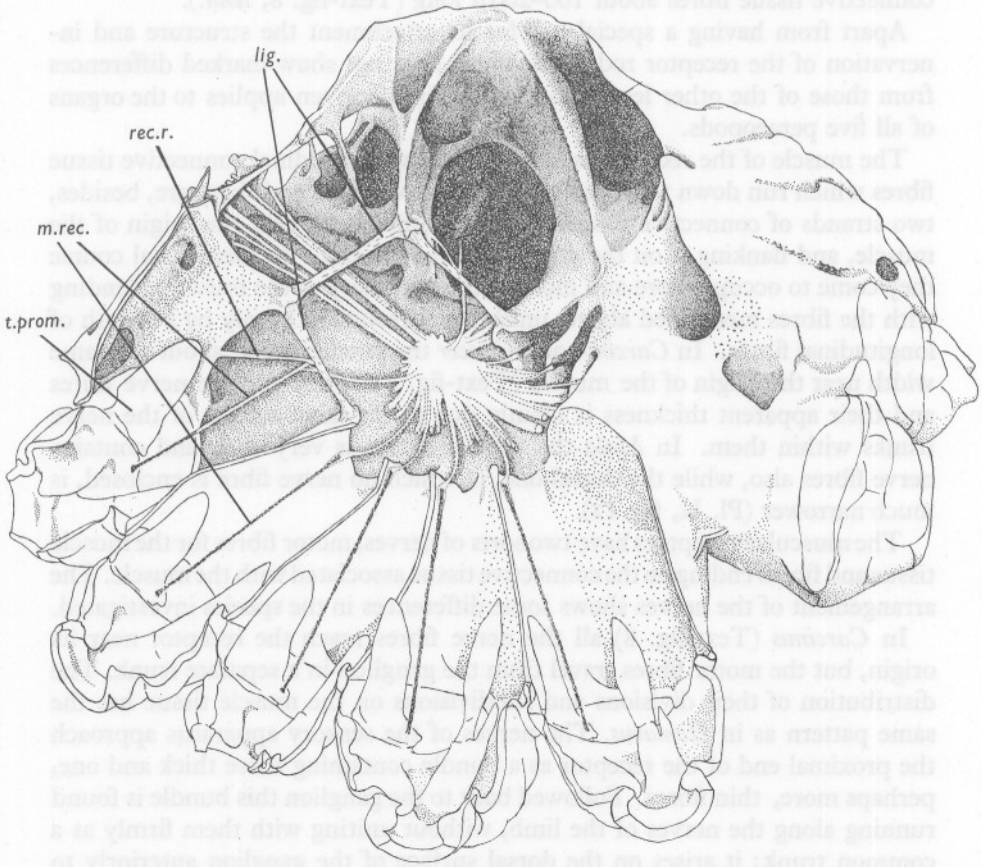
In *Cancer* and in *Carcinus* the rods project at a more acute angle from the edges of the endopleural plates, close beneath them. As the endopleural plates and the receptor rods are prolonged farther towards the mid-line of the body than in *Maia*, only a small distance separates the ends of the rods of the opposite sides. The ligamentous connexions between the corners of the endopleural plates of the two sides and between these plates and the endosternites are stronger than in *Maia*; in *Carcinus* there are also short muscles here.

In *Maia* the receptor rod is thickened at its terminal part and is slightly bent (Pl. II, fig. 10). In *Carcinus* it may be almost straight as in *Maia*, or there may be a more pronounced bend at the tip (Pl. II, fig. 9). In *Cancer* the rod curves and tapers into a point. In all these crabs the muscular receptor originates near the tip of the rod and runs at an acute angle to it to

[1] Pearson, in his monograph of *Cancer* (1908) designates this plate as the endosternite of the 8th somite, that is, of the 4th thoracic segment. Drach's denomination has been adopted here, although without knowledge of the development of this arthrophragm there is no certainty that the lower part of the plate in question is not derived from the lateral part of the sternum. The number (2nd) of this endopleurite is due to the fact, known since the work of Milne Edwards (1834, 1851), that each endopleurite fuses with the endosternite of the following segment and not with that of its own. To be exact, they do not fuse directly but join to form a horizontal plate (lame de jonction of Drach). The ventral border of the 2nd endopleurite plate is free since the other part of the arthrophragm, an endosternite plate ascending from the sternum and fusing with the endopleurite plate, is here missing.

insert on the rim of the coxa, near the ventral border of the tendon of the m. promotor coxopoditis; in its course it passes on the ventral side of this muscle, between it and the m. depressor basipoditis.

In the 5th to 8th thoracic segments, in which no receptor rods are present, the muscular receptors originate directly on the posterior surface of the endosternites close to their mesial border at a level higher than that of



Text-fig. 6. *Maia squinado*. Endophragmal skeleton with parts of the peraeopods dissected on the left side to show the muscular receptors (*m.rec.*). *rec.r.*, receptor rod; *t.prom.*, tendon of m. promotor coxopoditis; *lig.*, ligaments of the 2nd endopleurite.

the dorsal surface of the ganglionic mass (Text-fig. 6). From this point of attachment the receptor in each segment runs between the promotor and depressor muscles on the posterior surface of the endosternite, being separated from the chitin of this plate only by a thin layer of the fibres of the m. promotor (Text-fig. 7).

The distal attachments of the receptors in the 2nd to 5th peraeopods are

not exactly at the same points in various species. In *Cancer* they insert, as in the chela, on the rim of the coxa close to the base of the promotor tendon, but in *Maia* and *Carcinus* they insert in the base of the tendon itself. The arrangement of the receptors in *Maia* is shown in Text-fig. 6. At the distal insertion the muscle tissue extends up to the chitin, but at the proximal end of the receptor its myofibril bundles are fixed to the chitin by a short tendon of connective tissue fibres about 100–200 μ long (Text-fig. 8, *tend.*).

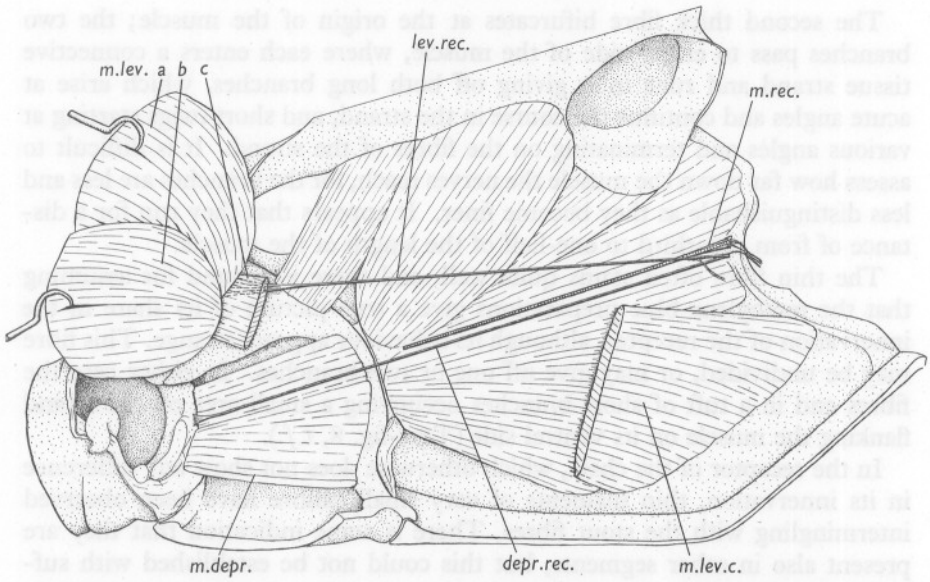
Apart from having a special rod for its attachment the structure and innervation of the receptor rod of the chela does not show marked differences from those of the other legs, and the description given applies to the organs of all five peraeopods.

The muscle of the receptor is surrounded by longitudinal connective tissue fibres which run down to its insertion. At its proximal end there are, besides, two strands of connective tissue attached to the chitin near the origin of the muscle, and flanking it on the dorsal and ventral side. In their distal course they come to occupy more and more of the periphery of the muscle, blending with the fibres mentioned above, until it is surrounded evenly by a sheath of longitudinal fibres. In *Carcinus* and *Cancer* the strands are of about the same width near the origin of the muscle (Text-fig. 8). They enclose nerve fibres and their apparent thickness is mainly due to the large calibre of the nerve trunks within them. In *Maia* the ventral strand is very wide and contains nerve fibres also, while the dorsal one, in which no nerve fibre is enclosed, is much narrower (Pl. II, fig. 12).

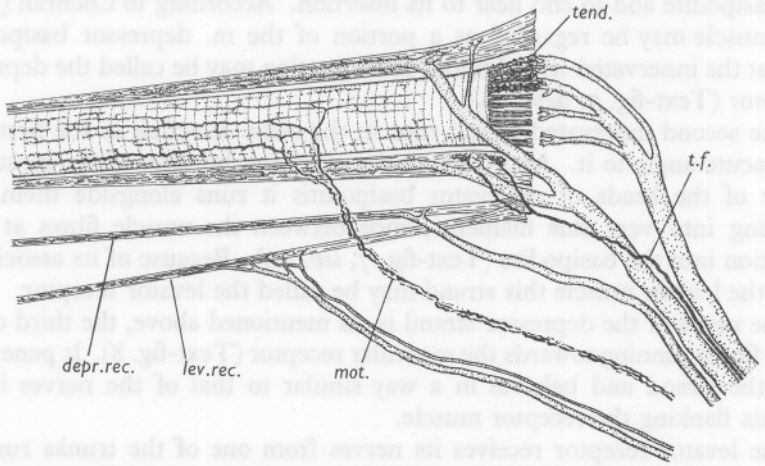
The muscular receptors have two sorts of nerves, motor fibres for the muscle tissue and fibres ending on the connective tissue associated with the muscle. The arrangement of the nerves shows some differences in the species investigated.

In *Carcinus* (Text-fig. 8) all the nerve fibres reach the receptor near its origin, but the motor fibres travel from the ganglion in a separate trunk. The distribution of their divisions and subdivisions on the muscle tissue has the same pattern as in *Homarus*. The nerves of the sensory apparatus approach the proximal end of the receptor as a bundle containing three thick and one, perhaps more, thin fibres. Followed back to the ganglion this bundle is found running along the nerves of the limb, without uniting with them firmly as a common trunk; it arises on the dorsal surface of the ganglion anteriorly to the other nerves of the same segment. In the 4th segment it has to travel upwards to reach the muscle arising on the receptor rod.

One of the three thick fibres approaches the receptor directly opposite its end and breaks up into several stout branches which pass on to the short tendon of the muscle and supply it with dense ramifications. In methylene-blue preparations little can be seen of their finest divisions, but it can safely be assumed that they end among the elements of the tendon. One or two nerve branches can sometimes be seen extending a little farther, between the bundles of myofibrils, but no relation to the latter has been noticed.



Text-fig. 7. *Carcinus maenas*. Posterior view of the endosternite separating the 5th and the 6th thoracic segments of the left side with parts of the coxa and the basipodite of the 3rd peraeopod. *m.rec.*, muscular receptor; *lev.rec.*, *depr.rec.*, levator and depressor receptors; *m.depr.*, short head of m. depressor basipoditis; *m.lev. a*, *b*, *c*, portions of m. levator basipoditis. The muscle bundles, the middle part of which is cut away (*m.lev.c*), originate, as shown in the figure, on the ventral part of the endosternite plate; they can be regarded as a branch of the strong head of the levator muscle (*m.lev.b*) which originates on the anterior surface of the endosternite of the next following segment (not seen in the figure).



Text-fig. 8. *Carcinus maenas*. Proximal parts of the thoracico-coxal receptors. The semi-diagrammatic representation applies to each of the 4th to 8th thoracic segments of the left side. The receptor muscle is seen flanked by two strands of connective tissue into which penetrate branches of a thick nerve fibre. *tend.*, tendon of the receptor muscle; branches of the nerve fibre ending on it have been partly cut to show the fibres of the tendon drawn somewhat diagrammatically. *t.f.*, thin fibre ending on the ventral strand; *mot.*, motor nerves of the receptor muscle. *lev.rec.*, *depr.rec.*, levator and depressor receptors with their innervation. For the sake of clarity the levator depressor is drawn in a position different from that in Text-fig. 7.

The second thick fibre bifurcates at the origin of the muscle; the two branches pass to either side of the muscle, where each enters a connective tissue strand and runs in it giving off both long branches, which arise at acute angles and continue the course in the strand, and short twigs starting at various angles and terminating on the fibres of the strand. It is difficult to assess how far down the muscle the nerves reach, for the branches are less and less distinguishable as they become finer. It appears that they run for a distance of from one-third to one-half of the length of the muscle.

The thin fibre often stains quite well, and there is ground for assuming that the methylene-blue preparations give a true picture of its share in the innervation of the receptor, although its behaviour appears strange. This fibre may be undivided, or may give off one or two branches. In either case the fibres end in a tuft of short branches occupying a small area on the strand flanking the muscle on its ventral side (Text-fig. 8, *t.f.*).

In the receptor of the chela, which otherwise does not show any difference in its innervation, thin filaments of very small calibre have been observed intermingling with the stout fibres. There is some indication that they are present also in other segments, but this could not be established with sufficient certainty.

The third of the thick fibres approaching the receptor is the element of an innervated elastic strand. There are two such strands, both originating near to the proximal end of the receptor (Text-fig. 8, Pl. II, fig. 11). One of them runs near and parallel to the receptor muscle, but extends farther, to become applied to the bundles of a short muscle stretching between the coxa and the basipodite and to end near to its insertion. According to Cochran (1935) this muscle may be regarded as a portion of the m. depressor basipoditis, so that the innervated strand under consideration may be called the depressor receptor (Text-fig. 7, *depr.rec.*).

The second innervated strand runs in the same direction as the first, at a very acute angle to it. Approaching the overlying bundles of the most posterior of the heads of m. levator basipoditis it runs alongside them and, splitting into very fine filaments, ends between the muscle fibres at their insertion into the basipodite (Text-fig. 7, *lev.rec.*). Because of its association with the levator muscle this strand may be called the levator receptor.

The nerve of the depressor strand is, as mentioned above, the third of the thick fibres running towards the muscular receptor (Text-fig. 8). It penetrates into the strand and behaves in a way similar to that of the nerves in the strands flanking the receptor muscle.

The levator receptor receives its nerves from one of the trunks running from the ganglion to the limbs. Two comparatively thick fibres reach the strand at a certain distance from its origin and give off branches which divide in their turn (Text-fig. 8, Pl. II, fig. 11).

Compared with the elements of the system of innervated strands in *Homarus*

those in *Carcinus* show a simpler arrangement as there are two strands only, and the suspensory ligament is missing. As regards their innervation, however, it would be premature to draw a similar conclusion for the technical difficulties are such that other elements may yet be detected. It is also understandable that no details can be given about the behaviour of the various nerve elements in these strands, the dimensions of which may go down to 10 μ and in the thickest parts are in the range of 50–60 μ.

In the 4th thoracic segment the innervated strands originate on the receptor rods close to the attachment of the muscle and in all probability their distal insertions are the same as in other segments, but the observations have been hampered by the difficulty of obtaining preparations with these organs intact along their whole length.

In *Cancer* the arrangement of various receptor elements is similar to that in *Carcinus*. The innervated strands are also present. *Cancer* was less thoroughly examined than *Carcinus*, the latter being, despite its smaller size, more suitable for dissection.

In *Maia* the independence of the motor and sensory nerves of the muscular receptor is particularly manifest as the motor fibres run with the nerves of the promotor and depressor muscles, and reach the receptor at a distance from its proximal end. Two fibres at least supply the receptor, and it is interesting to note that one of these is a branch of a fibre which also supplies the promotor muscle. Reaching the receptor the motor fibres bifurcate and their branches run in opposite directions, ramifying in the usual way.

As in *Carcinus*, three thick and at least one thin fibre approach the receptor muscle at its origin. One of the thick fibres is destined for the short tendon and its situation is the same as previously described (Pl. II, fig. 12). The two others penetrate into the connective tissue strand flanking the muscle on its ventral side and branch in this strand in the same manner as in *Carcinus*.

The thin fibre runs together with the thick ones. It gives off short branches, all of which appear to end on the connective tissue strand at its proximal end. This fibre did not stain so well in *Maia* as in *Carcinus* and the picture of its course was not so clear.

In the receptor of the chela the arrangement of the three thick fibres is basically the same, although at first sight it may seem to be different (Pl. II, fig. 10). This is due to the fact that the two thick fibres penetrating the connective tissue strand can split into branches before reaching the receptor, and these branches enter the strand at a distance one from another. The very thin fibres running with the thick ones occur in *Maia*, too. They appear to associate with the thick fibre which supplies the short tendon of the muscle.

The innervated strands have not been found in *Maia*. It is, of course, possible that if they are in a different position they might easily be overlooked. However, the occurrence in *Maia* of the same number of thick nerve fibres, and the fact that one of them supplies the depressor receptor in *Carcinus*, gives

probability to the supposition that the system of innervated strands in *Maia* has been reduced and one of its elements has become associated with the muscular receptor. A comparative study of these organs in various species of Brachyura could possibly throw some light on this problem.

In all crabs investigated a coxo-basipodite receptor, with bipolar nerve cells, is present. Owing to the different shape of the coxa in crabs, the position of this receptor is relatively more distal than in *Homarus* and does not come into the picture in preparations of the muscular receptor.

Hints on dissection

With crabs the main part of the dissection aimed at exposing the receptors consists in carefully cleaning away the liver; particular caution is necessary with regard to the organ in the 4th thoracic segment where it is attached to the receptor rod.

In *Maia* this rod can be found more easily from the dorsal side. On removing the liver piece by piece one finds a flaccid ligament connecting the endopleurites of the opposite sides (Text-fig. 6, *lig.*) and this guides one to the inner corners of these plates. This region must be cleaned with care in order not to damage the other ligament running backwards from the corner of the endopleurite plate on which the tip of the receptor rod is attached.

In *Carcinus* and *Cancer* it is preferable to look for the receptor rod from below in order to find its origin on the ventral border of the 2nd endopleurite. To make the access easier, parts of the sternum should be removed as far as possible, and the liver strands taken out. It must be realized that the receptor rod is very fragile and can be broken at a slight pull of the forceps. Its origin can be found on the border of the endopleurite plate at a point more laterally than in *Maia*. On moving the rod with fine forceps one can locate the point of its tip at which the receptor muscle is attached. The preparations of the rods with the receptors can be made by cutting out the rods with all the adjacent parts, i.e. muscles, nerves, remains of the liver, etc. The whole is put into methylene-blue solution and the tissues sorted out under a dissecting microscope. The rod with the receptor can be thus isolated and attached with fine pins to the paraffin plate on which it remains until the preparation is to be put into xylol.

The receptors in other segments can be stained *in situ*, but then only their proximal parts on the median borders of the endosternites can be made visible. For detailed study each endosternite should be cut out with parts of the coxa and the basipodite as in the preparation shown in Text-fig. 7. This is a simple matter, but there is one vulnerable point, viz. the connexion of the nerves with the receptor, and the utmost care must be taken in avoiding any pulling on these nerves. Therefore, before cutting through the sternites, it is important to sever the nerves, vessels and each strand which might tear the nerves. After the endosternite plate has been cut out it should be pinned on to a paraffin plate with its posterior surface upwards. The muscle bundles covering the receptor should be pulled aside and pinned down, but this must be done progressively. Little practice is necessary to recognize the receptor if only a small portion of it becomes stained; it can then be safely freed from overlying tissues. In every case of doubt about its further course the preparations should be put back into staining solution and examined after a while.

The innervated strand of the depressor receptor in *Carcinus* and *Cancer*, running parallel to the receptor muscle, can be found without difficulty, provided one does not cut the tissues around this muscle too freely at the beginning of the staining, because the fine innervated strand cannot then be distinguished and may be torn away.

The levator receptor can be found by pulling cautiously aside the bundles of the levator muscle. Here again it is advisable to do this by steps, proceeding each time as far as the course of the strand can be traced and leaving the preparation in the staining solution until it is discernible.

Some observations on other species

A few observations were made with *Astacus astacus*, *Palinurus vulgaris* and *Eupagurus bernhardus*; in each of these the receptor organs in the coxal region have been found. Although they have not been investigated in detail, some of their features are worth mentioning since they show that the anatomy of the receptors varies in different species.

In *Astacus* the general arrangement of the receptors is similar to that of *Homarus*. Receptor rods are present in the 4th to 8th thoracic segments; they arise from the bases of the pillars of the endosternites; in *Astacus*, as the sternites of these segments become progressively broader posteriorly the rods stand farther away from the nerve cord; there is no rigid connexion between the sternites of the 7th and 8th segments, and here the rods arise, not from the hard part of the endosternite, but from the arthrodial membrane behind it. As far as they have been determined, the structure and innervation of the muscular receptor, the elastic receptor and the coxo-basipodite receptor, resemble those of *Homarus*. Because of the more lateral position of the rods in the hinder segments, the nerves of the receptors are correspondingly longer in these segments. The suspensory ligament and elastic strands are again similar to those of the lobster, but with differences in the details of the arrangement and innervation of the elastic strands.

In *Palinurus* the receptor rods are present in all five thoracic segments, but their disposition in conformity with differences in structure of the endophragmal skeleton is not the same as in *Homarus*. It is only in the 4th thoracic segment that the endosternites arise near the median line of the body and have the receptor rods originating at their bases; in this segment *Palinurus* has long rods extending upwards and backwards as far as the roof of the sternal canal. In the 5th to 8th thoracic segments, in which the basal parts of the endosternites are situated at a considerable distance from the mid-line of the body, the receptor rods project from the upper parts of the endosternites, not far from the horizontal plates of the mesophragms; they originate on the posterior surface of the endosternite plates near their inner border, and are directed inwards. In all segments the rods are thin and very flexible.

The muscular receptor attaches to the rod, but the elastic receptor appears to be missing. At any rate it is not present in the immediate vicinity of the muscular one. A coxo-basipodite receptor is present. There are some strands of connective tissue which presumably correspond to the innervated elastic strands of *Homarus*, but their extension and connexions have not been sufficiently determined. *Palinurus* proved a difficult object for this kind of investigation, for in the specimens dissected there was soft yellowish tissue filling

up the sternal canal and enveloping the outgoing nerve trunks; it made it difficult to find the receptors and prevented the stain penetrating.

In *Eupagurus bernhardus* the receptor rods are missing, so that the muscular receptors, the only ones which have been found, arise directly on the endosternites. They insert near the rim of the coxa.

DISCUSSION

The receptor organs described are remarkable in many respects. Not only are several of them present near to one another, but their structures show essential differences within the Decapoda. Thus in *Homarus* there are (1) an elastic strand with numerous nerve cells attached to it, (2) a thin muscle with a complex innervation, and (3) several elastic strands with numerous nerve fibres ending on them. In the Brachyura the organs under (1) seem to be missing in the thoracico-coxal articulation, while the muscular receptor has a more complicated structure. Both in the Brachyura and the Astacura different species show variations in the detailed arrangements of the receptors.

Several of these organs show an unusual feature in that the cell body of the receptor neuron is not situated near its peripheric endings. It is understandable that doubts may arise as to whether the observations were correct as to this point. As a rule, when the search for some nervous element has been unsuccessful, it is advisable, instead of stating that they are missing, to say that they have not been found, and, admittedly, the observations recorded in the present paper may be liable to amendments in the future. In this case, however, the histological evidence can be interpreted in only one sense, which is that the fibres terminating on the tendinous parts of the muscular receptors and on the innervated elastic strands are emitted by neurons of which the cell bodies are situated in the central nervous system. As these fibres are obviously afferent in nature the conclusion must be drawn that in the Crustacea sensory neurons can develop, as in vertebrates, a long process which behaves functionally as a dendrite, but which otherwise may be indistinguishable from an axon. In the organs under consideration various stages in the elongation of the dendrites can be observed. In the muscular receptors in *Homarus* the fibres of the sensory neurons differ in appearance from ordinary nerves; as they do not extend far from the ganglion there is not much difference in shape and dimensions between them and those of the receptor organs in the dorsal muscles. In the 8th thoracic segment of *Homarus*, where the receptor organs originate at a greater distance from the neural cord, the dendrites of their sensory neurons are elongated and look like ordinary nerve fibres. The same is true of their aspect in crabs, and in the hinder thoracic segments in *Astacus*. The nerves of the innervated elastic strands have various dispositions, some, such as those of the additional strands in *Homarus* and of the depressor receptor in *Carcinus*, associate with the nerve fibres of the muscular receptor,

while others travel in the nerve trunks of the leg, and, until their branches are seen to reach the strands, are practically indistinguishable among the ordinary fibres.

The structure of the muscular receptor in *Homarus* resembles in certain features that of the receptor organs in the dorsal muscles of the same animal. The aspect of the muscle and the pattern of its motor innervation appear almost identical. The connexion of the muscle and the receptor neurons is effected on the same principle, that is, the dendrites of the latter end on the connective tissue linked with the muscle but not on the muscular tissue itself. On the other hand there are important differences. One, the absence of the peripheral nerve-cell bodies has just been discussed; the other is in the position of the sensory terminations, which is at the end of the receptor muscle in the leg, but always at some distance from the attachments of the receptors in the dorsal muscles. A further difference is the presence in the coxal receptors of two sensory neurons (or even three, as in *Maia*) ending at the same muscle. The question arises whether there is evidence for considering them to have various functions. Their aspect in *Homarus* does not provide support for such a view. In crabs, however, they exhibit such differentiation in the disposition of their endings that the assumption of their having different natures has a high degree of probability.

The elastic receptor of the thoracico-coxal joint in *Homarus* and *Astacus* is so like that of the coxo-basipodite joint and the other receptors farther down the leg, that it must be considered as belonging to the same series. It is strange that it should be well developed and situated so near the muscular receptor in these animals and yet be, apparently, absent in the other species investigated.

As regards the innervated elastic strands, their very existence, in the vicinity of other receptor organs, is puzzling, apart from their structure. The ending of thick nerve fibres in elastic strands is a most unusual feature. Moreover, the levator and depressor systems receive different sets of nerves, of various kinds. It is difficult to assess how much value may be attached to these differences, but it is reasonable to assume that each anatomical difference is likely to have a functional meaning and sets a problem to be solved.

The suspensory ligament has been described as a component of the system of innervated strands and it certainly plays an important role in it. It is, however, not evident whether this is its only function. Being made of connective tissue it can only serve to offer resistance to some pulling force, but why this should be necessary in this region, apart from giving a point of attachment to the innervated strands, it is difficult to say. To the conjecture that it might give support to the ganglion it may be objected that its firm attachments are at the endosternites lateral to the median line of the body and, besides, in the 8th thoracic segment where the ligament is particularly well developed, it cannot have such a function because of the more anterior position of the ganglion.

As stated in the introductory remarks, the occurrence of proprioceptors in the coxal articulations was predicted. The possibility of their existence was adumbrated by Bethe (1897) who, experimenting on compensatory eye movements in *Carcinus maenas*, expressed the view that besides the reflexes elicited by the eyes and the statocysts, a 'third factor' may play a role. Dijkgraaf (1956*a*, *b*) has demonstrated that proprioceptors must be there. They are indeed. But now the question of their function remains to be answered, for it seems most unlikely that such organs have no other role than to participate in the compensatory eye reflexes in which, as Bethe's and Dijkgraaf's experiments have shown, they play only a subordinate part.

Their number, variety and structure indicate that there is in the coxal region of decapod crustaceans a complex apparatus whose elements, or a part of them, are instrumental in registering the position of the legs with respect to the thorax. What may be the function of each of them remains to be determined.

SUMMARY

In the 4th to 8th thoracic segments of decapod Crustacea, at the bases of the peraeopods, sensory organs of various kinds have been found. They have been observed in *Homarus vulgaris*, *Astacus astacus*, *Palinurus vulgaris*, *Eupagurus bernhardus*, *Carcinus maenas*, *Maia squinado* and described in greater detail for *Homarus*, *Carcinus* and *Maia*.

In all species examined there is in each peraeopod a proprioceptor consisting of a thin muscle with various nerve elements which extends from a point of the endophragmal skeleton situated near the ventral ganglia to the anteroventral part of the coxa. In the 4th to 7th thoracic segments of *Homarus*, in the 4th to 8th of *Palinurus* and *Astacus*, and in the 4th of the Brachyura, the receptor muscle is proximally attached to the tip of a chitinous projection of the endophragmal skeleton for which the term 'receptor rod' is proposed. In other instances it originates on the plate of the endosternite.

The nerve components of this 'muscular receptor' are of two sorts: (1) motor nerves spreading their branches over the whole length of the muscle, and (2) processes of the sensory neurons distributing their ramifications on the connective tissue associated with the muscle at its proximal end. The arrangement of the sensory elements is different in various species, but they all exhibit one feature, unusual in invertebrates, viz. their cell-bodies are situated within the central nervous system and not outside it.

In *Homarus* and *Astacus* there is a second receptor organ having the same attachments as the former and running close to it. It has been called 'elastic receptor' since it is composed of fibres with elastic properties; they form a sort of tube in which a row of bipolar nerve cells and their processes are enclosed. In all other species investigated this organ appears to be missing.

In all species investigated there is a sensory organ spanning the articulation between the coxa and the basipodite. It is made up of a strand of elastic

fibres and a row of sensory nerve cells. This coxo-basipodite receptor belongs to a system of receptors of similar structure which occur in all articulations of the legs.

A different system of sensory organs consists of innervated elastic strands. As they are associated with the two muscles inserting into the basipodite they may be called the 'depressor receptor' and 'levator receptor' respectively. In *Homarus* and *Astacus* this system consists of two strands arising on the receptor rods and two others connected with a special connective tissue band termed the suspensory ligament. In *Carcinus* and *Cancer* it is simpler, being represented by two strands originating near the proximal end of the receptor muscle. In *Maia* these organs have not been found. The strands are abundantly supplied with nerve fibres considered to be processes of sensory nerve cells located in the central nervous system.

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EXPLANATION OF PLATES

PLATE I

All photomicrographs are made from *Homarus vulgaris*.

Fig. 1. Receptor organs of the thoracico-coxal articulation of the 5th thoracic segment in connexion with the ganglion seen from above. On the left side both the muscular and the elastic receptors are present; on the right side the elastic receptor is removed. *rec.r.*, upper parts of the receptor rods cut from the endosternites.

Fig. 2. Proximal parts of the muscular (*m.rec.*) and the elastic (*el.rec.*) receptors of the right side.

Fig. 3. Muscular receptor of the right side from Fig. 1 under higher magnification.

Fig. 4. Proximal part of the muscular receptor of the left side. Note its attachment to the receptor rod (*rec.r.*). In the bundle of nerves connecting the receptor with the ganglion are included fibres of the additional strands (cf. Text-figs. 3, 5); the strands themselves are not seen.

Fig. 5. Proximal part of the additional strand of the levator receptor with nerve fibre branching in it.

Fig. 6. Middle part of the coxo-basipodite receptor. The axons of nerve cells are in this preparation more apart than usual; in their proximal course they unite into a compact bundle.

PLATE II

Fig. 7. *Homarus vulgaris*. Suspensory ligament (*lig.*) of the right side of the 2nd thoracic segment with the main strands of the levator (*lev.rec.*) and depressor (*depr.rec.*) receptors. Additional strands are removed.

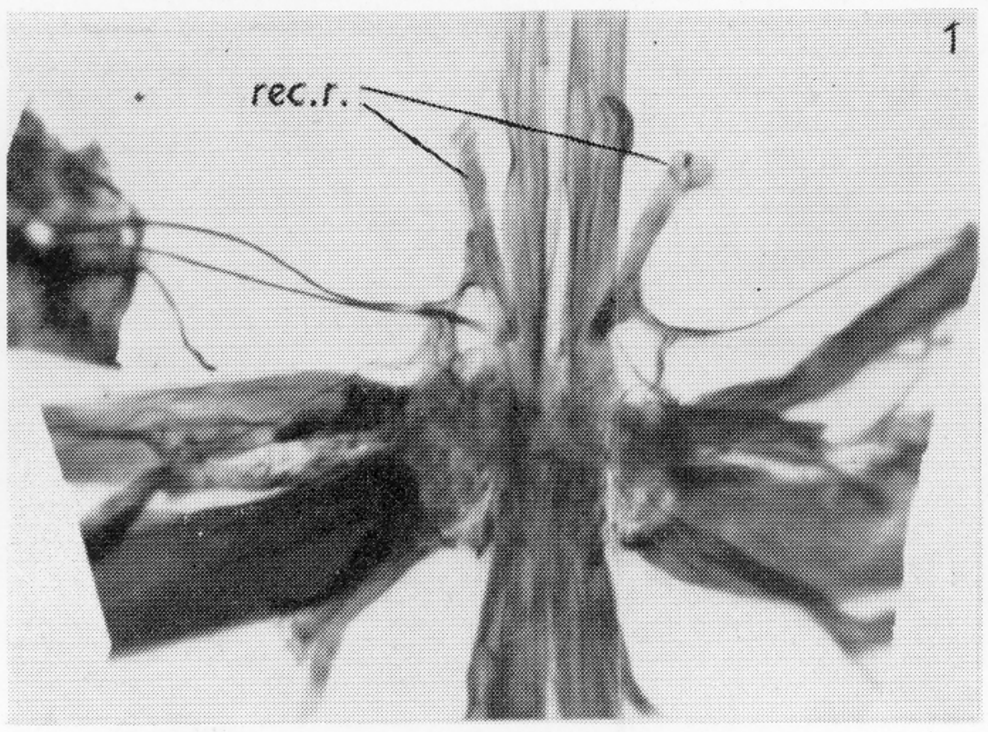
Fig. 8. *H. vulgaris*. Nerve fibres of the depressor receptor (cf. Text-fig. 5). *ad.*, branches of the fibre of the additional strand; the division of the nerve fibre at a distance from the main strand, as seen in this preparation, is less common.

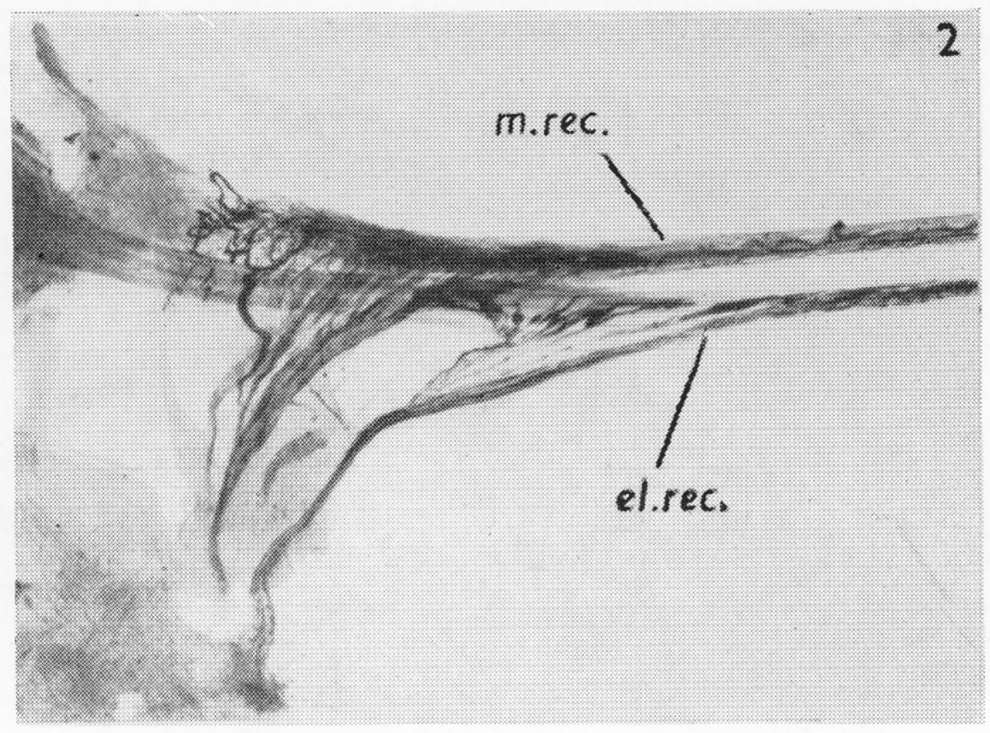
Fig. 9. *Carcinus maenas*. Receptor rod with the muscular receptor (*m.rec.*). The nerves are incomplete and somewhat displaced.

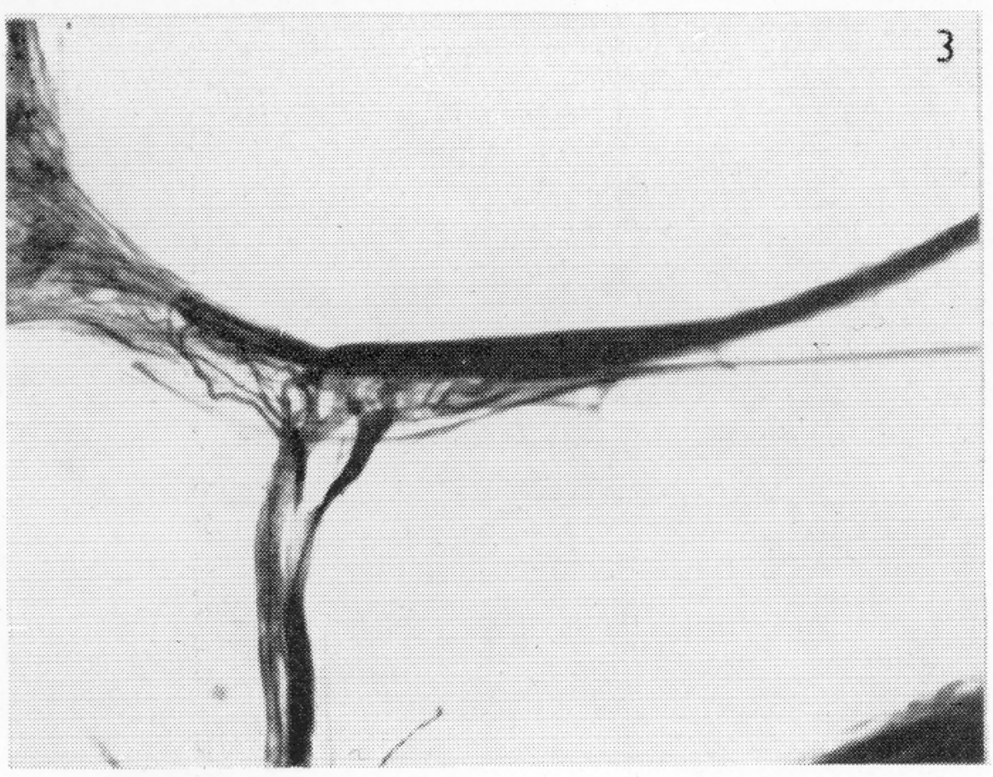
Fig. 10. *Maia squinado*. Receptor rod with the muscular receptor (*m.rec.*) and its nerves. *a*, fibre ending on the tendon; *b*, two fibres branching before reaching the receptor muscle; in the photograph their outlines are confluent but in fact there are two.

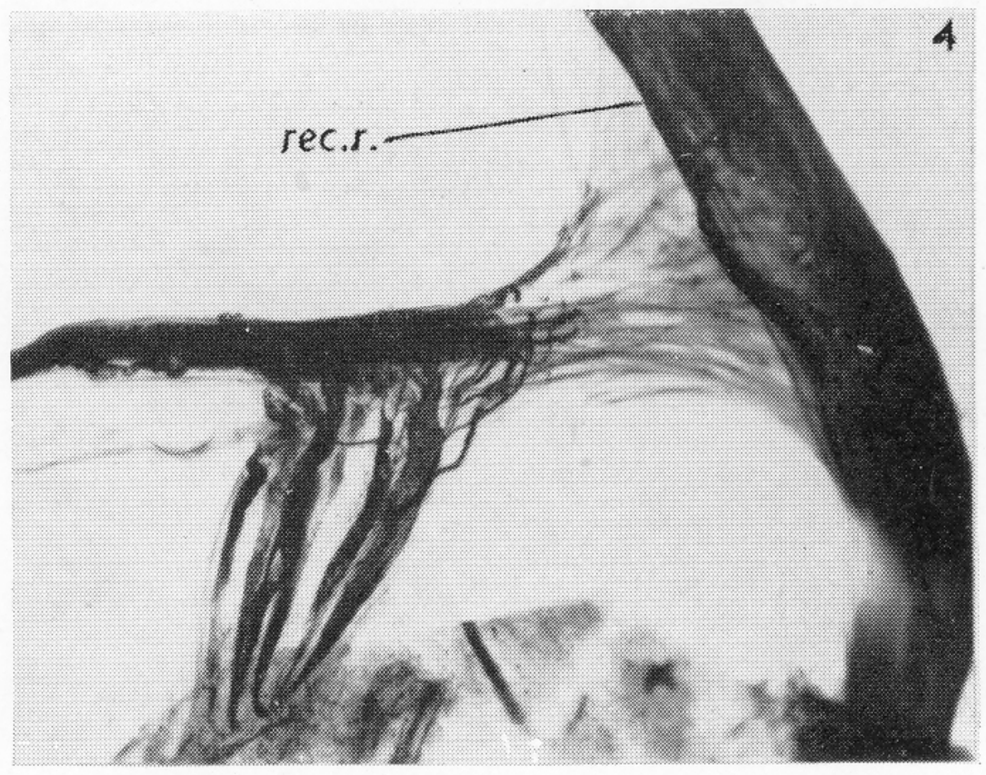
Fig. 11. *Carcinus maenas*. Proximal part of the muscular receptor of the 8th thoracic segment of the left side. *depr.rec.*, depressor receptor; *lev.rec.*, levator receptor. Note the nerve fibres of the levator receptor (cf. Text-fig. 8).

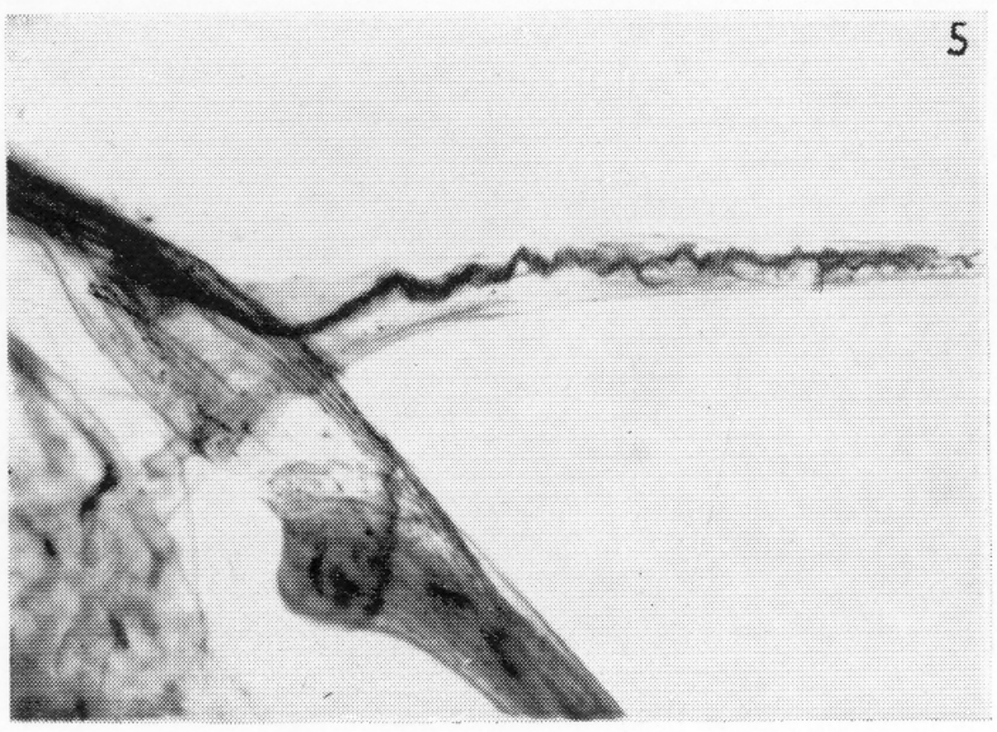
Fig. 12. *Maia squinado*. Proximal part of the muscular receptor of the 6th segment of the left side with branches of the nerve fibre innervating the tendon and with the two nerve fibres penetrating into the strand flanking the receptor muscle.

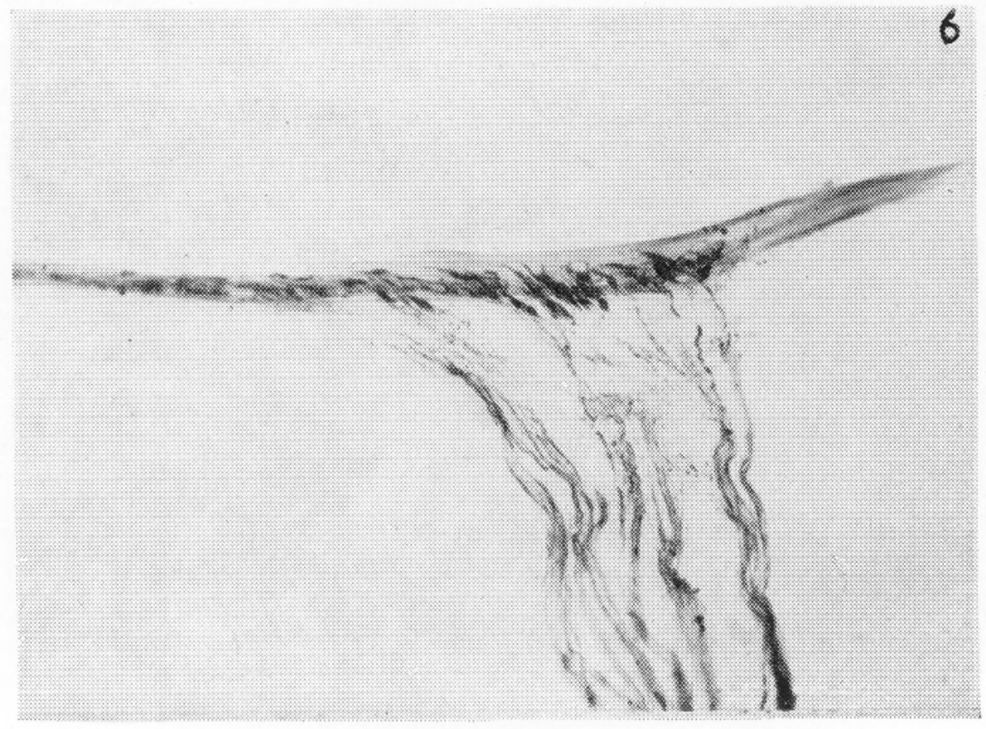












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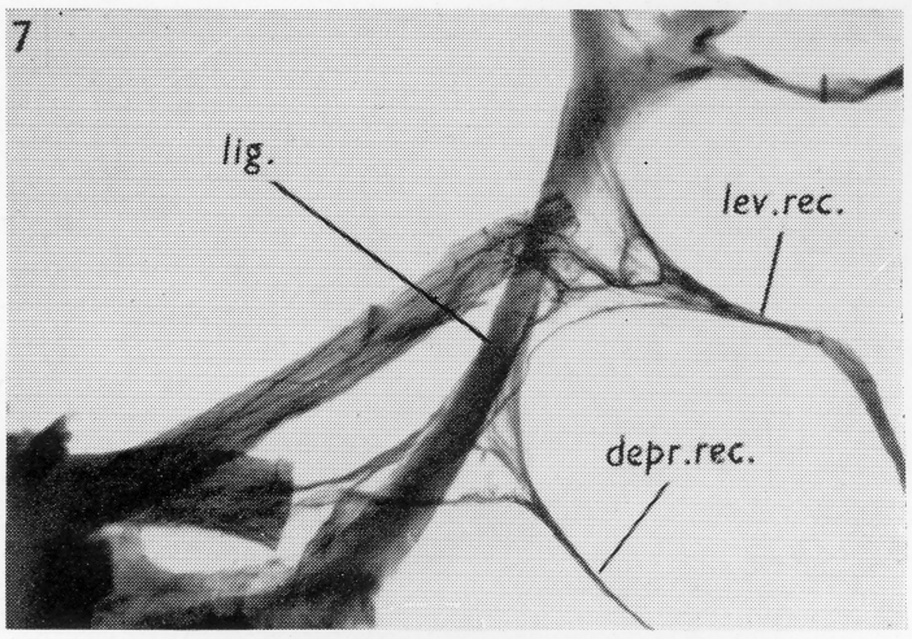
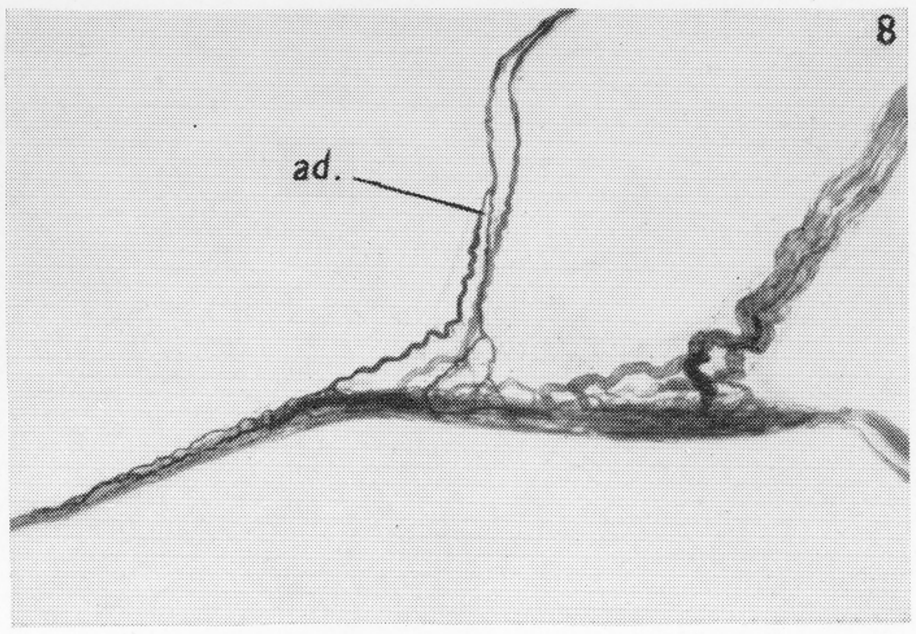
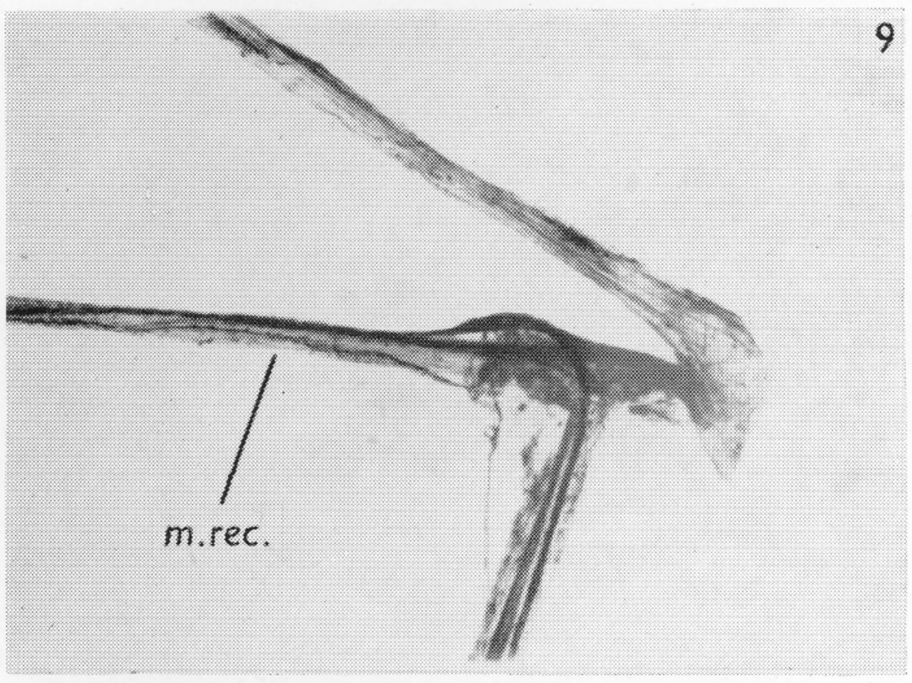

7
lig.
lev.rec.
depr.rec.
2 mm


8
ad.
500 μ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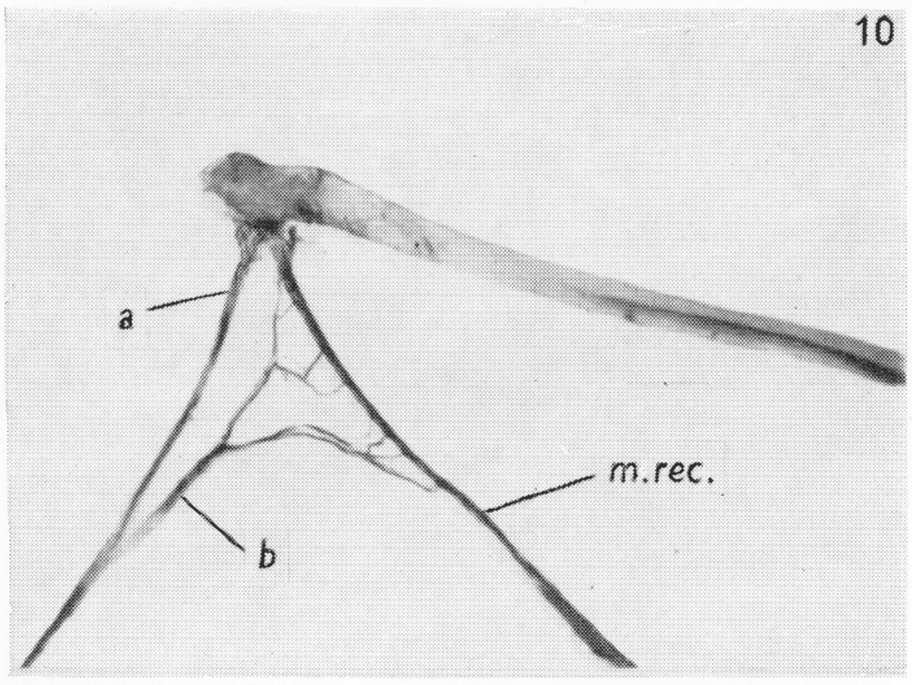
m.rec.
500 μ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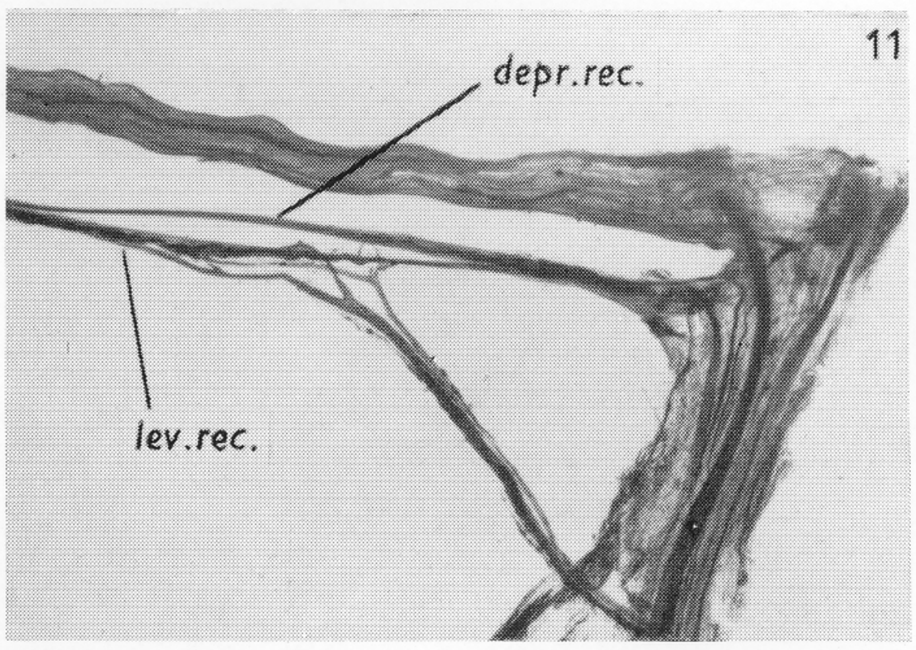
a
b
m.rec.
2 mm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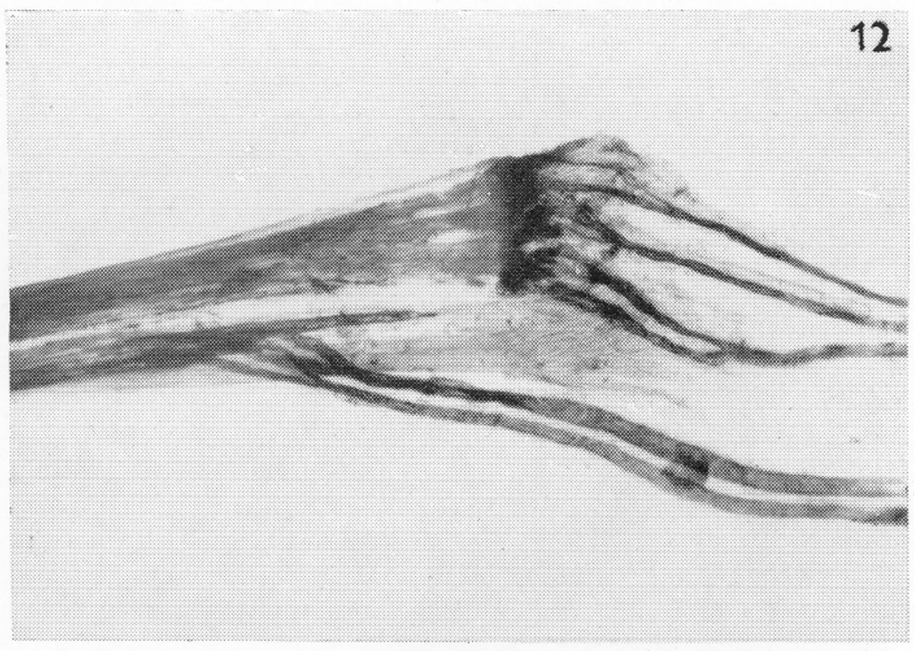
depr.rec.
lev.rec.
500 μ


12
500 μ

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SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

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(Text-figs. 1–13)

The light of *Chaetopterus* has a bluish hue. From visual examination Lankester (1868) judged that the emission spectrum extended from about 440 to 550 mμ (wavelengths estimated by Harvey, 1952). Other polychaetes said to produce bluish luminescence are found in the families Alciopidae, Syllidae and Terebellidae. The light of Tomopteridae and Cirratulidae is described as yellow or yellow-green (Harvey, 1955). The spectral composition of the light of polynoids has now been measured. It is yellow-green in colour, with maximal emission at about 515 mμ (Nicol, 1957).

The spectral composition of the light of *Chaetopterus variopedatus* is here described. Various physiological aspects of the response, some of them pertinent to the present investigation, have already been dealt with (Nicol, 1952*a–c*). The light is produced by a luminescent secretion discharged into the surrounding sea water. When the glands on segment XII discharge, the light rises to maximal intensity in about 14 sec, and the whole response lasts some 5 min.

MATERIALS AND METHODS

Chaetopterus was removed from its tube, and the anterior region (head) was cut off. The head was pinned out in a black dish, and light was evoked by electrical stimulation of the luminescent glands lying at the bases of the aliform notopodia (segment XII) (Nicol, 1952*a*, *b*).

To analyse the spectral composition of the light, a multiplier phototube and a series of coloured filters were used. The photomultiplier was connected to a cathode-ray oscilloscope, and photographic records were made of the deflexion of the oscilloscope trace on moving paper.

The filters used were Ilford spectrum filters nos. 601–608, covering the visible range (about 400–700 mμ), Chance's purple (OV 1), and an ultra-violet filter transmitting from about 300–400 mμ. A set of filters was mounted in an opaque disc which could be rotated beneath the cathode of a photomultiplier tube. Apertures were cut at regular intervals about the margin of the disc, and a filter was placed over each aperture. The disc was arranged so that the filter-covered apertures passed across the face of the photocathode (arrangement shown in Fig. 1). The dish containing the animal was placed under the disc, close to the filters.

Since the light varies in intensity, it was necessary to have some method of registering changes in light intensity, while records of intensity of filtered light in different spectral regions were obtained. This was accomplished by using a series of identical filters (hereafter called reference filters), one of which was placed between each of the other spectral filters. By this means it was possible to gauge the relative light intensity at the beginning and end of each measurement made with a given spectral filter. For reference filters I employed either Ilford blue-green 603, or Ilford green 604. From the intensity of the light passed by the reference filters, it was possible to correct the records obtained with other spectral filters, so that all the data referred to light of the same initial energy-content before filtration.

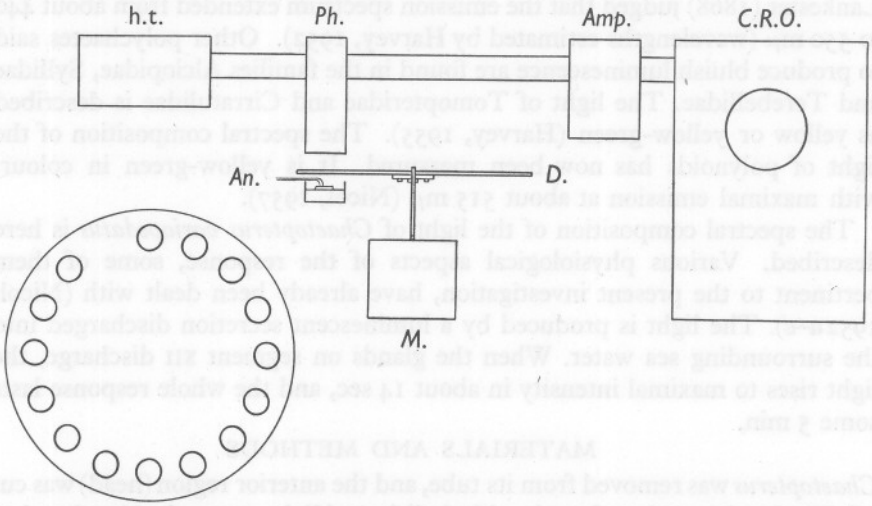

Fig. 1. Diagram of apparatus. *Amp.*, amplifier; *An.*, animal; *D.*, disc; *C.R.O.*, cathode-ray oscilloscope; *h.t.*, high tension supply; *M.*, variable speed motor. The disc is shown in surface view at the lower left.

In order to reduce the disparity in magnitude of responses given with the various filters, neutral filters were used in conjunction with Ilford spectrum filters nos. 601–604. They were either Chance's neutral glass or Ilford neutral density filters. Four combinations of filters that were used are shown in Table 1. The filters are given in the order in which they passed across the face of the multiplier phototube. A blank opaque space was left between each pair of contiguous filters to separate the records clearly. At one point on the disc there was a double blank space as a position-marker, to show when the disc had made one complete rotation, and to provide a means of relating the seriated responses to the filters in their order of rotation. Thus, in disc I, when the filters were rotated in order from red to violet, the photographic trace would show: nil deflexion, long duration (=double space); deflexion (=blue-green filter); nil deflexion, short duration (=single space); deflexion (=red filter);

nil deflexion, short duration (=single space); deflexion (=blue-green filter); etc. Some records, described later, are shown in Figs. 2 and 3.

The transmission of all filters was measured in a spectrophotometer (Unicam, S.P. 500).

The photomultiplier was an E.M.I. no. 6685, having high sensitivity in the violet and very low sensitivity in the red. The spectral sensitivity of the

TABLE 1. FOUR COMBINATIONS OF FILTERS, LISTED IN ORDER OF ROTATION

Disc I

Double space

1. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
2. Ilford red 608
3. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
4. Ilford orange 607
5. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
6. Ilford yellow 606
7. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
8. Ilford yellow-green 605
9. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
10. Ilford green 604 + Ilford neutral density (D. 0·5)
11. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
12. Ilford blue 602 + Ilford neutral density (D. 0·5)
13. Ilford blue-green 603 + Ilford neutral density (D. 0·5)
14. Ilford violet 601
15. Ilford blue-green 603 + Ilford neutral density (D. 0·5)

Disc II

Double space

1. Ilford green 604
2. Ilford orange 607
3. Ilford green 604
4. Ilford yellow 606
5. Ilford green 604
6. Ilford yellow-green 605
7. Ilford green 604
8. Ilford blue-green 603 + Chance neutral ON 31
9. Ilford green 604
10. Ilford blue 602 + Chance neutral ON 32
11. Ilford green 604
12. Ilford violet 601 + Chance neutral ON 33
13. Ilford green 604

Disc III

Double space

1. Ilford green 604
2. Ultra-violet
3. Ilford green 604
4. Ilford yellow 606
5. Ilford green 604
6. Ilford yellow-green 605
7. Ilford green 604
8. Ilford blue-green 603 + Chance neutral ON 31
9. Ilford green 604
10. Ilford blue 602 + Chance neutral ON 32
11. Ilford green 604
12. Ilford violet 601 + Chance neutrals ON 32 + ON 33
13. Ilford green 604
14. Chance OV 1
15. Ilford green 604

Disc IV

Double space

1. Ilford red 608
2. Ilford green 604
3. Ilford orange 607
4. Ilford green 604
5. Ilford yellow 606
6. Ilford green 604
7. Ilford yellow-green 605
8. Ilford green 604
9. Ilford blue-green 603 + Chance neutral ON 31
10. Ilford green 604
11. Ilford blue 602 + Chance neutral ON 32
12. Ilford green 604
13. Ilford violet 601 + Chance neutral ON 33
14. Ilford green 604
15. Chance OV 1
16. Ilford green 604

photocathode of this tube was determined by the National Physical Laboratory. Voltage for the photomultiplier was supplied by a stabilized power pack. The mains voltage for oscilloscope and power pack was held steady by a voltage stabilizer.

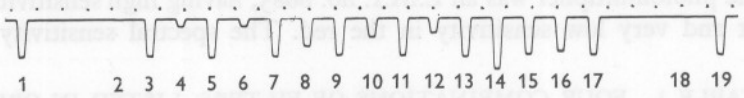

Fig. 2

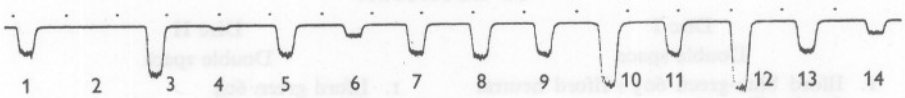

Fig. 3

Fig. 2. Photographic record of oscillograph deflexions given by artificial light source (lamp 2360° K + Chance blue-green OB 2), interrupted by rotation of disc IV. Responses as follows: 1, green 604; double space; 2, red 608; 3, green 604; 4, orange 607; 5, green 604; 6, yellow 606; 7, green 604; 8, yellow-green 605; 9, green 604; 10, blue-green 603; 11, green 604; 12, blue 602; 13, green 604; 14, violet 601; 15, green 604; 16, purple OV 1; 17, green 604; double space; 18, red 608; 19, green 604.

Fig. 3. Similar record for the light of *Chaetopterus*, interrupted by disc III. Responses as follows: 1, green 604; 2, ultra-violet; 3, green 604; 4, yellow 606; 5, green 604; 6, yellow-green 605; 7, green 604; 8, blue-green 603; 9, green 604; 10, blue 602; 11, green 604; 12, violet 601; 13, green 604; 14, deep purple OV 1. Time, both records, $\frac{1}{5}$ sec.

In order to calculate the relative spectral energy of a light source by the method here adopted, it is necessary to know the combined effect of spectral sensitivity of the photomultiplier (S_λ) and spectral transmission of each filter (T_λ). Let R_x be the response for a given filter x, and E_λ the relative spectral energy of emitted light. Then

$$R_x \propto E_\lambda \int S_\lambda T_\lambda \, d\lambda,$$

$$\therefore \; E_\lambda \propto \frac{R_x}{\int S_\lambda T_\lambda \, d\lambda}.$$

Plots of $S_\lambda T_\lambda$ against λ are given in Figs. 4 and 5. The areas under curves $S_\lambda T_\lambda$ were used to represent the integrals for each filter

$$\eta_x = \int S_\lambda T_\lambda \, d\lambda.$$

The mean wavelength (mean λ) for each filter was taken from the centre of gravity of the areas under the curves. Values for η_x and mean λ are given in Table 2.

All measurements of *Chaetopterus* light were made at a room-temperature of 18–19° C.

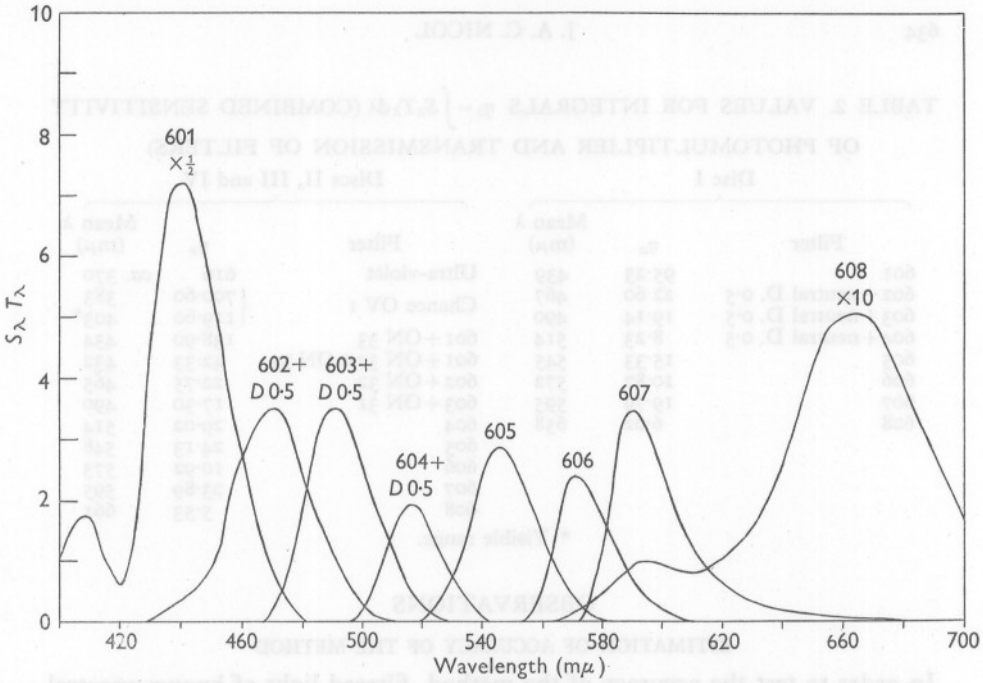

Fig. 4. Plots of $S_\lambda T_\lambda$ against λ for the series of Ilford gelatine filters used in disc I. S_λ = sensitivity of photomultiplier 6685; T_λ = transmission of filters. An Ilford neutral density filter (density D. = 0·5) was used with each of filters 602 to 604. All filters were mounted between two pieces of Perspex.

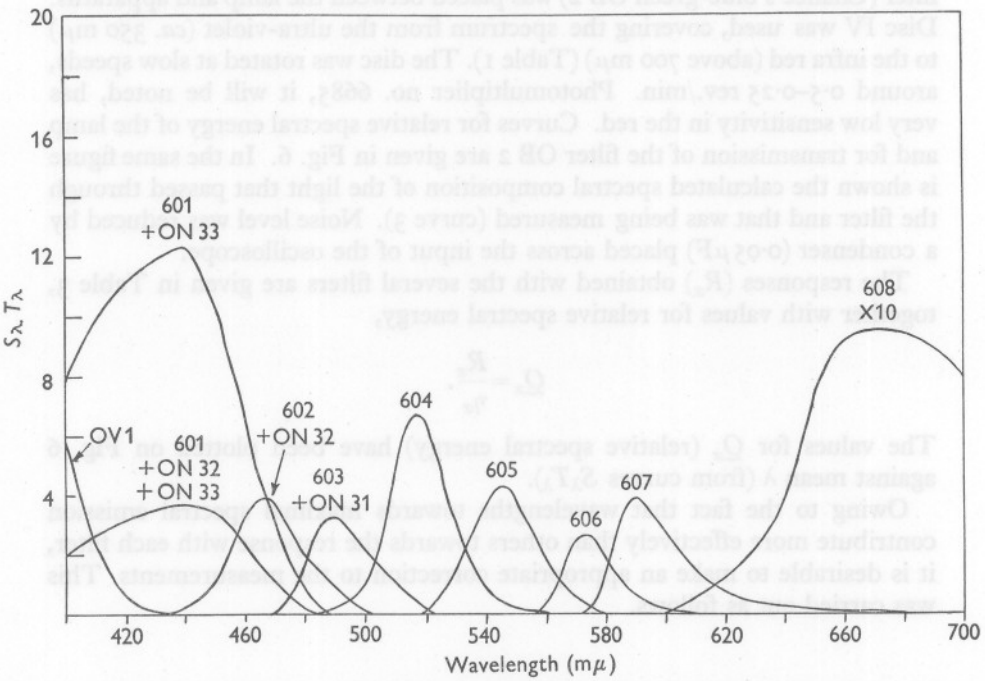

Fig. 5. Plots of $S_\lambda T_\lambda$ for the various filters used in discs II, III and IV. Filters 601 to 608 were gelatine, mounted in glass; the remainder glass.

TABLE 2. VALUES FOR INTEGRALS $\eta_\lambda = \int S_\lambda T_\lambda \, d\lambda$ (COMBINED SENSITIVITY OF PHOTOMULTIPLIER AND TRANSMISSION OF FILTERS)

Disc I			Discs II, III and IV		
Filter	η_x	Mean λ (mμ)	Filter	η_x	Mean λ (mμ)
601	95·23	439	Ultra-violet	616	*ca.* 370
602 + neutral D. 0·5	22·60	467	Chance OV 1	700·60	383
603 + neutral D. 0·5	19·14	490		119·60	403*
604 + neutral D. 0·5	8·23	514	601 + ON 33	138·90	434
605	15·33	545	601 + ON 32 + ON 33	42·33	432
606	10·87	572	602 + ON 32	22·75	465
607	19·79	595	603 + ON 31	17·30	490
608	6·02	658	604	29·02	514
			605	24·13	548
			606	10·92	573
			607	23·89	595
			608	5·53	661

* Visible range.

OBSERVATIONS

ESTIMATION OF ACCURACY OF THE METHOD

In order to test the accuracy of the method, filtered light of known spectral composition was measured by means of a disc of filters, photomultiplier and oscilloscope. Constant light was provided from a substandard lamp of colour temperature 2360° K, obtained from the National Physical Laboratory. A blue filter (Chance's blue-green OB 2) was placed between the lamp and apparatus. Disc IV was used, covering the spectrum from the ultra-violet (*ca.* 350 mμ) to the infra red (above 700 mμ) (Table 1). The disc was rotated at slow speeds, around 0·5–0·25 rev./min. Photomultiplier no. 6685, it will be noted, has very low sensitivity in the red. Curves for relative spectral energy of the lamp and for transmission of the filter OB 2 are given in Fig. 6. In the same figure is shown the calculated spectral composition of the light that passed through the filter and that was being measured (curve 3). Noise level was reduced by a condenser (0·05 μF) placed across the input of the oscilloscope.

The responses (R_x) obtained with the several filters are given in Table 3, together with values for relative spectral energy,

$$Q_x = \frac{R_x}{\eta_x}.$$

The values for Q_x (relative spectral energy) have been plotted on Fig. 6 against mean λ (from curves $S_\lambda T_\lambda$).

Owing to the fact that wavelengths towards maximal spectral emission contribute more effectively than others towards the response with each filter, it is desirable to make an appropriate correction to the measurements. This was carried out as follows.

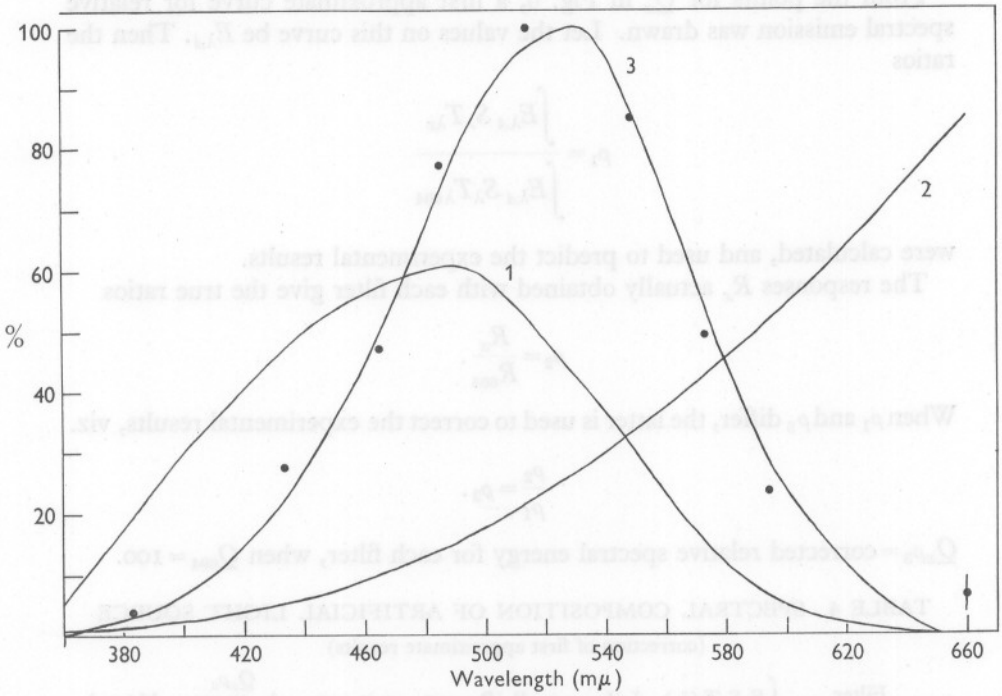

Fig. 6. Curves for (1) transmission (%) of a blue filter, Chance OB 2; (2) spectral emission of a substandard lamp (colour temperature 2360° K), and (3) calculated spectral composition of light passed by filter OB 2 ($T_\lambda \mathcal{J}_\lambda$). Relative $\mathcal{J}_\lambda$ based on $\mathcal{J}=1$ at $\lambda=590$ mμ (from Skogland, 1929). Relative $T_\lambda \mathcal{J}_\lambda$ based on $T\mathcal{J}=100$ at $\lambda=530$ mμ. Curve (2), $\times 50$. The points are measured values for spectral composition of light passed by filter OB 2.

TABLE 3. MEASUREMENT OF SPECTRAL COMPOSITION OF AN ARTIFICIAL LIGHT SOURCE

Lamp of colour temperature 2360° K + Chance blue-green filter OB 2. Responses and first approximation of relative spectral energy.

Filter	Mean λ (mμ)	Response R_x	$R_x/\eta_x = Q_x$
OV 1	383	10	0·0143
601 + ON 33	434	15	0·1080
602 + ON 32	465	4·2	0·1846
603 + ON 31	490	5·2	0·3006
604	514	11·3	0·3894
605	548	8·0	0·3315
606	573	2·1	0·1923
607	595	2·2	0·0921
608	661	0·15?	0·0271?

From the points for Q_x in Fig. 6, a first approximate curve for relative spectral emission was drawn. Let the values on this curve be $E_{\lambda A}$. Then the ratios

$$\rho_1 = \frac{\int E_{\lambda A} S_\lambda T_{\lambda x}}{\int E_{\lambda A} S_\lambda T_{\lambda 604}}$$

were calculated, and used to predict the experimental results.

The responses R_x actually obtained with each filter give the true ratios

$$\rho_2 = \frac{R_x}{R_{604}}.$$

When ρ_1 and ρ_2 differ, the latter is used to correct the experimental results, viz.

$$\frac{\rho_2}{\rho_1} = \rho_3.$$

$Q_x\rho_3$ = corrected relative spectral energy for each filter, when $Q_{604} = 100$.

TABLE 4. SPECTRAL COMPOSITION OF ARTIFICIAL LIGHT SOURCE

(correction of first approximate results)

Filter	$\int E_\lambda S_\lambda T_\lambda(\zeta_x)$	$\zeta_x/\zeta_{604} = \rho_1$	$R_x/R_{604} = \rho_2$	$\rho_2/\rho_1 = \rho_3$	$Q_x\rho_3$ $\lambda_{530} \equiv 100$	Mean λ
OV 1	201·0	1·16	0·885	0·763	2·79	395
601 + ON 33	227·7	1·32	1·33	1·007	27·83	445
602 + ON 32	66·66	0·385	0·372	0·966	45·63	466
603 + ON 31	79·34	0·459	0·460	1·002	77·08	491
604	173·0	—	—	—	97·56	516
605	108·75	0·629	0·708	1·126	95·51	542
606	26·67	0·154	0·186	1·208	59·45	572
607	31·00	0·179	0·195	1·089	25·65	592
608	2·27	0·013	0·013?	1?	6·93?	622

In Table 4 are given the details of these calculations for filtered blue light from the substandard lamp. The second column lists areas of the curves $E_{\lambda A} S_\lambda T_{\lambda x}$ plotted against $\lambda(\zeta_x)$. Columns 3–5 give values of ρ_1, ρ_2 and ρ_3, for the various filters. The sixth column $Q_x\rho_3$ gives relative spectral energy for each filter, based on $\lambda_{530} \equiv 100$, the estimated region of maximal emission. The last column shows recalculated values for mean λ, based on curves $E_{\lambda A} S_\lambda T_{\lambda x}$.

The final corrected values for relative spectral energy for each filter are plotted on Fig. 7, together with the calculated relative energy curve (based on $\mathcal{J}_\lambda T_\lambda$). The degree of agreement, which can be seen from inspection, seems reasonable enough to trust the method for measurement of animal luminescence.

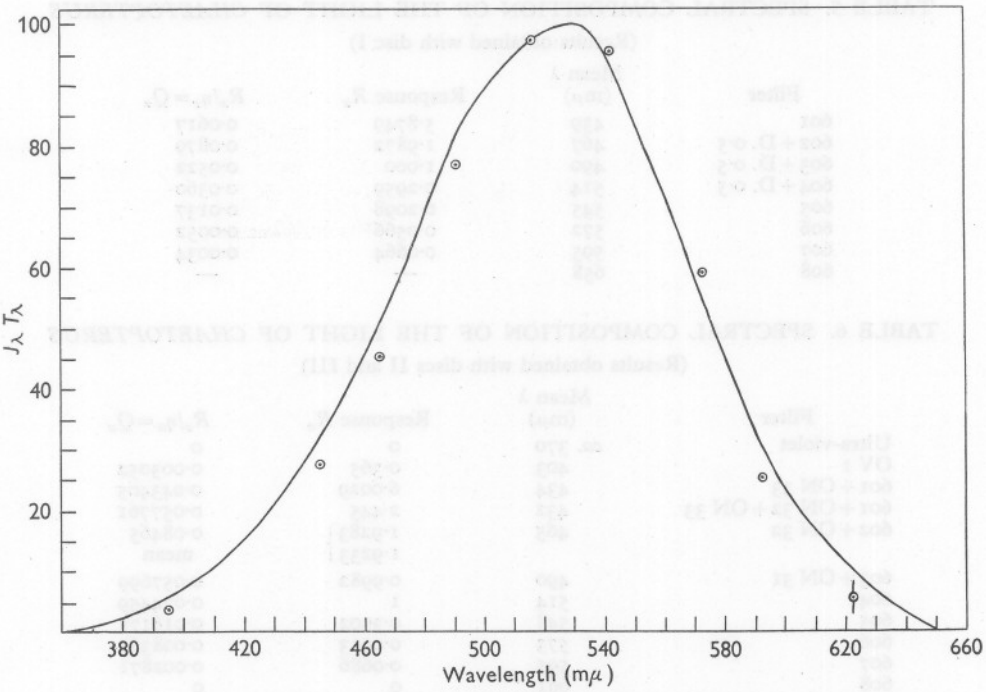

Fig. 7. Curve for relative spectral energy of artificial light (lamp 2360° K + Chance OB 2). The points are corrected measurements made with the various filters, and plotted against mean λ (determined from curves $E_{\lambda A} S_\lambda T_{\lambda x}$).

MEASUREMENTS OF THE LIGHT OF *CHAETOPTERUS*

As a first attempt, the light of *Chaetopterus* was measured by means of disc I, containing Ilford filters 601 to 608. This disc was designed for green light. It was rotated at various speeds, varying from 1 to 3 rev./sec. The data obtained are summarized in Table 5, and first approximate estimations of relative spectral energy are plotted against λ in Fig. 8 (mean λ for each filter based on curves $S_\lambda T_\lambda$).

From these preliminary results it appeared that the light possessed a maximum well into the blue, around 460 mμ, and discs II and III were devised, accordingly, to extend the spectral range of analysis. Discs II and III were spun at low speeds, around 0·5 rev./min, at which rate it was possible to use a condenser (0·05 μF) to filter off most of the noise. The data obtained with discs II and III are shown in Table 6, and values for relative spectral energy are plotted in Fig. 9 against mean λ (derived from curves $S_\lambda T_\lambda$).

In order to correct these values, the same procedure was employed, as described in the previous section. First approximate values for relative

TABLE 5. SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

(Results obtained with disc I)

Filter	Mean λ (mμ)	Response R_x	$R_x/\eta_x = Q_x$
601	439	5·8749	0·0617
602+D. 0·5	467	1·9872	0·0879
603+D. 0·5	490	1·000	0·0522
604+D. 0·5	514	0·2959	0·0360
605	545	0·2098	0·0137
606	572	0·0566	0·0052
607	595	0·0664	0·0034
608	658	—	—

TABLE 6. SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

(Results obtained with discs II and III)

Filter	Mean λ (mμ)	Response R_x	$R_x/\eta_x = Q_x$
Ultra-violet	*ca.* 370	0	0
OV 1	403	0·365	0·003052
601+ON 33	434	6·0029	0·043405
601+ON 32+ON 33	432	2·445	0·057761
602+ON 32	465	1·9283 1·9233	0·08465 mean
603+ON 31	490	0·9982	0·057699
604	514	1	0·034459
605	548	0·3902	0·016171
606	573	0·0913	0·008361
607	595	0·0686	0·002871
608	661	0	0

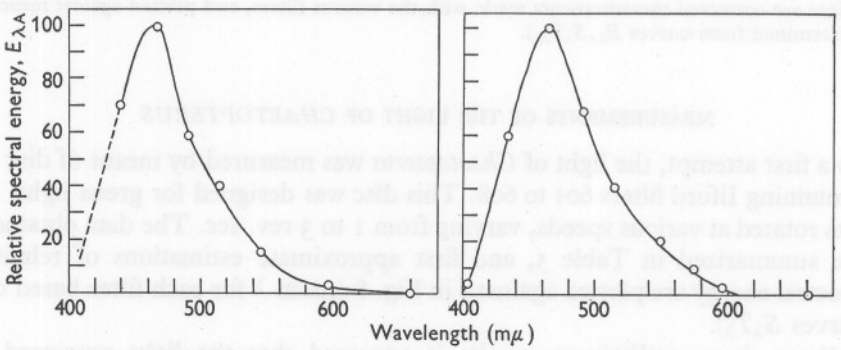

Fig. 8 Fig. 9

Fig. 8. Spectral composition of the light of *Chaetopterus*. Approximate curve based on records obtained with disc I. Mean λ for each filter obtained from curves $S_\lambda T_\lambda$.

Fig. 9. Spectral composition of the light of *Chaetopterus*. Approximate curve based on records obtained with discs II and III. Mean λ for each filter obtained from curves $S_\lambda T_\lambda$.

spectral emission $E_{\lambda A}$ were estimated from a curve resembling that in Fig. 9, and these values were used to draw curves for $E_{\lambda A}S_\lambda T_{\lambda x}$ (Fig. 10). Computed values are listed in Table 7, together with subsequent calculations to determine corrected values for spectral emission. Final values are collected in Fig. 11, which depicts a corrected spectral emission curve. Maximal emission occurs at about 465 mμ, well into the blue. There is no emission in the ultra-violet, and emission in the red, above 600 mμ, is negligible.

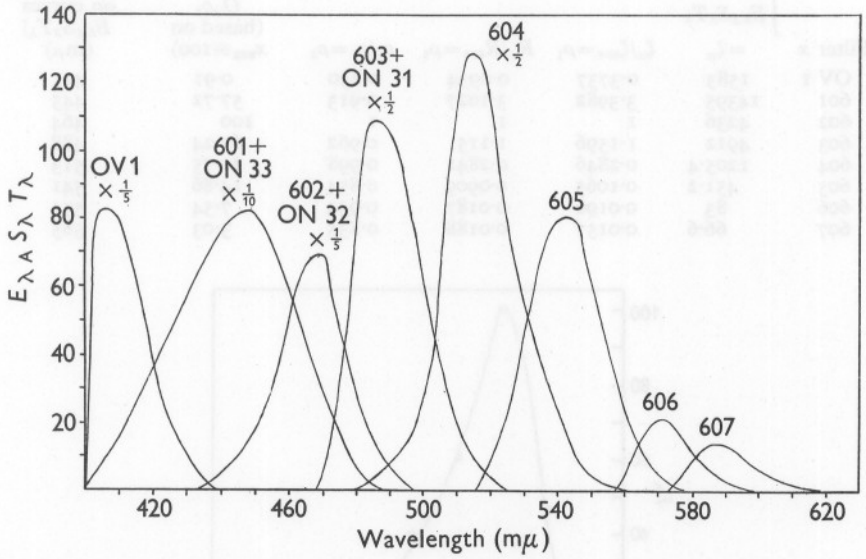

Fig. 10. Curves for $E_{\lambda A}S_\lambda T_\lambda$ against λ, based on first approximate measurements of relative spectral emission of *Chaetopterus* light.

COMMENT

Most of the light of *Chaetopterus* is concentrated in the blue region of the spectrum, more so than that of any animal hitherto measured. *Cypridina* has a somewhat similar emission spectrum, with a maximum at *ca.* 480 mμ (Coblentz & Hughes, 1926). Polynoid light is greenish, with maximal emission at about 515 mμ (Nicol, 1957).

The biological significance of the light of *Chaetopterus* still awaits an explanation. *Chaetopterus* is light-sensitive, and presumably could detect its own light. However, the spectral sensitivity of *Chaetopterus* in unknown, so it is not possible to relate this to the colour of the luminescence. *Chaetopterus* is preyed upon by various animals, including *Limulus* and coastal fish, which may have occasion to perceive the light.

Absorption curves are available for the eye pigments (rhodopsins) of marine coastal fish, and the curves can be used to represent the spectral sensitivity of

these animals (Fig. 12) (Wald, 1946; Kampa, 1953). The spectral sensitivity curve of *Limulus* has been determined (Graham & Hartline, 1935). This has a maximum at 520 mμ (Fig. 12). In Fig. 13 I have drawn curves for 'luminous flux' of *Chaetopterus* light, based on visibility values taken from the curves of

TABLE 7. SPECTRAL COMPOSITION OF THE LIGHT OF *CHAETOPTERUS*

(Correction of first approximate results)

Filter x	$\int E_{\lambda A} S_\lambda T_\lambda = \zeta_x$	$\zeta_x/\zeta_{602} = \rho_1$	$R_x/R_{602} = \rho_2$	$\rho_2/\rho_1 = \rho_3$	$Q_x\rho_3$ (based on $x_{602} \equiv 100$)	Mean λ (based on curves $E_{\lambda A} S_\lambda T_\lambda$) (mμ)
OV 1	1583	0·3737	0·0934	0·250	0·91	411
601	14395	3·3982	3·1027	0·913	57·72	443
602	4236	1	1	1	100	464
603	4912	1·1596	1·115	0·962	61·24	488
604	1205·4	0·2846	0·2841	0·998	40·75	513
605	451·2	0·1065	0·0909	0·854	14·86	541
606	83	0·0196	0·0187	0·954	7·54	571
607	66·6	0·0157	0·0188	0·835	3·03	585

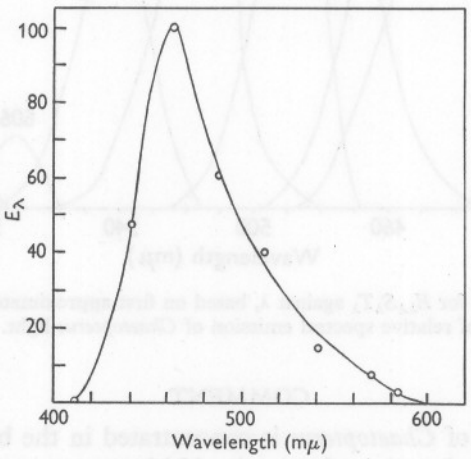

Fig. 11. Corrected values for relative spectral energy of *Chaetopterus* light, and a spectral emission curve based on these values.

Fig. 12, and on human scotopic vision (C.I.E. values). The luminous efficiency of radiation is given by the ratio of total luminous flux to total radiant flux (Harvey, 1940). For human scotopic vision, *Chaetopterus* light is 67% efficient; for fish having visual purples with maxima at 505 mμ, *Chaetopterus* light is 71% efficient; and for the eye of *Limulus*, *Chaetopterus* light is 56% efficient.

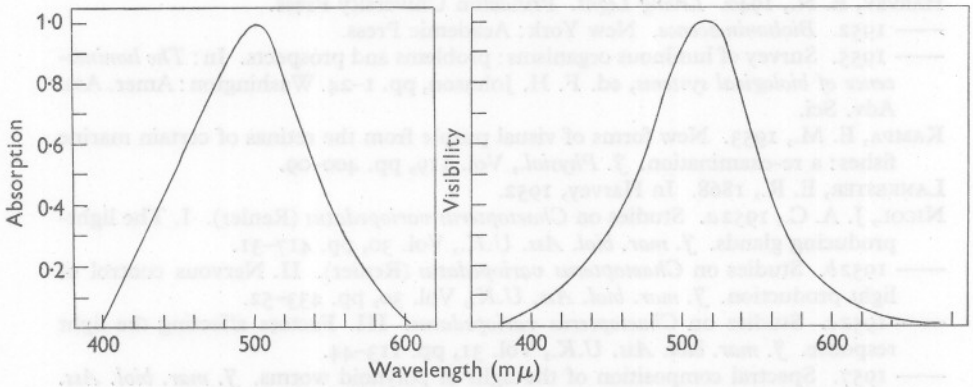

Fig. 12. Left, generalized absorption curve for visual purple of coastal marine fish (based on measurements of Wald, 1946, and Kampa, 1953). Right, visibility curve for *Limulus* (based on measurements of Graham & Hartline, 1935).

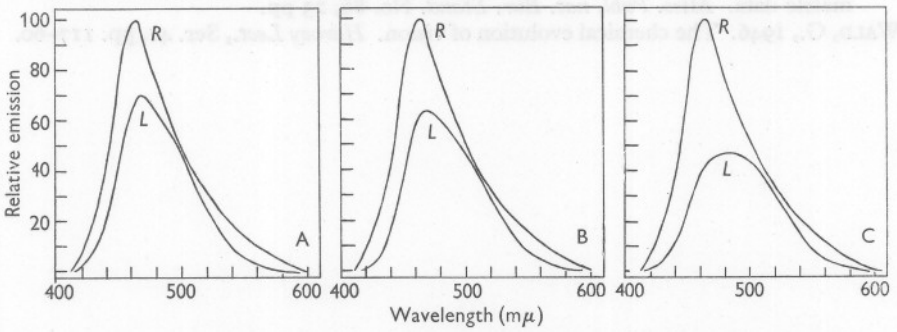

Fig. 13. Relative spectral energy curves (radiant flux) of *Chaetopterus* light, and estimated curves of luminous flux based on fish rhodopsin (A), human scotopic vision (B), and *Limulus* vision (C). *R*, radiant flux; *L*, luminous flux.

SUMMARY

The spectral composition of the light of *Chaetopterus variopedatus* has been measured by means of spectral filters and multiplier phototube. Spectral emission extends from about 405 to 605 mμ, with a maximum at about 465 mμ. The spectral curve of *Chaetopterus* light is compared with a human visibility curve (scotopic vision), a visibility curve for *Limulus*, and an absorption curve for fish visual purple. Luminous efficiencies, based on these curves, are calculated.

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J. mar. biol. Ass. U.K. (1957) 36, 643–650
Printed in Great Britain

A NEW MARINE DINOFLAGELLATE: *EXUVIAELLA MARIAE-LEBOURIAE* N.SP.

By MARY PARKE and DOROTHY BALLANTINE
The Plymouth Laboratory

(Text-figs. 1–18)

Exuviaella mariae-lebouriae n.sp., Parke & Ballantine

Exuviaella apora Schiller pro parte, in Lebour, 1925, (non *E. apora* Schiller, 1918).
Exuviaella apora Schiller, in Martin, 1929.

Diagnosis

Cell ovoid to almost sphaeroidal in face view of right or left valve, lenticular to almost sphaeroidal in view showing junction of valves, in both views flagellar pole flattened, length (10) 14–17 (22), breadth (9) 11–15 (20), thickness (5) 6–8 (18) μ. Two valves of cellulose, each with a striated band at margin, band wider in larger cells, striations about 0·5 μ apart, remainder of valve surface with poroids, apparently in rows, 0·25 μ apart, poroids 0·2–0·25 μ diameter; right valve with shallow indentation, about 2 μ wide, at flagellar pole, usually lying to left of centre line; left valve with small projecting flange, about 2 μ wide, bearing flagellar pores and fitting into and over indentation on right valve; the two flagellar pores of unequal size, in apical view larger nearly triangular, smaller circular, in left valve view smaller pore to left of larger. Two flagella, one emerging from larger pore undulating parallel to, and round, flagellar pole, 2·5–3 times body length; the other, 1·25–1·5 times body length, emerging from smaller pore. One obvious, usually ovoid, pusule, 1·5–4 μ in length, in left valve view close to surface on the right side near flagellar pole, opening to exterior by canal to larger flagellar pore; second smaller pusule sometimes present but connexion to exterior not visible. Nucleus posterior, broadly ellipsoidal in valve view. Chromatophores golden-brown, usually two in smaller cells, large, parietal, saucer-shaped with deeply lobed margins, with a single large pyrenoid on inner face of each lying in anterior part of body; in larger cells chromatophores smaller and more numerous. Disc-shaped starch grains surrounding pyrenoids and in stroma; lipoid reserve absent. Nutrition phototrophic. Trichites distributed in peripheral cytoplasm, more numerous in region of junction of valves. Non-toxic to fish.

Asexual reproduction by fission in the motile state into two daughter-cells of equal or unequal size.

Isolated from sea-water sample taken near Knap Buoy, Plymouth Sound,

from 8 m depth on 30 June 1949 (type culture); also from St German's River in tow net sample on 24 June 1957. Type culture (Plymouth no. 18) at the Laboratory of the Marine Biological Association, Plymouth.

Named in honour of Dr Marie V. Lebour on the occasion of her 80th birthday.

Cellula duabus valvis (materia cellulosa consistentibus) induta, sinistra atque dextra, forma ovali vel sphaerali ut videtur pro superficie utriusque valvae, lenticulari vel fere sphaerali pro conjunctione valvarum; planata extremitate qua oriuntur flagella; longa (10) 14–17 (22) μ, lata (9) 11–15 (20) μ, crassa (5) 6–8 (18) μ; margine utriusque valvae striolata, latius in majoribus cellulis, striolis 0·5 μ separatis, valvis pro cetero perforatis minutissimis porulis latis 0·20–0·25 μ, distributis—ut videtur—in ordinibus regularibus 0·25 μ separatis; valva dextra indentata sinu haud profundo, lato fere 2 μ, ad extremitatem qua oriuntur flagella paulum sinistraliter ex norma posito; valva sinistra praedita parvo processu, eminente super sinum valvae dextrae, quem sinum idem replet. Eodem processu perforato a duobus poris ad exitum flagellorum; quibus poris disparibus magnitudine; majore dextro, fere triangulari, minore sinistro, circulari (ut videtur in aspectu sinistrae valvae). Duobus flagellis, altero emergente ex majore poro, undulante circum situm originis suae, longiore 2·5–3plo quam cellula; altero emergente ex minore poro, longiore 1·25–1·5plo quam cellula. Pusulis duabus, altera (quam semper facile potest videre) longa 1·5–4 μ, in sinistra valva posita, sub superficie, dextraliter prope originem flagellorum, aperiente externe per canaliculam in porum majorem flagelli, altero nonnunquam absente, invisibili ut aperit externe.

Legend to Figs. 1–9

Figs. 1–9. *Exuviaella mariae-lebouriae* n.sp.

(Figs. 1–2, ×5000; Figs. 3–9, ×2500)

c, chromatophore; *et*, ejecting trichite; *g*, granules in pusule; *lf*, 'longitudinal' flagellum; *m*, mitochondrion?; *n*, nucleus; *nsb*, narrow striated band at margin of valve; *p*, pyrenoid; *pu*, pusule; *s*, starch bodies; *sp*, 2nd pusule; *t*, trichite; *tf*, 'transverse' flagellum; *wsb*, wide striated band at margin of valve.

Fig. 1. Left valve view of small individual with two large chromatophores; valve shows large and small flagellar pores and a narrow striated margin.

Fig. 2. Right valve view of large individual with six chromatophores and two pusules, the larger containing granules in Brownian movement; three pyrenoids surrounded by disc-shaped starch bodies; valve shows wide striated margin and indentation at flagellar pole; the projecting flange of the left valve, bearing the flagellar pores, is seen in the indentation.

Fig. 3. View of flagellar pole showing large and small flagellar pores.

Fig. 4. Empty valves of cell showing flagellar pores on flange of left, and indentation in right, valve.

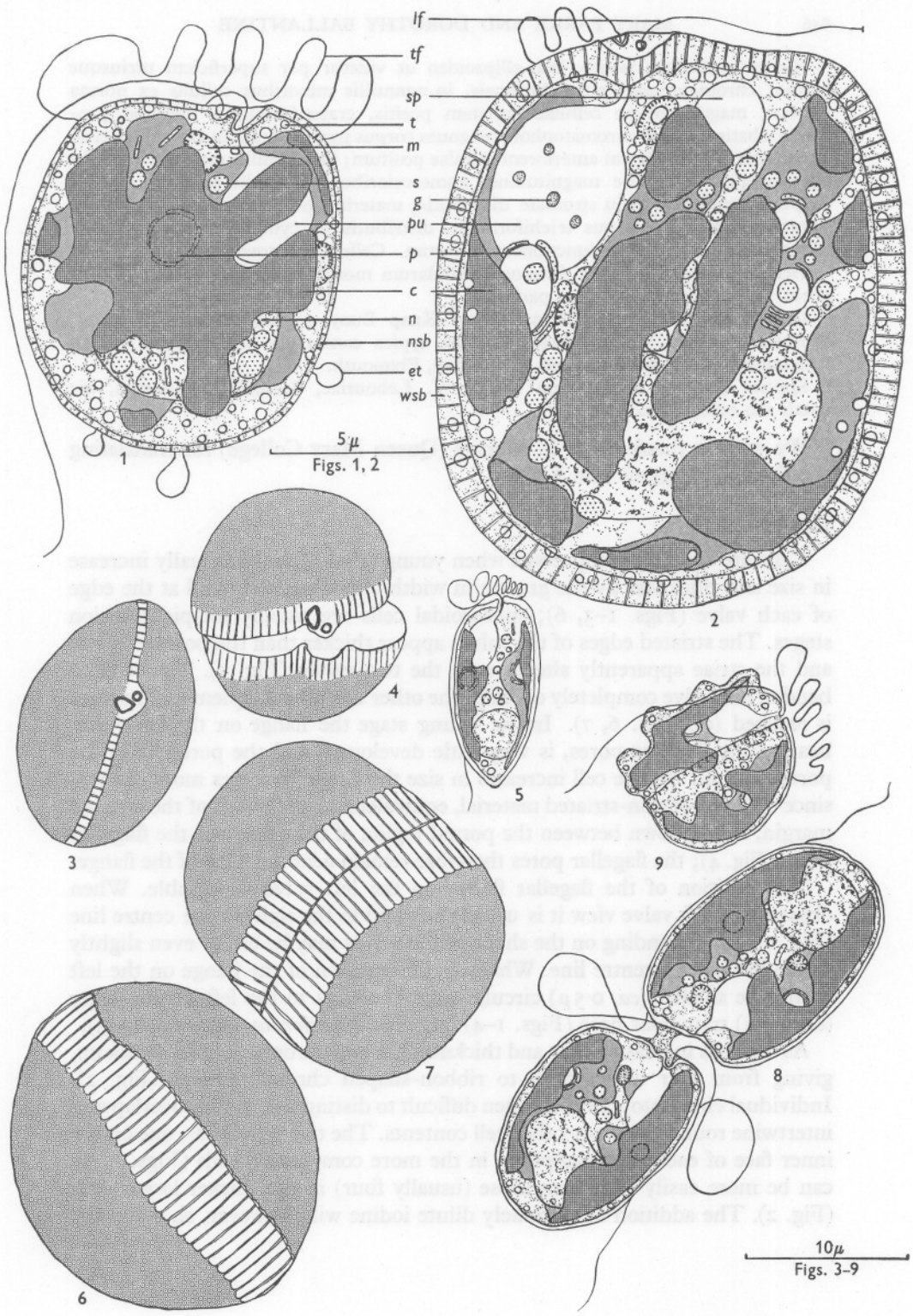
Fig. 5. Optical section of young compressed cell in side view (junction of valves—left valve on left of diagram) showing connection of pusule to larger flagellar pore.

Fig. 6. Side view of large, nearly sphaeroidal, individual with the wide striated margins to the valves still overlapping.

Fig. 7. Early fission stage with valves not overlapping; the wide striated margins of both valves are clearly visible.

Fig. 8. Late fission stage: daughter-cells still joined by narrow connexion near flagellar pole.

Fig. 9. Newly separated daughter-cell with one valve.



Figs. 1–9

Nucleo posteriore posito, late ellipsoideo ut videtur per superficiem utriusque valvae; chromatophoris aureo-brunneis, in nonnullis minoribus cellulis ex norma duobus, magnis, prope cellulae parietem positis, crateriformibus, margine profunde lobatis, quoque chromatophoro magnum corpus pyrenoideum in aspectu interno continente, versus partem anteriorem cellulae positum; in nonnullis majoribus cellulis chromatophoris minore magnitudine, numerosioribus. Granulis amylosis circum corpora pyrenoidea et in stromate distributis; materia lipoidea absente. Nutritione phototrophica. Corporibus trichiformibus distributis in cytoplasmate superficiali, numerosioribus prope conjunctionem valvarum. Cellula non toxica piscibus.

Generans asexualiter per fissionem cellularum motilium ad duas cellulas filiolas pares vel impares magnitudine pariendas.

Isolata exemplis aquae marinae prope Knap Buoy, regione Plymouth Sound, profund. 8 metr., 30 jun. 1949. Cultura typica conservata (Plym. num. 18) ad Laboratorium Marine Biological Association, Plymouth.

Species dedicata in honorem Mariae V. Lebouriae, doctoris scientiarum, die natali suo octogesimo.

We wish to thank Dr J. E. Morton (Queen Mary College) for translating the English diagnosis into Latin.

Description

Cells are strongly compressed when young (Fig. 5), but gradually increase in size and thickness by the growth in width of the striated band at the edge of each valve (Figs. 1–3, 6); sphaeroidal cells are usually incipient fission stages. The striated edges of the valves appear thicker than the poroid region, and the striae apparently alternate on the two valves (Fig. 7). The striated band of one valve completely overlaps the other until the incipient fission stage is reached (cf. Figs. 6, 7). In the young stage the flange on the left valve, bearing the flagellar pores, is very little developed, and the pores lie in the poroid region. As the cell increases in size the flange becomes more obvious since a region of non-striated material, equivalent to the width of the striated margin, is laid down between the poroid region of the valve and the flagellar pores (Fig. 4); the flagellar pores therefore remain near the edge of the flange.

The position of the flagellar flange on the left valve is variable. When observed in left valve view it is usually situated to the right of the centre line (Fig. 1), but depending on the shape of the valves may be on, or even slightly to the left of, the centre line. Whatever the position of the flange on the left valve, the smaller (*ca.* 0·5 μ) circular pore is always to the left of the larger (*ca.* 1·5 μ) triangular pore (Figs. 1–4) (cf. *Porella perforata*, Braarud, 1945).

As the cells increase in size and thickness the two chromatophores break up, giving from four to six disc- to ribbon-shaped chromatophores (Fig. 2). Individual chromatophores are then difficult to distinguish as they overlap and intertwine round the many other cell contents. The two pyrenoids, one on the inner face of each chromatophore in the more compressed cells (Figs. 1, 5), can be more easily seen than those (usually four) in the thicker larger cells (Fig. 2). The addition of extremely dilute iodine will, however, show up the

pyrenoids more clearly by staining them orange-brown. This dilute iodine also stains blue the very numerous disc-shaped bodies, up to 1 μ in diameter, which we take to be starch (Figs. 1, 2 and 5). They surround the pyrenoids and are also freely distributed in the cytoplasm. Both pyrenoids and starch grains are masked by the staining of other cell contents when strong iodine is used. No lipoid reserve has been detected by the use of osmium tetroxide, Sudan black and Sudan IV.

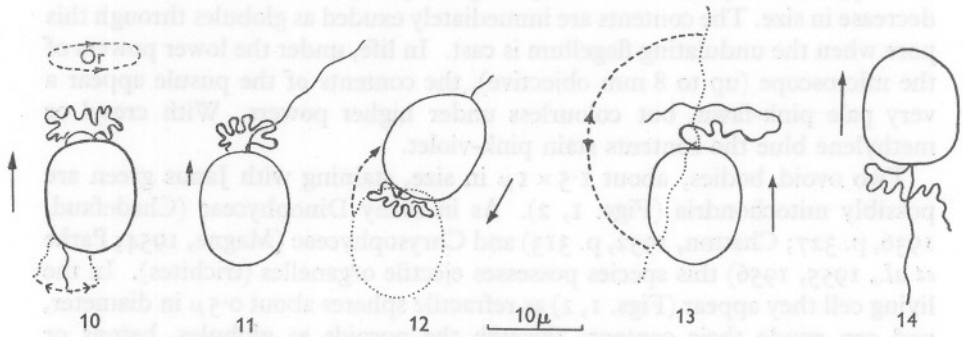
Tests with graphite (cf. Parke, Manton & Clarke, 1955, p. 582) have given no evidence of phagotrophy. Minute granules (about 0·5 μ) showing Brownian movement have, however, been found in the large, but not in the small, pusule (Fig. 2). The origin of these granules is unknown. The large pusule (Figs. 1, 2 and 5), which opens into the large flagellar pore, can be seen to increase or decrease in size. The contents are immediately exuded as globules through this pore when the undulating flagellum is cast. In life, under the lower powers of the microscope (up to 8 mm objective), the contents of the pusule appear a very pale pink-fawn, but colourless under higher powers. With cresyl or methylene blue the contents stain pink-violet.

Two ovoid bodies, about 1·5 × 1 μ in size, staining with Janus green are possibly mitochondria (Figs. 1, 2). As in many Dinophyceae (Chadefaud, 1936, p. 327; Chatton, 1952, p. 313) and Chrysophyceae (Magne, 1954; Parke *et al.*, 1955, 1956) this species possesses ejectile organelles (trichites). In the living cell they appear (Figs. 1, 2) as refractile spheres about 0·5 μ in diameter, and can exude their contents through the poroids as globules, batons or threads (Fig. 1). With cresyl or methylene blue they stain a deep clear blue (cf. Chrysophyceae, Parke *et al.*, 1955, 1956).

During swimming the undulating flagellum (≡ transverse flagellum of dinoflagellates possessing a girdle) always moves parallel to, and round, the flagellar pole, only the speed and amplitude of the undulations varying. The position of the so-called longitudinal flagellum varies with the speed of movement of the cell. During rapid swimming it is backwardly directed and vibrates quickly (Fig. 10). Movement of the cell is in an irregular double spiral with many changes of direction. When the cell changes direction the 'longitudinal' flagellum sweeps rapidly forward, the cell stops and the body immediately turns over to lie on the 'longitudinal' flagellum (Figs. 10–12). The cell then swims away in the new direction. Larger, more sphaeroidal, cells rotate relatively more slowly with a more rolling motion. During slow movement there is no rotation of the body. The cells usually move with the flagellar pole foremost, and with the 'longitudinal' flagellum either directed backwards, and not apparently moving, or sweeping slowly backwards and forwards in a half circle (Fig. 13). Occasionally the cell moves with the non-flagellar pole foremost (Fig. 14) for short periods. Although no stigma can be detected, this species shows a phototactic reaction when exposed to uneven illumination.

At the peak of growth a culture of this species in Erdschreiber solution will produce about 200,000 cells per ml., which is close to the production of cells (160,000/ml.) in a culture of *E. baltica* Lohmann (Plymouth no. 28).

Cell division takes place in the motile state. As the incipient fission stages gradually increase in thickness, the two valves move apart. At first the wide striated region of the valves is seen as two distinct bands (Fig. 7). After this stage these broad bands are not visible, and there appears to be an area of naked protoplasm between the two valves (Fig. 15). Division of the nucleus then occurs and the two new flagella are formed (Figs. 15, 16). Fission of the body starts at the non-flagellar pole and proceeds until the two daughter-cells are joined by only a narrow connexion near the flagellar pole (Figs. 8, 16–18).



Figs. 10–14. *Exuviaella mariae-lebouriae* n.sp. (× 1250). Cells showing positions of flagella in relation to the body during swimming. Arrows show direction of movement.

Fig. 10. 'Longitudinal' flagellum backwardly directed, vibrating rapidly, as in fast movement.

Fig. 11. 'Longitudinal' flagellum sweeps forward, cell slows down to change direction.

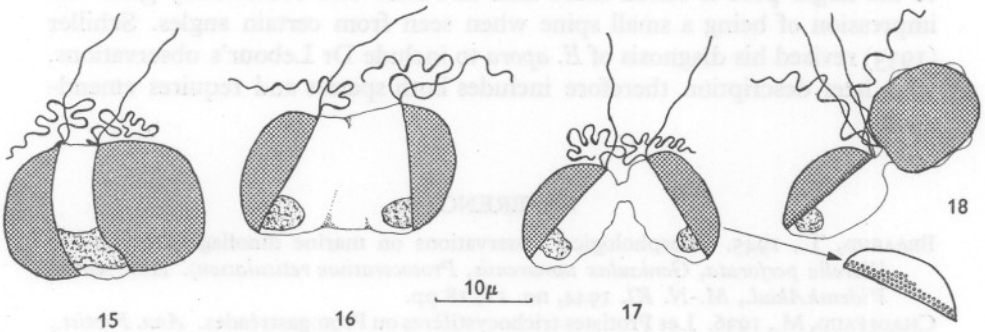
Fig. 12. Cell-body turns over to lie over the 'longitudinal' flagellum, to complete the change of direction.

Fig. 13. Cell showing action of flagella in slow movement with flagellar pole foremost. 'Transverse' flagellum moves with looser and slower undulations.

Fig. 14. Slow movement with non-flagellar pole foremost.

The two daughter-cells swim joined together for some time, then break apart. Each daughter-cell usually retains one valve and secretes one new one. Small cells with one valve and the remainder of the body showing a lobed outline are seen frequently (Fig. 9). Examination of the valves on late fission stages and newly separated daughter-cells shows that they either lack, or have only very narrow striated margins (Figs. 9, 17); the flange bearing the flagellar pores is also very small (see p. 646). It is thought that the prominent flange and the wide striated margin of the incipient fission stage is either cast or resorbed during fission. If this is the case both daughter-cells will develop new flagellar pores and this is consistent with the evidence obtained from the examination of the valves of young specimens.

Of the species which show a superficial resemblance to *E. mariae-lebouriae*, *E. compressa* Ostenfeld and *E. pusilla* Schiller differ in having only one flagellar pore; they can also be distinguished by other characters. *E. cordata* Ostenfeld appears rather similar but has a depression at the flagellar pole and has thick-walled valves which apparently lack striated margins. *E. baltica* Lohmann is similar to *E. mariae-lebouriae* in having two flagellar pores and striated margins to the valves (Woloszynska, 1928; also Plymouth Culture no. 28—private communication from Professor T. Braarud and our own observations using a light microscope). *E. baltica* differs, however, in being smaller and almost spherical, in having smaller flagellar pores, in lacking poroids



Figs. 15–18. *Exuviaella mariae-lebouriae* n.sp. (× 1250). Stages in cell division (see also Figs. 7–9). Valves are indicated by stippled area.

Fig. 15. Early fission stage: the two new flagella are formed and the valves lie apart, leaving an area of naked protoplasm; the broad striated bands at the margins of the valves of incipient fission stages cannot be seen.

Fig. 16. Nucleus has divided, and cell begins to show indentations at poles.

Fig. 17. Later stage of fission, showing position of valves. The inset diagram of one valve shows the poroids extending to the margin of the valve, i.e. striated area is lacking.

Fig. 18. Last stage of fission before daughter-cells break apart; one daughter-cell has twisted round with respect to the other, showing one valve in face view; new valves are not yet formed.

and in the chromatophores being much more distinct and more deeply pigmented, although both species produce starch as a reserve product. *E. apora* Schiller (1918, p. 258) is larger (30–32 μ × 21–26 μ) than *E. mariae-lebouriae* and the valves lack poroids. In the original diagnosis of *E. apora* there is no mention of the edges of the valves being striated, nor is the number of flagellar pores given. Lebour (1925) placed specimens (16–22 μ long) found near Plymouth in Schiller's *E. apora*, but states: 'It is possible that there are here two separate species....' In these specimens she records the presence of two flagellar pores and striated margins in the older cells. She also records the breaking up of the two chromatophores into small spheres (cf. Martin, 1929, p. 10). No poroids in the valves were observed by Dr Lebour, but these can be seen only with critical brightfield illumination and objectives of very high resolution or

with dark-ground illumination using a 4 mm objective. We are certain that our material is identical with that described and figured by Dr Lebour and therefore designate her Plymouth specimens, placed by her in *E. apora* Schiller, as *E. mariae-lebouriae* n.sp. (non *E. apora* Schiller). Martin (1929) records *E. apora* from New Jersey and states he has 'no hesitation in applying this name in Lebour's sense to our material. Whether it is the same as Schiller's original species is less certain.' In his description Martin mentions that a small spine is sometimes present on the left valve but that it is seen with difficulty and only in certain positions. We have not observed spines on the left valve in our material, but in some specimens the margin of the larger pore is raised more than in others and occasionally gives the impression of being a small spine when seen from certain angles. Schiller (1933) revised his diagnosis of *E. apora* to include Dr Lebour's observations. This later description therefore includes both species and requires emendation.

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THE PHOTOSENSITIVE PIGMENTS IN THE RETINAE OF DEEP-SEA FISH

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(Text-figs. 1 and 2)

The deep-sea fishes might be expected to have eyes specialized for their environment because this differs in some striking respects from that of terrestrial and shallow water animals. The groups of mid-water oceanic fish on which most of these experiments were made live in the 'twilight' zone of the ocean. Here daylight, much attenuated by the sea water through which it has passed, is blue-green in colour, and the light given by the luminescent organs of animals is an important fraction of the total light available (Clarke & Wertheim, 1956). These animals probably have two visual tasks, the first that of perceiving the daylight above by which they must regulate their daily vertical migrations, and second seeing the small flashing photophores of other animals or the small shadows of other animals against daylight which serve to guide them to their food and their mates and to warn them of the presence of enemies. These two tasks do not demand the same kind of eye.

To see small spots of light efficiently a large collecting pupil is needed, and a large eye such as the eye of an oceanic squid, provided that it can form a good image, will have very distinct advantages over a small one. To see a very large field such as that given by the daylight coming through sea water the size of the eye is not important, but only the aperture, i.e. a relationship between size of pupil and the other dimensions of the eye. But whatever the structure and use of the eye the efficiency with which the retina absorbs the light quanta incident on it will be of the first importance. The light penetrating oceanic waters best is blue-green in colour, and the deeper the ocean is penetrated the more and more the penetrating light becomes confined to a narrow band of wavelengths around 475 μ (Jerlov, 1947–8). This fact has suggested to Marshall (1954) that the eyes of deep-sea fish would be especially sensitive to such blue light, a prediction which has been borne out by experiment (Denton & Warren, 1956).

METHODS

The eyes of many deep-sea fish are quite small and are not in general available in such numbers as to make the classical methods of extraction useful. The measurements were therefore made on intact retinae using new methods

described in detail elsewhere (Denton & Wyllie, 1955; Denton, 1954; Denton & Walker, 1957) which demand only very small areas of retina. Such methods have the added advantage of giving directly the density of pigment in the retina, a quantity essential to an evaluation of the possible sensitivity of the eye. The method is briefly as follows: (1) Under Ringer's solution the retina is dissected from the dark adapted eye. It is floated rod-side uppermost into a chamber made by fixing a ring of wax on to a microscope slide and then, after filling with Ringer's solution, this chamber is closed with a cover glass. (2) An image of the retina is thrown by a $\frac{2}{3}$ in. objective on to a diaphragm and the retina moved until the image of a uniform part of the retina in which the rods are upright is seen to fall on the hole in the diaphragm. The eye of the observer is replaced by a photomultiplier tube which thus collects light which has passed through one thickness of a small area of retina. (3) The colour and intensity of the light reaching the retina can be changed by neutral and colour filters placed between the light source and the substage condenser of the microscope. The output of the photomultiplier is measured with a Cossor oscillograph (Model 1049). (4) Measurements are made for a series of colour filters both before and after bleaching the retina with strong white light. The assumption is made (Denton & Walker, 1957) that the retina contains no photosensitive pigment appreciably absorbing deep red light of wavelength about 650 mμ, and that this light can be used as a reference light showing changes in sensitivity of the light source and recording system. Corrections are thus calculated which are used for measurements with other colour filters. The apparatus is very robust and, since the measuring instrument is virtually without inertia, it can be used aboard ship without any special difficulty. The apparatus was not appreciably disturbed by the movement of the ship in any but the heaviest seas.

MATERIAL

The experiments were made on freshly caught deep-sea fish; some aboard R.V. *Sarsia*, and others aboard R.R.S. *Discovery II*. Aboard R.V. *Sarsia* the fish were caught in the Bay of Biscay off the continental shelf by verticals hauls made from 2000 m with a 2 m stramin ring trawl. Aboard R.R.S. *Discovery II* the fish were caught in an Isaacs Kidd mid-water trawl fished at various depths estimated at being between 200 and 1500 m. The catch was generally brought up either at twilight or after dark and care taken not to expose the fish used for experiments to bright lights. Some of the fish used were alive when brought to the surface but others were dead. Since the haul with the Isaacs Kidd trawl was generally for 4 h it is possible that some fish had been dead for 4 h before experiments were begun.

RESULTS

EFFECT OF TIME ON THE DIFFERENCE CURVE

On bleaching a retina by exposing it to a bright light a chain of reactions is started which continues in the dark. These reactions were first described by Kühne (1878) in his classical work on visual purple. The retina of the frog, which Kühne used extensively, is rose pink in colour when unbleached and passes, following exposure to a bright light, through orange and yellow to become finally colourless. Similarly, following bleaching, the photosensitive pigments in the retinae of deep-sea fish, which are all golden in colour when unbleached, undergo a series of reactions in which the products have absorption spectra displaced progressively farther towards the ultra-violet. This is shown in Figs. 1 A and B, in which difference curves (a difference curve shows the change in density between unbleached and bleached retinae as a function of wavelength) at various times following bleaching are given. No matter how long a time is given after bleaching, the products of bleaching are always appreciably more heavily absorbing in the deep blue and near ultra-violet than the unbleached pigment from which they were formed. This is very characteristic of this group of golden pigments. Rhodopsin and porphyropsin pigments in the intact retina usually give products of bleaching in which the absorption in the deep blue and near ultra-violet is very like, or less, than that of the unbleached pigment.

For the deep-sea fish the dark reactions go on very slowly after the first hour following bleaching. Most of the difference curves given here are of difference in density between an unbleached retina and the retina an hour after bleaching.

EFFECT OF TIME AFTER DEATH OF THE ANIMAL AT WHICH MEASUREMENTS ARE BEGUN

To find the possible effect of the death of an animal for a period of 4 h before observations are made (4 h was the time of a typical haul), measurements were made on the retinae of a *Chauliodus sloanei* which was caught alive. One retina was dissected and used immediately after death, whilst the other retina was dissected and used 4 h later. Fig. 1 C shows that the difference curves are very similar except that the dark reactions following bleaching have gone less far in the later preparation. The consequent distortion of the curve is very slight over most of the visual spectrum and insufficient to displace the wavelength of maximum difference in density.

The maximum density change on bleaching was smaller for the 'older' preparation. The maximum density change for the first retina being 0·67 and of the second 0·40. It was the rule in these experiments that high retinal densities were always found in those fish caught alive.

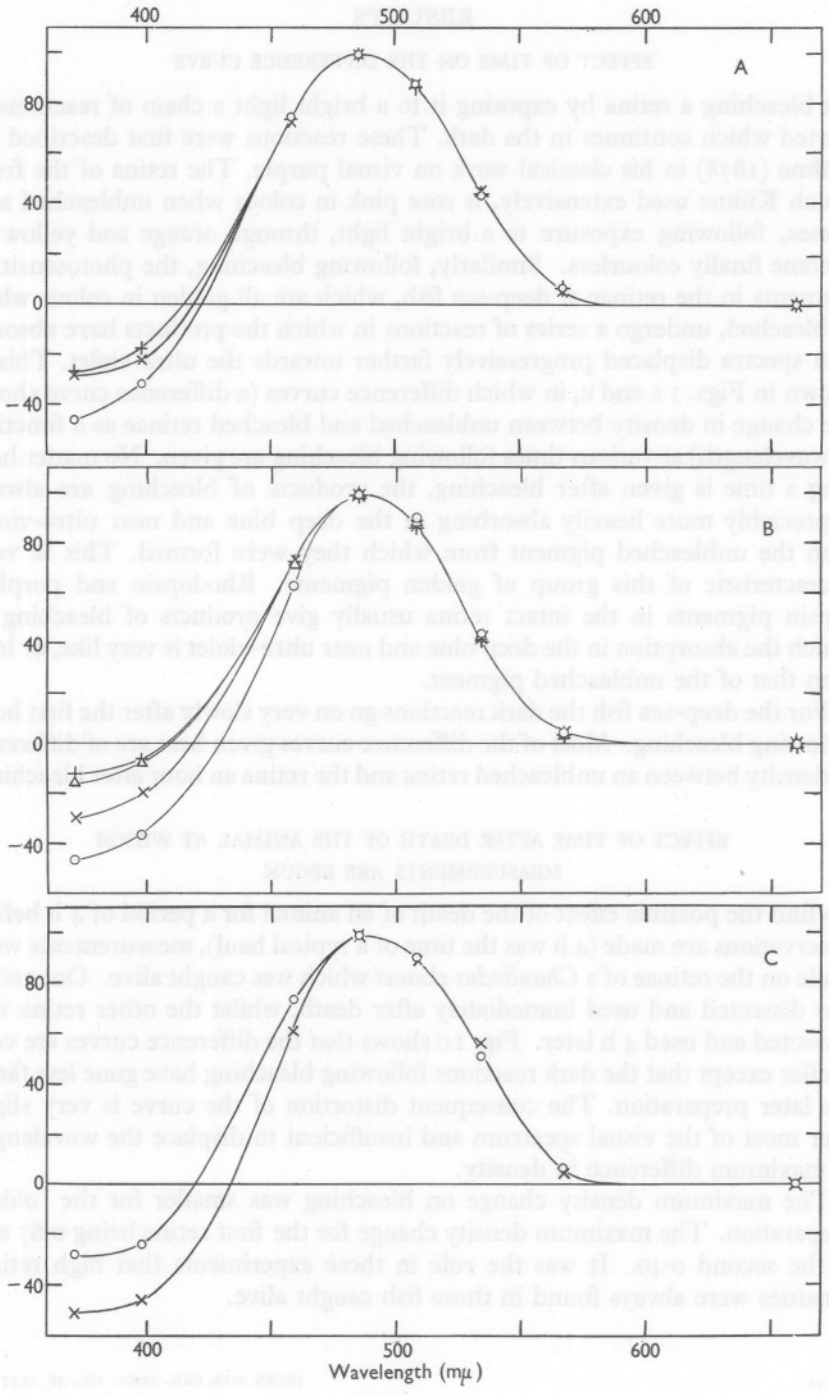

Fig. 1

DENSITY OF PIGMENT

The density change on bleaching was measured for all the preparations used (Table 1). The maximum density change was always for light of wavelengths around 485 mμ. When the measurements were completed it was always possible to see the small area of colourless bleached retina in the otherwise golden-coloured retina, and thus confirm that only one thickness of retina had been used for the measurements on which the density change is based.

TABLE 1. DENSITY CHANGE ON BLEACHING FOR LIGHT OF WAVELENGTH 485 Mμ

Family	Species	Max. density change
Melamphaidae	*Melamphaës megalops* Lütken	0·19
,,	*Melamphaës unicornis* Gilbert	0·56
Synaphobranchidae	*Synaphobranchus kaupi* Johnson	0·27
Sternoptychidae	*Argyropelecus hemigymnus* Cocco	1·08
,,	*Argyropelecus aculeatus* C.V.	1·20*
,,	*Argyropelecus olfersii* (Cuvier)	0·78
Chauliodontidae	*Chauliodus sloanei sloanei* Schneider	0·67
,,	*Chauliodus danae* Regan & Trewavas	0·46
Myctophidae	*Lampanyctus ater* Tåning	0·31
,,	*Diaphus rafinesquei* (Cocco)	0·43
,,	*Lampadena braueri* Zugmayer	0·21*
,,	*Myctophum punctatum* Rafinesque	0·41
Gonostomatidae	*Gonostoma elongatum* Günther	1·01
Searsidae	*Searsia* sp.	1·21
Diretmidae	*Diretmus argenteus* Johnson	0·98*
Argentinidae	*Opisthoproctus soleatus* Vaillant	0·54
Stomiatidae	*Stomias boa* (Risso)	0·79
Melanostomiatidae	*Flagellostomias* sp.	0·58

* For these retinae only the density change at 485 mμ was measured and not the difference curve.

To these we may add *Conger vulgaris*, 0·58 (see Denton & Walker, 1957).

Of the oceanic fish examined only one, a surface-living fish, *Scombresox saurus*, had a rose-coloured retina. The maximum density change for its retina was at 508 mμ and was 0·60 and the difference curve typical of the coastal fish.

SHAPE OF ABSORPTION CURVES

Parts of all retinae were examined visually in white light. All were found to have golden-coloured pigments except the gar fish (*Scombresox saurus*), which was rose-coloured, and the myctophid *Diaphus rafinesquei* (Cocco), which was

Legend to Fig. 1

Fig. 1. Curves show difference in density between unbleached and bleached retina plotted against wavelength. The maximum fall in density on bleaching is made equal to 100%. A, *Argyropelecus hemigymnus* Cocco: ○——○, 4–20 min after bleaching; ×——×, 35–45 min. after bleaching; +——+, 60–70 min after bleaching. B, *Gonostoma elongatum* Günther: ○——○, 1 h after bleaching; ×——×, 2 h after bleaching; △——△, 6 h after bleaching; +——+, 24 h after bleaching. C, *Chauliodus sloanei sloanei* Schneider, showing the effect of death of animal on the density difference curve between unbleached and bleached retina. The measurements on bleached retina were made 1 h after bleaching. ○——○, retina dissected immediately after death; ×——×, retina dissected 4 h after death.

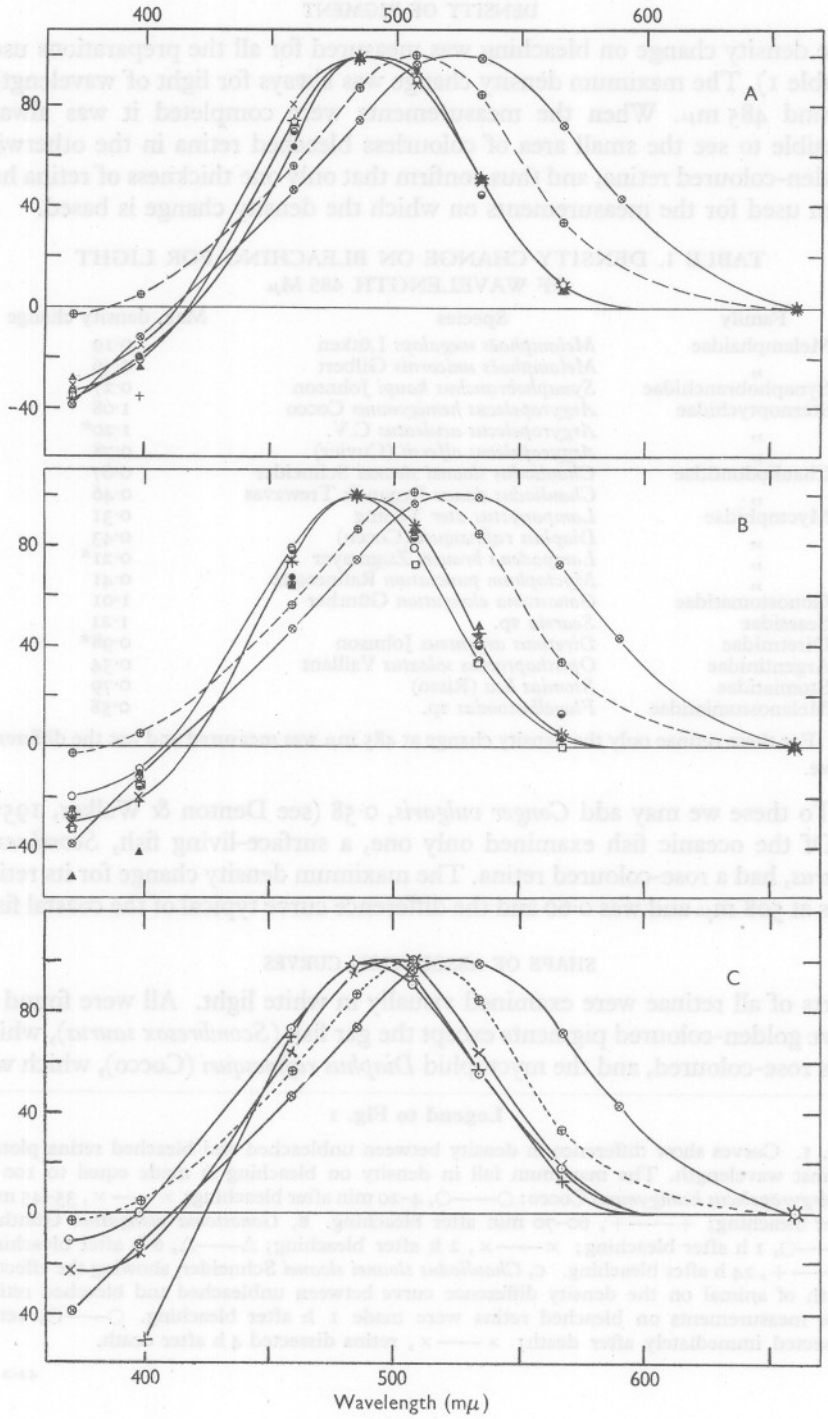

Fig. 2

noted as having a colour intermediate between that of the conger and the gar-fish, and was later found to give an absorption curve that fell between those for these two fish.

The results for the fish are plotted in three groups: (1) the difference curve very closely resembles that of the conger eel (Fig. 2A); (2) the maxima of absorption are displaced a little farther towards the blue than the conger eel (Fig. 2B); (3) the maxima of absorption are displaced a little farther towards the red than the conger eel (Fig. 2C).

One other species, *Argyropelecus aculeatus* C.V., was examined visually and found to have a golden-coloured retina, but absorption curves were not measured on it.

DISCUSSION

A good number of visual photosensitive pigments are now known and recent work, particularly by Dartnall and his collaborators, has shown that the types of scotopic visual pigments are more varied than was at first thought. The broad generalization, however, made by Wald (1945–6) that freshwater fish have retinae containing principally purple-coloured pigments (porphyropsins), whilst the coastal marine fish have retinae containing principally rose-coloured pigments (rhodopsins) remains substantially true. As a result of the present experiments it seems likely that the great majority of deep-sea fish, if not all, have retinae containing principally golden-coloured pigments and thus form a third great grouping. Denton & Warren (1956) have suggested the names chrysopsins or visual golds for these golden-coloured pigments. On the basis of the experiments described here we cannot eliminate the possibility that some of these golden-coloured retinae contain mixtures of pigments. [Miss M. A. Walker (private communication) finds that a digitonin extract of the retinae from six *Diaphus rafinesquei* (Cocco) caught in the same haul as the one used in the experiment described above, contained in fact only one photosensitive pigment.]

The difference curves shown in Fig. 2 for deep-sea fish differ from those measured on rhodopsin and porphyropsin retinae in that the increase in density

Legend to Fig. 2

Fig. 2. Curves showing density difference between unbleached and bleached retinae plotted against wavelength. The maximum fall in density for each retina is made equal to 100%. A, Curves for the following species: ○—○, *Conger conger*; ×—×, *Myctophum punctatum* Rafinesque; +, *Flagellostomias* sp.; ●—●, *Melamphaës megalops* Lütken; ▲, *Chauliodus sloanei sloanei* Schneider; ◒, *Opisthoproctus soleatus* Vaillant. For comparison: ⊕ - - - ⊕, *Cottus bubalis*; ⊗—⊗, sea trout. B, Curves for the following species: ○—○, *Argyropelecus olfersii* (Cuvier); +, *Argyropelecus hemigymnus* Cocco; ×—×, *Gonostoma elongatum* Günther; ▲, *Chauliodus danae* Regan & Trewavas; ●, *Melamphaës unicornis* Gilbert; ◒, *Searsia* sp.; ■, *Synaphobranchus kaupi* Johnson. For comparison: ⊕ - - - ⊕, *Cottus bubalis*; ⊗—⊗, sea trout. C, Curves for the following species: ○—○, *Lampanyctus ater* Tåning; +—+, *Stomias boa* (Risso); ×—×, *Diaphus rafinesquei* (Cocco). For comparison: ⊕ - - - ⊕, *Cottus bubalis*; ⊗—⊗, sea trout.

on bleaching for wavelengths between 380 and 400 mμ is much greater. This characteristic, which they share with the conger eel and the silver freshwater eel (Carlisle & Denton, unpublished observations) and which must represent a difference in the course of the dark reactions following bleaching, gives another reason for grouping the pigments of these fish together.

Wald (1938–9) has shown that the colour of the principal retinal photosensitive pigment of a freshwater or coastal marine fish is correlated with the fishes' enviroment (more exactly that in which it spawns) rather than with its family affiliations. Here again, for the deep-sea fish, we find fishes of the most varied appearance, habits and families sharing the characteristic of golden-coloured retinae, a property which they share with no other vertebrates so far studied.

The limit to the depth at which daylight could be detected

The known ways of assessing the sensitivity of an animal's eye, that of studying the animal's behaviour or by recording the change in nervous activity of the eye when lights are flashed into it, are not easily used on deep-sea fish, which are difficult to keep alive for more than a few hours and then only aboard a ship whose movements would make electrophysiological recording almost impossible. Even when such methods can be used it is difficult to be sure that behavioural responses are really made at the limit of the animal's sensitivity or that electrophysiological recordings are made from the most sensitive receptor and nervous elements. In this paper the method of approach is that of comparing the eyes of the deep-sea fish with our own and trying to assess what advantages and disadvantages may be given to them by any peculiarities of their eyes in the particular environment in which they live. Clarke (1936) has made estimates of the same type using the known sensitivity of the sun-fish (*Lepomis*) as the starting-point for his calculations.

Clarke & Wertheim (1956) give the energy of penetrating daylight at 610 m (the remaining daylight will effectively all be of wavelength around 475 mμ) as 10^{-6} μW cm^2, which corresponds to a flux of 10^{-5} ergs/sec/cm^2. The incident flux required at the eye for the human just to see a large uniform field of this wavelength is given by Denton & Pirenne (1954) as 10^{-7} ergs/sec/cm^2 of retina, or approximately 4×10^{-7} ergs/sec/cm^2 at the pupil. This would imply that at 610 m in sunlight, in the part of the ocean where Clarke & Wertheim made their measurements, the penetrating sunlight for an observer looking upwards would be about $\times 25$ above threshold. The oceanic waters of Clarke & Wertheim reduced penetrating daylight (at these depths only blue-green light is left) to about 10% for approximately every 120 m and the absorption of oceanic water would, therefore, set the depth at which daylight could just be detected by the human eye at about 950 m. The value given by direct observation by Beebe (1935) is about 550 m, but this refers to daylight in a horizontal sense since the windows of his bathysphere faced towards its side.

Light cannot be effective for vision unless it is absorbed by the photosensitive pigments of the retina, and in this respect the eyes of the deep-sea fish probably have considerable advantages over our own. These include (1) the pupils of deep-sea fish are, relative to the other dimensions of the eye, very much larger than human pupils. For the conger we can easily calculate (see Le Grand, 1948) that the gain in retinal illumination due to this factor is about $\times 2{\cdot}5$. It would be difficult to calculate the gains for some fish, e.g. *Chauliodus sloanei*, because the crystalline lens does not fill the pupil, but we can easily show that even an eye with no dioptric system and with light falling directly on to the photosensitive surface the gain would be $\times 5$, and this is the maximum possible gain. (2) The eye media of the human eye absorb about 50% of light of 500 mμ as it passes from the cornea to the retina. This absorption will almost certainly be much less in the eye media of deep-sea fish because the lenses can be seen to be very transparent and the eyes are very much smaller than human eyes. This may give the deep-sea fish a gain of $\times 2$ in retinal illumination over the human. (3) The density of retinal photosensitive material is usually very much greater in the deep-sea fish than the human. Rushton (1956) gives the human retinal density of rhodopsin for light of 500 mμ as about 0·15, while we find that retinal densities of 1·0 or more are not uncommon in deep-sea fish. This will mean that the human retina will absorb about 30% of blue-green light incident on it whilst the deep-sea fish will absorb about 90% of blue-green light incident on it, thus giving the deep-sea fish a gain of $\times 3$ over the human.

Taking these three factors we may suppose that if a deep-sea fish and a human were both looking at the same large field of blue-green light, the number of quanta absorbed/cm^2 of retina/sec would be between 15–30 times greater for a deep-sea fish than for the human.

This suggests that if man and deep-sea fish are equally efficient at extracting information from absorbed quanta, then the deep-sea fish would see daylight at depths between 130 and 170 m deeper than could man. This would put the maximum depth at which it could see daylight at about 1100 m.

Light of a given wavelength can only be absorbed in packets of energy corresponding to the energy hv of the quantum of that wavelength (h is Planck's constant and v is the frequency of the light waves). The energy of the quantum, for light of 475 mμ, the blue-green light which penetrates oceanic waters best (Jerlov, 1947–8), is about 4×10^{-12} ergs. Even at the absolute threshold for the human eye when looking at a large field the number of quanta *absorbed* by the retinal photosensitive pigments is quite large; Denton & Pirenne give the value of 3000 quanta/cm^2 of retina/sec, a number which leaves a very large margin for improvement in the efficiency of detection. This limit to vision may be set by spontaneous activity in the retina which, to use the jargon of radar, constitutes a 'noise' amongst which the 'signal' of the external light must be detected. Now a likely site of spontaneous activity

seems to be the spontaneous breakdown (in the dark) of the visual photosensitive molecules within the rods which, since light acts by breaking down the molecules, would give rise to nervous activity of exactly the same type as that given by a dim background light. The rate at which human visual purple would have to break down in the dark in order to be the limiting factor in the detection of light, was calculated as being 0·0005 %/h by Denton & Pirenne. We know that in extracts with digitonin it breaks down at the much higher rate of 1 %/h (St George, 1952), whilst Barlow (1956, 1957) has calculated the consequences of the idea that retinal 'noise' sets the limit to visual performance and has, moreover, shown experimentally that many of the predictions of his theory hold good. Reconsidering the possible gain in sensitivity of the deep-sea fish over the human with the idea of retinal 'noise' in mind, we have as before the same advantages because of the greater aperture and greater transparency of eye media, but the extra density of pigment would be much less advantageous because an increase in density is not only accompanied by an increase in signal given by the more effective absorption of the incident light quanta, but also by an increase in 'noise' consequent in the increase in the amount of visual pigment which achieves this extra absorption. The 'noise' will go up as the square root of the density of pigment in the rod and the signal as the fraction of light absorbed. The optimum density of pigment is such that 71·5 % of the light is absorbed (density of 0·55) (Denton & Pirenne) and then the gain over the human would only be $\times 1{\cdot}25$, not $\times 3$, as simple computation of absorption might suggest. The higher densities found in some deep-sea fish would give an even smaller gain than $\times 1{\cdot}25$ over the human. The deep-sea fish probably has, however, an advantage over man for, with an eye at a lower temperature and a photosensitive pigment which although similar in shape to that of visual purple is displaced towards the blue, the spontaneous rate of breakdown of visual photosensitive pigment might be expected to be much lower. To have an idea of the order of such an effect we may consider, as Stiles (1948) and Barlow (1957) have done, a simplified picture where the molecules of pigment have thermal energies distributed in accordance with Boltzmann's distribution, when a reduction in temperature from the mammalian temperature to that of a deep-sea fish will make the pigment $\times 10$ more stable, whilst the effect of the shift of maxima towards the blue from 502 to 485 mμ might be expected to be accompanied by a further tenfold increase in stability. Bridges (1956) finds that in a mixture of two extracted visual photosensitive pigments with maxima at 522 and 533 mμ respectively, the first broke down spontaneously in the dark at a rate forty times more slowly than the second (see also Dartnall, 1955).

Thus on the basis of the 'noise' theory allowing for a more stable retina we arrive at a revised estimate of the sensitivity gain of the deep-sea fish eye over the human eye of 60–120 times instead of 15–30 times, giving an extra range of vision of daylight of about 40 m deeper than that calculated above, and

putting the maximum depth at which the deep-sea fish can see daylight at about 1150 m.

We have not taken account of the possibility of extra physiological summation in area and time in the retinae of deep-sea fish, but the eyes of deep-sea fish are often small and would not permit of much extra area summation over that found in humans, whilst against physiological summation obtained by the absorption of quanta over larger areas and times must be set the possibility of probability summation between independent retinal units. The argument is, however, not a profitable one to pursue because as the intensity of daylight penetrating the ocean falls with depth, the light given by luminescent creatures becomes more and more predominant and no matter how sensitive the eye, the daylight is small compared with this light and the problem is one of intensity discrimination not one of absolute sensitivity. Our estimate of 1150 m is already down at depths at which this must be true.

We are grateful to Mr N. B. Marshall and Dr W. A. H. Rushton for their advice and help, and to the Director of the National Institute of Oceanography for his kindness in giving permission to carry out experiments aboard R.R.S. *Discovery II*. We also wish to express our thanks to Captain C. A. Hoodless and the crew of R.V. *Sarsia* and to Captain S. S. F. Dalgleish and crew of the R.R.S. *Discovery II* for their enthusiastic co-operation.

SUMMARY

Measurements were made on the intact retinae dissected from freshly caught deep-sea fish. The unbleached retinae of such fish are not rose-pink like the retinae of most coastal fish or purple like the retinae of most freshwater fish, but are golden in colour.

The golden colours are of photosensitive pigments which give retinal absorption curves similar in shape to frog's rhodopsin, but with maxima of absorption displaced on the average about 15 mμ towards the blue end of the spectrum. The names 'chrysopsins' or visual golds are suggested for this group of pigments.

The density of such photosensitive pigments is often very high. Retinal density changes on bleaching of more than 1·0 has been found for several deep-sea fish. These probably correspond to absolute retinal densities of pigment of about 1·3, i.e. the absorption of 95% of blue-green light striking the retina.

The conger and silver freshwater eels have retinae containing similar golden-coloured pigments. These eels begin their lives in the deep ocean and return there when mature to spawn.

The significance of this type of photosensitive pigment in the vision of deep-sea fish is discussed, and an estimate is made of the depths at which deep-sea fish will see daylight.

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Note added in proof

F. W. Muntz has recently confirmed (*Science*, 1957, Vol. 125, pp. 1142–3) that deep-sea fish have golden-coloured retinae. He has also shown that *Bathylagus wesethi* Bolin has a retinae containing a mixture of two photosensitive pigments.

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STUDIES IN THE GENUS *FUCUS* L.

II. DISTRIBUTION AND ECOLOGY OF FORMS OF *FUCUS DISTICHUS* L. EMEND. POWELL IN BRITAIN AND IRELAND

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(With Plates I–IV and Text-figs. 1–5)

CONTENTS

INTRODUCTION

In part I of this series (Powell, 1957) the species *Fucus distichus* L. was re-established and emended to include the following four subspecies: subsp. *distichus*, subsp. *anceps* (Harv. et Ward ex Carruthers) Powell, subsp. *edentatus* (De la Pyl.) Powell, and subsp. *evanescens* (C. Ag.) Powell. Of these subspecies, only *anceps*[1] and *edentatus* have been found in the British Isles. Their distribution and ecology in Britain and Ireland are now described.

[1] Throughout the text subspecific names have to be referred to constantly, and will be cited normally as a straight trinomial, e.g. *F(ucus) distichus anceps*. Forms and other lower categories are indicated in the usual way, e.g. *F. vesiculosus* f. *linearis*. Often, to avoid tedious repetition, it is adequate to refer simply to the final epithet, whether subspecies or form, e.g. *anceps*, or *linearis*, alone. Among names of other organisms there are some in which the genus here automatically indicates a single species (e.g. *Alaria esculenta*, *Chthamalus stellatus*), and the specific name can often be dropped.

It is probable that, until the present century, authentic specimens of any form of *Fucus distichus* L. emend. Powell were known in the British Isles only from Kilkee, Co. Clare, Ireland.[1] There, in 1863, W. H. Harvey and N. B. Ward found and described *F. anceps* (see Powell, 1957, for references). Many of the larger herbaria in Britain contain specimens of '*F. anceps*' from Kilkee, most of the specimens being distributed by E. M. Holmes (*Algae Britannicae Rariores Exsiccatae*, Fasc. X, No. 240). As the data on numerous herbarium specimens examined testify, several other collections were made at Kilkee later in the 19th century, the latest known date being September 1897 (collected by 'E. George').

The first authentic British record of *F. distichus edentatus* is that of Börgesen (1903) for the Shetland Islands (14–16 July 1902). He reported that 'well-developed, typical specimens, agreeing exactly with my Faeröese specimens referred to [*F. inflatus*] f. *edentata* (De la Pyl.) Rosenv., occurred abundantly near Lerwick'.

Batters (1902) and Newton (1931) both list *F. anceps* Harv. & Ward as a distinct species (with Kilkee as the only locality) and both mention, but with some doubt, a record by Traill (1885) of '*F. distichus*'.[2]

I first became interested in *F. distichus* during the summer of 1951 when with Dr J. R. Lewis (Leeds) I carried out an ecological survey of the north coast of Scotland. One of the most interesting findings of the survey was the discovery of *F. distichus anceps* along a limited and very exposed stretch of the north coast of Caithness. This remains the only record of any form of *F. distichus* for the mainland of Britain, and in a preliminary announcement of the find (Powell & Lewis, 1952) Börgesen's nomenclature was followed.

During succeeding years I have had opportunities of taking part in several phycological surveys of various parts of the coast of north and west Britain and Ireland, as follows: Fair Isle and part of the Mainland of Shetland in 1952, and parts of the west of Ireland in 1953, in each case with colleagues Dr E. M. Burrows (Liverpool), Dr E. Conway (Glasgow) and Dr S. M. Lodge (Liverpool); and the island of Lewis-Harris (Outer Hebrides) in 1954. These expeditions have yielded further information about the distribution

[1] All other early British records of fucoids that might possibly have referred to this species (e.g. the '*F. distichus*', '*F. inflatus*' and '*F. linearis*' of various authors) have been carefully considered, and almost certainly all refer to forms of either *F. ceranoides* L. or *F. vesiculosus* L. Thus '*F. distichus*' of Lightfoot (1777, p. 912) was probably a very narrow form of *F. ceranoides*; and '*F. inflatus*' Lightfoot (1777, p. 910) and '*F. linearis*' Hudson (1762, p. 467) were forms of *F. vesiculosus*.

[2] Traill (1885, p. 11) records '115. *Fucus distichus*. Cast ashore at Port-Seton (J. R. Henderson, 1882). Only one specimen found. Identified by E. M. Holmes.' I have made unsuccessful efforts to trace this specimen; it is *not* in Herb. Traill (University of Edinburgh), Herb. Holmes, Herb. Batters or General Algal Herb. (British Museum), or Herb. Kew. The specimen probably cannot be traced now and it would seem best to disregard this very doubtful record.

Text-fig. 1. Map to show localities (numbered 1–11) at which *Fucus distichus* has been found in Britain and Ireland. Subsp. *anceps* has been found at localities 1–9, and subsp. *edentatus* at localities 4, 10 and 11.

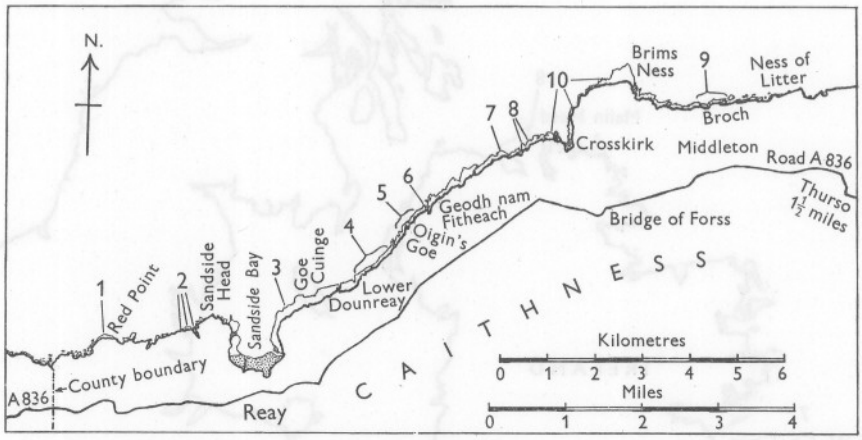
and ecology of forms of *F. distichus*; also, a number of additional valid British records have come to my notice from various sources and are discussed below.

FUCUS DISTICHUS L. EMEND. POWELL, SUBSP. *ANCEPS* (HARV. ET WARD EX CARRUTHERS) POWELL (Pl. I)

DISTRIBUTION

Scotland (see Text-figs. 1, 2)

CAITHNESS. Found, intermittently, only along a limited stretch (about 12 miles) of the north coast, from a point about 3 miles west of Holborn Head (near Thurso) westwards to near the county boundary with Sutherland (July–September 1951). It is possible that the range may extend slightly farther, both east and west, on reefs that are difficult to reach. The principal reefs on which *anceps* was found in the 1951 survey are shown in Text-fig. 2, sites 1–9; more recently (August 1954 and June 1956) Dr E. Conway (accompanied by my wife, Grace Powell, in 1956) has found the plant also at the three sites marked 10.



Text-fig. 2. Map of part of the north coast of Caithness. The principal sites at which subsp. *anceps* has been found are numbered 1–10 (see text).

ORKNEY ISLANDS. Recorded only from three sites, all on the west coast of the Mainland of Orkney. The plants from sites 1 and 2 (Text-fig. 1, locality 2), situated just south and just north of Bay of Skaill, were collected by James Sinclair (Orkney) in 1938 and 1939, respectively. I first heard of them through correspondence with Dr Søren Lund (Charlottenlund, Denmark), and later Mr Sinclair kindly allowed me to examine and identify his her-

barium specimens and to refer to his records here. Details are (1) Hole o'Rowe, Sandwick, Orkney (59° 3′ 4″ N., 3° 21′ 21″ W.), 16 October 1938, common in one spot on an exposed ledge of rock, material all sterile, sheet no. 445 in Herb. J. Sinclair; (2) exposed coast below Garson, Northdyke, Sandwick, Orkney (59° 3′ 40″ N., 3° 21′ W.), 7 May 1939, common on flat rocks, all five herbarium specimens fertile, sheet no. 511 in Herb. J. Sinclair.

For the third Orkney record I am indebted to Dr A. J. Southward (Plymouth), who in May 1953 found one small patch of *anceps* on an exposed reef near Brough Head, north-west Orkney Mainland (Text-fig. 1, locality 3; approximate position 59° 8′ 16″ N., 3° 19′ 39″ W.); the area occupied by the plant was several metres long by 0·5 m wide, on the upper shore among *Chthamalus stellatus* (Poli); material fertile.

FAIR ISLE. Found only at two sites in June–July 1952. At North Gavel, a very exposed site (59° 32′ 28″ N., 1° 35′ 49·5″ W.), *anceps* was fairly common on high-level ledges and rock steps (see Burrows, Conway, Lodge & Powell, 1954). At a second site, occasional scattered plants were found on extremely exposed reefs (59° 30′ 53″ N., 1° 39′ 7·5″ W.) immediately to the west of the South Lighthouse.

OUTER HEBRIDES. *Island of Lewis-Harris.* Cotton (1912, pp. 23–6), in relating the zonation of fucoids in parts of the west of Ireland to the rest of Britain,[1] and to other places in Europe, mentions (p. 23) 'An additional species, *F. inflatus*, was recorded by Börgesen for the Shetland Isles and Mr E. M. Holmes has lately received a specimen of this boreal species from Lewis, so possibly it is a regular constituent of the association in the north of Scotland.' The specimens from Lewis referred to by Cotton are now located in Herb. Kew, and detailed examination has proved that the plants are true *F. distichus* subsp. *anceps*. There are three specimens in Herb. Kew, on separate sheets, as follows: (*a*) a single narrow specimen, labelled '*Fucus inflatus* var. *distichus*, Butt of Lewis, N.B. Coll. W. J. Gibson. April 1909. Comm. E. M. Holmes.' Another label on the sheet indicates that the plant was actually named by F. Börgesen; and attached to the sheet is a letter from W. J. Gibson ('The Nicholson Institute, Stornoway') to E. M. Holmes dated 21 April 1909, stating that the material was collected 'last week' (i.e. about 14 April 1909). Specimen (*b*) is a duplicate of (*a*), labelled similarly, and mounted singly on a separate sheet. (*c*) On another sheet (beside three specimens of authentic '*Fucus anceps*, Kilkee') is mounted one plant labelled '*Fucus distichus*? Stornoway, N.B. Comm. E. M. H. May '09.' I am inclined to think that this is simply another duplicate Gibson specimen from 'Butt of Lewis' that Holmes sent on to someone else (or possibly to Kew) in May 1909; certainly it could not really have been collected in the sheltered environs of 'Stornoway'. All three specimens are fertile.

[1] Curiously, however, Cotton omits to mention in this general discussion Harvey's important record of '*F. anceps*' from Kilkee.

In July–August 1954 I was able to investigate the extreme northern tip of Lewis, but only the accessible parts of the shore north of a line running east to west from just south of Aird Dell on the west coast to just north of Port Skegirsta on the east coast. I found subsp. *anceps* only at two sites (close together; 58° 30′ 3″ N., 6° 13′ 19″ W.) on very exposed reefs, facing E.N.E., at the foot of the headland named Buaile na Faing, which is about 2 miles south-east of the Butt of Lewis. The littoral area of the actual headland and small islets comprising the true Butt of Lewis is precipitous and inaccessible without a rope or a boat and could not be investigated in 1954. Possibly the location 'Butt of Lewis' cited by W. J. Gibson is used in a broad sense, to include some few miles of the northern tip of Lewis.

St Kilda. Algae from the 1952 marine biological expedition to St Kilda (Gauld, Bagenal & Connell, 1953) were identified by me. *F. distichus* subsp. *anceps* (listed as *F. inflatus* f. *distichus*) was found in small quantity (a few plants) at one site only—at the top of the *Balanus balanoides* (L.) belt, on rather steeply sloping rocks at the head of Glen Bay, on the north side of Hirta (57° 49′ 16″ N., 8° 35′ 50″ W.). T. B. Bagenal (Millport) revisited the Glen Bay site on 14 July 1956 and again found *anceps*, in late fertile condition. He reports that the fucoid had greatly increased in amount since 1952, forming a belt up to 1 m wide at the head of the bay, and had spread (although not continuously) along about 100 m of shore altogether.

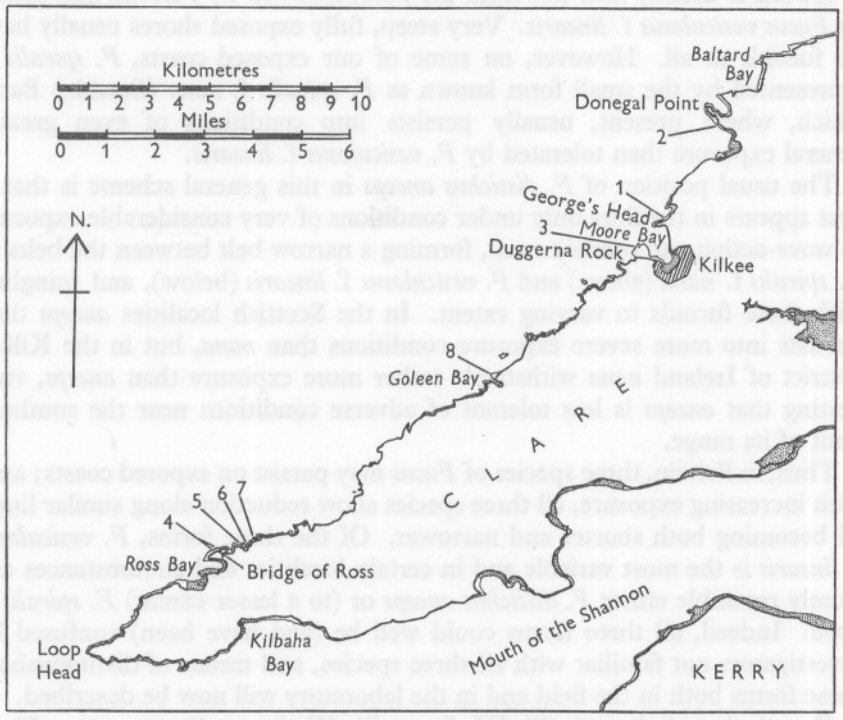
Ireland (see Text-figs. 1, 3)

KILKEE DISTRICT, Co. Clare. (Text-fig. 3.) In July 1953 *anceps* was found at the precise site (Duggerna Rock) at Kilkee where W. H. Harvey first recorded it 90 years before. During the 1953 survey the plant was found also on exposed rocks at several other localities in south-west Co. Clare, both north and south of Kilkee, between Donegal Point and Ross Bay, the exact sites being: (1) George's Head (north side, well inshore, on reefs facing N.N.W.); (2) Donegal Point (midway along south-west flank; the Point itself is a sheer 100 ft. cliff); (3) Duggerna Rock, Kilkee (and on two reefs immediately adjacent to and west of the Rock); (4)–(7) at four separate exposed sites, all within 1 mile of coast, just north of Ross Bay (i.e. from near Bridge of Ross, north-east for about a mile); (8) Goleen Bay (exposed reefs at northern entrance to Bay).

Also in 1953, J. R. Lewis surveyed other parts of the coast of Ireland and found *anceps* at two additional, isolated, exposed sites (Text-fig. 1, localities 8 and 9) as follows:

MALIN HEAD (the northernmost point of Co. Donegal), 4 July 1953, on reefs facing N.N.W. about 250 yards west of Malin Tower (55° 22′ 53″ N., 7° 22′ 56″ W.).

KERRY HEAD, Co. Kerry (52° 25′ 9″ N., 9° 56′ 44″ W.), 6 June 1953. This is the most southerly record of any form of *F. distichus* in Europe.



Text-fig. 3. Map of south-west part of Co. Clare. The sites at which subsp. *anceps* has been found are numbered 1–8 (see text).

DISTINCTION FROM OTHER FUCOIDS

The distribution and ecology of *F. distichus anceps* is most conveniently considered in relation to the other fucoids found in Britain. On sheltered rocky shores, as is well known, the zonation of the littoral Fucaceae association follows a fairly standard pattern. The species occur in more or less well-defined belts in the following order from high-water level downwards: *Pelvetia canaliculata* (L.) Dec'ne et Thur., *Fucus spiralis* L., *Ascophyllum nodosum* (L.) Le Jol./*Fucus vesiculosus* L., *F. serratus* L. With increasing exposure to wave-action some of these dominants are replaced either by other algal species or by animals, but some persist usually in a modified and often reduced form. *Ascophyllum* is usually the first of the series to be eliminated by increasing exposure, followed by the normal bladdered form of *Fucus vesiculosus*, and then *F. serratus*; thus the fucoid zonation on fairly exposed and moderately steep shores is often as follows: *Pelvetia*, reduced plants of *Fucus spiralis*, *F. vesiculosus* f. *linearis* (Huds.) Powell (=f. *evesiculosus* auctt.). With further increase in exposure, or on steeper shores, the normal form of

F. spiralis is usually next lost from the flora, followed by *Pelvetia* and finally by *Fucus vesiculosus* f. *linearis*. Very steep, fully exposed shores usually have no fucoids at all. However, on some of our exposed coasts, *F. spiralis* is represented by the small form known as *F. spiralis* f. *nana* (Stackh.) Batt., which, where present, usually persists into conditions of even greater general exposure than tolerated by *F. vesiculosus* f. *linearis*.

The usual position of *F. distichus anceps* in this general scheme is that it first appears in the flora only under conditions of very considerable exposure to wave-action and oceanic swell, forming a narrow belt between the belts of *F. spiralis* f. *nana* (above) and *F. vesiculosus* f. *linearis* (below), and mingling with these fucoids to varying extent. In the Scottish localities *anceps* then persists into more severe exposure conditions than *nana*, but in the Kilkee district of Ireland *nana* withstands rather more exposure than *anceps*, suggesting that *anceps* is less tolerant of adverse conditions near the southern limit of its range.

Thus, in Britain, three species of *Fucus* may persist on exposed coasts; and, with increasing exposure, all three species show reduction along similar lines, all becoming both shorter and narrower. Of the three forms, *F. vesiculosus* f. *linearis* is the most variable and in certain localities and circumstances can closely resemble either *F. distichus anceps* or (to a lesser extent) *F. spiralis* f. *nana*. Indeed, all three forms could well be (and have been) confused by investigators not familiar with all three species, and means of distinguishing these forms both in the field and in the laboratory will now be described.

F. vesiculosus f. *linearis* (Pl. III, fig. 2, Pl. IV, fig. 1; Cotton, 1912, Pl. I; frontispiece, *Rev. Algologique*, T. 5, fasc. 3–4, 1931; Harvey, 1950, for photograph of plants on Lundy) is extremely variable in form and in conditions of considerable exposure may be reduced to rather erect stunted tufts only a few inches in length and with narrow fronds (but never so narrow as fronds of *anceps* growing at the same site). Fundamentally *linearis* is distinguished from *anceps* by the fact that it is unisexual and dioecious, while *anceps* is invariably hermaphrodite (it should be noted, however, that very old conceptacles of *anceps* may have released all antheridia and may then show a few remaining oogonia only). Also, the midrib in the younger branches of *linearis* is always very distinct and the lateral alae clearly differentiated (even in very narrow thalli), whereas in *anceps* the midrib and the lateral wings are not very sharply differentiated, the distal branches often being practically oval in section (see Plates I, III and IV). These two characters serve to distinguish the two forms in any circumstances and, in addition, *anceps* usually has a variable (small) number of small caecostomata (not present in either *linearis* or *nana*).

At certain exposed places in south-west England and Wales (e.g. the very exposed islands of Lundy and Skokholm) and in the west of Ireland, *linearis* may develop long, narrow, pointed receptacles, very reminiscent of *anceps* (see

Pl. IV, fig. 1). Gillham (1954, p. 217) records '*Fucus inflatus* L.? (*F. anceps* Harv. et Ward)' for Skokholm and Grassholm, but comments that 'it is possible that the plants are merely an extreme rough-water form of *F. vesiculosus*'. In view of the distribution of *anceps* outlined in the present paper, it is practically certain that the plants in question were merely small and narrow *F. vesiculosus* f. *linearis*;[1] Dr Gillham now agrees with this view.

F. spiralis f. *nana* (Pl. IV, fig. 2) varies in size from a few to *ca.* 10 cm in length and has narrow, strap-like thalli, either unbranched or with few dichotomies, and with very distinct midrib and lateral wings. The receptacles are usually small, terminal, globular, and have the sterile rim of tissue characteristic of this species; conceptacles hermaphrodite. The prominent midrib and the shape of receptacle readily distinguish this form from *anceps*; and the hermaphrodite conceptacles, and sterile rim to the receptacles, distinguish it from the most reduced forms of *linearis*.

It is usual for plants of *nana* to have all the apices fertile at the same time; this is a common feature also in *anceps*, and to a lesser extent in *linearis*, especially when the last two forms are growing under the most rigorous conditions that even they can tolerate. The development of this feature in the least favourable environmental circumstances is doubtless of value for the survival of the species.

ECOLOGY AT PARTICULAR SITES

Scotland

Caithness

The 1951 survey included an examination of many sites on the north, north-east and north-west coasts of Scotland (Sutherland and Caithness), but *F. distichus anceps* was found only on very exposed reefs at the sites indicated in Text-fig. 2. Geologically the reefs of the north coast of Caithness are formed of the remarkable Caithness Flagstones (a group of Middle Old Red Standstone), and form virtually unbroken and often very extensive sheets of rock, sloping either very gently or more or less steeply, sometimes from well above effective high-water level down into deep water. More usually, however, the reefs occur in a series one behind the other and more or less parallel with the coast-line, all dipping seawards and with the outermost being very much more exposed than the inner reefs which are comparatively sheltered.

Most of the reefs face north-west or north and, since they dip down directly into deep water and are not protected by offshore reefs or islands, are fully exposed both to oceanic swell and to all the wave-action produced by more local winds. Even during periods of local calm weather these reefs are constantly subject to oceanic swell which breaks as it travels inshore and on the gently inclined reefs sweeps upshore at great speed and may inundate all the lower half of the effective littoral zone even at low tide. As a result, there is a considerable increase in the effective height of the littoral zone, and the littoral plants and animals are able to occupy wider (vertical) zones without suffering undue desiccation. Also the communities of plants and animals present, in the upper littoral especially, are usually much more open than in sheltered localities. The

[1] This belief was strengthened when the author had an opportunity to examine some exposed parts of the shore of Skokholm during September 1956. *F. vesiculosus* f. *linearis* was common but no plants of *F. distichus anceps* were found.

general ecology of the dominant plants and animals found on these remarkable reefs has been described and illustrated by Lewis (1954).

In bays and other sheltered sites between the extensive Flagstone reefs, all the usual fucoids of sheltered British coasts were found. With increasing exposure, some of these were eliminated in the usual sequence and *F. vesiculosus* f. *linearis* became common in the upper part of the mid-littoral zone. On the upper shore, *Pelvetia canaliculata* and *Fucus spiralis* became represented by smaller plants, but *Pelvetia* was soon lost from the open reefs and *Fucus spiralis* persisted only as the small f. *nana*.

Moderately exposed (or very gently sloping) reefs characteristically showed the following zonation of dominant species from low-tide level upwards. *Sublittoral fringe*: dominated by *Alaria esculenta* (L.) Grev. *Mid-littoral zone*: first a broad belt of *Himanthalia elongata* (L.) S. F. Gray, merging upwards into a belt of *Rhodymenia palmata* (L.) Grev.; then a belt of *Gigartina stellata* (Stackh.) Batt./*Balanus balanoides*/*Mytilus edulis* L.; next a belt of *Fucus vesiculosus* f. *linearis*/*Balanus*/*Mytilus*, with the *Balanus* extending to a slightly higher level than the *Fucus*. *Supralittoral fringe*: dominated principally by a wide belt of *Porphyra umbilicalis* (L.) Kütz. (f. *umbilicalis*), with a weft of less conspicuous blue-green algae growing beneath the *Porphyra* plants and also extending to higher levels than *Porphyra*. Frequently patches of *Blidingia minima* (Näg.) Kylin occurred in the lower part of the *Porphyra* belt and extended into the upper part of the mid-littoral zone. Thus, *Fucus vesiculosus* f. *linearis* was often the only fucoid found on such a gently sloping reef.

On more exposed reefs (either those farther out or those with steeper slope) a belt of *F. spiralis* f. *nana* appeared in the lower half of the supralittoral *Porphyra* belt. (In some few instances it was possible to trace a full series of intermediate forms of *Fucus spiralis* from the typical form in shelter through to f. *nana* with more exposure, but more usually f. *nana* occurred as locally isolated populations on the more exposed reefs.) With still greater exposure (on the steeper reefs), *F. distichus anceps* appeared and formed a distinct belt, *ca.* 15–45 cm vertical range, at the level of the general upper limit of *Balanus balanoides*—i.e. between the belts of *Fucus spiralis* f. *nana* (above) and *F. vesiculosus* f. *linearis* (below) where these were also present. With still greater exposure, *F. vesiculosus* f. *linearis* and *F. spiralis* f. *nana* were in turn lost from the flora, leaving *F. distichus anceps* as the sole remaining fucoid on many of the steeper (most exposed) reefs. Still steeper reefs and vertical walls of rock had no fucoids at all; such sites were dominated principally by a high-level belt of *Porphyra*, mid-littoral *Balanus* and *Mytilus*, and *Alaria* on the lower shore.

On the more exposed reefs *Fucus distichus anceps* was often locally abundant (see Pl. I, fig. 1). The smallest plants were those growing at the most exposed sites; at rather less exposed sites the plants were larger and the largest of all were intermediate in size and habit between subsp. *anceps* and subsp. *edentatus* (see Pl. II, fig. 1). However, such large plants have been found at only a very few restricted sites where forms of *F. vesiculosus* and *F. spiralis* were less dominant than was usual with increasing shelter.

The uplifted, open communities of algae developed on the exposed reefs became confined to ever narrower and more exclusive belts on the more sheltered inshore reefs. It is possible that competition from forms of more successful fucoids (*F. spiralis* and *F. vesiculosus*) prevents the establishment (to any great extent) of intermediate forms of *F. distichus* on reefs with intermediate exposure conditions. Or, stated otherwise, *F. distichus anceps* is most abundant on the more exposed reefs probably because generally it is only on these reefs that a suitable 'ecological niche' is regularly available that it can successfully occupy; the equivalent (but narrower) zone on more sheltered reefs becomes increasingly occupied by forms of *F. spiralis* and *F. vesiculosus*.

These general conclusions are based on an examination of many reefs. However, along the 12–15 miles of shoreline in question local variations from the zonation of Fucaceae outlined above were occasionally found. Sometimes these variations could be explained as the result of greater or less exposure very locally, caused by the particular configuration of the reef(s) in question (aspect, angle of slope, and relation to other nearby reefs)—e.g. the presence of a patch of *F. spiralis* f. *nana* above belts of *Pelvetia* and typical *Fucus spiralis* near the sheltered head of one of the inner reefs could be explained in terms of wave-action on the (more exposed) reef in front; waves and swell sweep up the outer reef and some splash dashes over and wets the small area of rock at a high level on the reef behind, just sufficiently for *F. spiralis* f. *nana* to develop there. Observations such as this serve to emphasize that, although *nana* and *anceps* were usually confined to the reefs most exposed to wave-action, these particular forms occur at a high level in a much extended littoral zone, and do not suffer most of the violence of swell and wave-action experienced by plants such as *Alaria* on the lower shore; on the other hand, the upper zones benefit from the almost constant spray of waves breaking lower down the shore.

On several very exposed reefs which otherwise lacked fucoids, patches of *anceps* were present only on the ends of the reefs most affected by spray from breaking waves; again it is probably the spray that is beneficial to this high-level form rather than any possible direct effect of wave-action.

Occasionally, both *linearis* and *nana* were absent from reefs where they were expected to occur. Possibly these reefs are stripped of such populations during exceptionally rough weather.

Fair Isle

At the North Gavel site on Fair Isle (see Burrows *et al.*, 1954) the survey party made a fairly accurately levelled shore transect, to compare the vertical zonation of dominant algae with that developed at the sheltered North Haven not far away. The transects and vertical zonations are given in detail in Burrows *et al.* (1954), which also includes photographs (Pl. 15) of the upper and lower parts of the exposed North Gavel site. The belts of dominant algae present were very similar to those described above for Caithness, but the configuration of the shore was interestingly different. Thus the lower shore, covered with *Alaria esculenta*, consisted of a gently sloping platform, which below low-water level sloped very steeply into deep water; the whole of the *Alaria* platform was constantly washed by swell even on calm days. Above the wide belt of *Alaria* the shore consisted of a series of steep sloping walls and rather flat narrow ledges, backed finally by cliffs. On the line of the transect, the steep mid-littoral faces bore little else but scattered tufts of *Gigartina stellata*, but on less steep mid-littoral slopes nearby, *Balanus balanoides*, *Mytilus edulis* and *Patella aspera* Lamarck were common, together with *Rhodymenia palmata*, *Gigartina stellata*, *Acrosiphonia centralis* (Lyngb.) Kjellm., *Scytosiphon lomentaria* (Lyngb.) Endl., *Callithamnion arbuscula* (Dillw.) Lyngb. and *Ceramium acanthonotum* Carm. ex Harv.; the smaller of these mid-littoral algae were mostly attached to the animals (as often they were in Caithness). Higher still, *Fucus distichus anceps* formed a narrow belt (*ca.* 0·6 m in vertical extent) on rock steps, and among and above it *F. spiralis* f. *nana* was particularly well developed, dominating rock steps through a vertical range of about 1·5 m. A belt of mixed *Porphyra umbilicalis* and *Blidingia minima* extended upshore for 1·5–2·1 m (vertical) on rather steep rock faces above *Fucus spiralis* f. *nana*.

The range of spring tides quoted in *The Admiralty Tide Tables* (1956) for Fair Isle is 1·74 m, but the vertical height of rather steep shore occupied by algae at the exposed North Gavel site was up to 6·1 m (from low-water level to the top of the

Blidingia minima zone). As shown in Burrows *et al.* (1954), the top of the *Alaria* belt corresponded approximately to observed high-water of a neap tide on a calm day, but even on such a day swell broke continuously at this site, and at high-water repeatedly flooded a zone extending upwards for 1·2–1·5 m above the theoretical high-water level (up to the lowest *anceps* plants), and splash from these waves wetted plants growing up to 2·4–2·7 m above high-water level (including all of the *anceps* belt and most of the main *nana* belt). Throughout most of the year the amount of wave-action experienced at this site will be very much greater, and it may be supposed that the high-level belts of reduced fucoids are frequently within the zone flooded by breaking waves, but probably are not often subjected to the maximum violence of waves breaking directly on them. The survival of belts of algae at these very high levels depends upon their being frequently wetted by swell, waves and splash, or else moistened by mist or rain; and the North Gavel site (facing north-east) is also favoured by shade cast by the cliff behind. Some small plants of *nana* were found, in complete shade, in a small gulley as much as 7·5 m above the main *nana* belt on the open ledges below; a trickle of fresh water kept the plants in the shaded gulley moist.

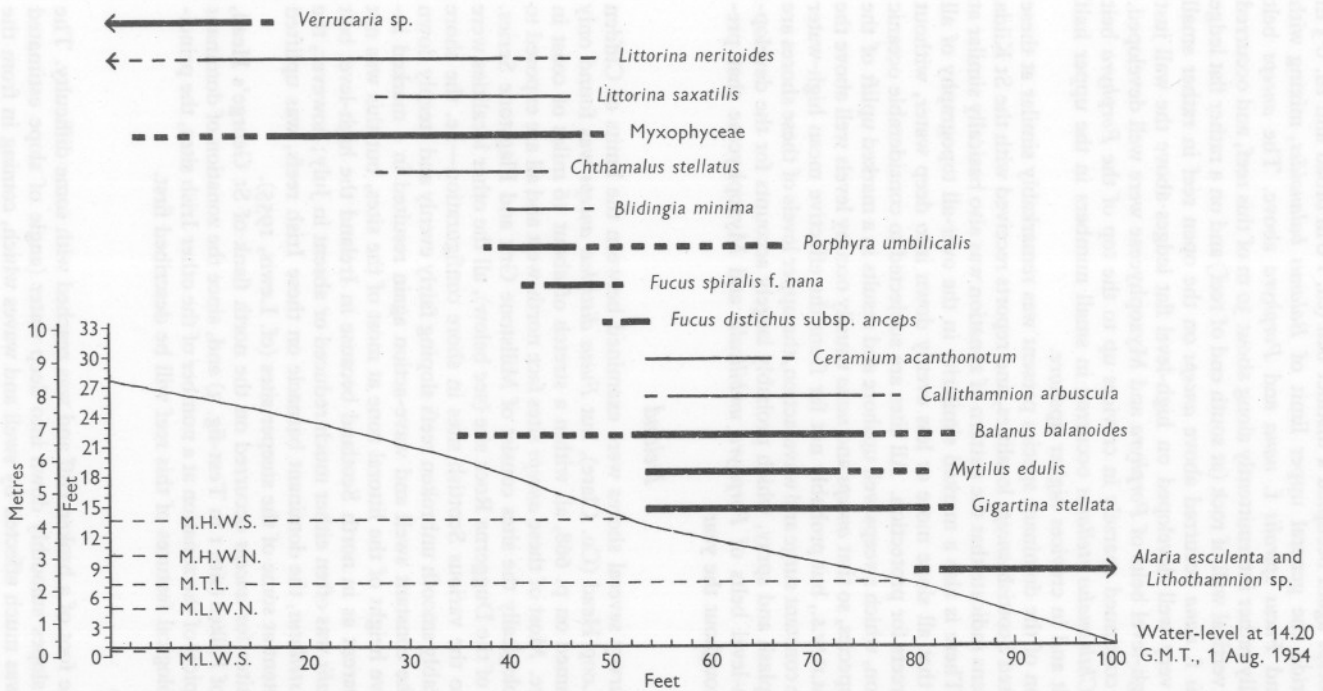
On the whole the plants of *anceps* were smaller than those found on the Caithness reefs and this is probably the result of more rigorous conditions at the North Gavel site, including relatively greater uplift of the whole belt as a result of the unusual (stepped) local rock configuration.

In a shallow high-level pool in the *anceps* belt at North Gavel, two plants of *Fucus distichus* were found which were distinctly narrower than the subsp. *anceps* of open rock and had much shorter receptacles; this narrow pool-plant was in fact intermediate in form between subsp. *anceps* and typical *F. distichus* (subsp. *distichus*) (see Powell, 1957).

At the second site on Fair Isle, a few patches only of *anceps* were found, on very exposed gently sloping reefs facing south-west. Neither *F. spiralis* f. *nana* nor *F. vesiculosus* f. *linearis* was found at or near this site and, as one moved toward more sheltered sites nearby, only one plant of *linearis* was observed. On broad flat reefs a short distance to the north, however, all the usual fucoids of shelter were found. *F. distichus anceps* seems to be only precariously established at this site, and was not found anywhere else on Fair Isle (much of the coast is precipitous and inaccessible); but, at Furse, some *F. spiralis* f. *nana* occurred on the upper shore and, passing into shelter nearby, a whole series of intermediate forms through to the typical form of *F. spiralis* was found.

Island of Lewis-Harris

The site at which *anceps* was found on Lewis in 1954 is accessible from land only by climbing down a 20 m cliff with the aid of a rope. Both the cliff and the shore below are composed of Lewisian Gneiss. The configuration of the shore was very similar to parts of Caithness in that the whole of the littoral zone consisted of a single reef of rather gentle slope for the most part (average *ca.* 15°), with a remarkably smooth and unbroken surface, and dipping directly down into deep water. The whole formed a small natural amphitheatre, limited behind and at each end by steep cliffs. In spite of difficulties, a profile of the shore was made and the zonation of the dominant species measured (Text-fig. 4). The theoretical range of spring tides at this site is *ca.* 4 m, but the coast is very exposed and subject to heavy swell, even though it lies on the east side of the Butt of Lewis. However, it will be seen from Text-fig. 4 that the zones of algae were not uplifted to quite the same extent (in relation to theoretical mean tide levels) as they were at North Gavel, Fair Isle. Thus at the Lewis site the belt of *Alaria* was uplifted only to about theoretical M.T.L., compared with M.H.W.N. (theoretical level) at North Gavel.



Text-fig. 4. Transect at Buaile na Faing headland, Island of Lewis, 1 August 1954. The belts occupied by the dominant species are shown by thick continuous lines, while the zonation of some of the less common species is shown by thinner unbroken lines; in each case the broken lines indicate decreasing frequency of occurrence. The vertical heights of belts were measured from a datum corresponding to the observed level of the sea at 14.20 G.M.T. (approximate predicted time of low water at Stornoway); on the vertical scale, this datum has been made to correspond to the height for low water predicted for Stornoway that day (1·0 ft.). The mean tidal heights indicated against the vertical scale are those given in *The Admiralty Tide Tables* (1956) for Stornoway—a sheltered harbour some 25 miles south of the transect site.

Fucus distichus anceps again occupied a distinct belt (*ca.* 1·0 m broad and *ca.* 0·5 m vertical range) astride the general upper limit of *Balanus balanoides*, mixing with *Gigartina* below and *Fucus spiralis* f. *nana* and *Porphyra* above. The *anceps* belt extended horizontally rather intermittently along about 30 m of this reef, and occurred also on an adjacent vertical wall of rock (at south end of reef) and on a rather flat ledge above it. *F. spiralis* f. *nana* occurred above *anceps* on the open reef in rather small quantity, but was very well developed on high-level flat ledges above the wall just mentioned. The high-level belts of *Porphyra* and Myxophyceae were well developed. *Balanus balanoides* continued sparsely in crevices up to the top of the *Porphyra* belt and even higher. *Chthamalus stellatus* occurred in small numbers in the upper half of the *Porphyra* belt and in crevices higher upshore.

Thus the zonation of the dominant species present was remarkably similar at these three widely separated Scottish *anceps* localities, and reports received with the St Kilda and Orkney specimens indicate that the pattern of zonation was also basically similar at those *anceps* sites. There is also a marked similarity in the over-all topography of all the *anceps* reefs in that all slope more or less evenly down into deep water, without offshore islands or reefs for protection. All sites are subjected to considerable oceanic swell and wave-action, which sweeps well upshore and results in a marked uplift of the zones of dominant species, so that *anceps* and *nana* usually occupy levels well above the *theoretical* level of M.H.W.S., but probably not far from the effective mean high-water level. Because of the constant surge and wave-action, the upper levels of these shores are much affected by splash and spray, which probably largely accounts for the development of good high-level belts of *Porphyra umbilicalis* and Myxophyceae that presumably persist throughout the year.

Ireland

During the 1953 survey several shores were examined between the limits of Clifden (Connemara) and Loop Head (Co. Clare), but *Fucus distichus anceps* was found only at the eight sites named on p. 668, all within a stretch of about 16 miles of coast in south-west Co. Clare. Most of these *anceps* sites face north-west and all are exposed to Atlantic swell. Geologically the sites consist of Millstone Grit and Flagstone Series. With the exception of the Duggerna Rock site (see below), all the other localities were essentially similar to the various Scottish sites in shore configuration—i.e. the shore consisted of remarkably smooth unbroken reefs sloping fairly evenly and steeply down into deep water. The constant swell and wave-action again resulted in a marked increase in the effective height of the littoral zone at most of the sites, but this was not so immediately apparent as in north Scotland because in Ireland the high-level belt of *Porphyra umbilicalis* was often either much reduced or absent in July; however, the belt of *Chthamalus stellatus*, the dominant barnacle on these Irish reefs, was uplifted to a considerable extent at some of the steeper sites (cf. Lewis, 1955).

One of the best sites for *anceps* occurred on the north flank of St George's Head, about 1 mile north of Kilkee (site 1 in Text-fig. 3) and, since the zonation of dominant species there was typical of the zonation at a number of the other Irish sites, the principal physical and ecological features of this reef will be described first.

St George's Head

The site lies at the foot of a broken cliff and was reached with some difficulty. The reef faces N.N.W., slopes smoothly down into deep water (angle of slope estimated to be 10–15°), and was much affected by swell and waves which, coming in from the south-west, mostly ran along the reef as well as slightly up it; the greatest violence of

wave-action occurred at the western end of the reef and it was here that the uplift of zones was greatest. Farther inshore (in a north-east direction) the severity of wave-action was less and the reef also becomes less steep. At the most exposed (south-west) end of the reef the upper shore was dominated by *Chthamalus stellatus* and a quite well developed (for Ireland) high-level belt of *Porphyra umbilicalis*; an excellent belt of *Fucus spiralis* f. *nana* occurred in the lower part of the *Porphyra* belt. A few yards farther into 'shelter' a fine belt of *Fucus distichus anceps* came in, and mixed with *F. spiralis* f. *nana* above and *Gigartina stellata*/*Chthamalus*/*Mytilus edulis* below. *Ceramium acanthonotum* occurred on the higher *Mytilus*, and *Callithamnion arbuscula* on *Chthamalus* and rock slightly lower. The lower shore was dominated by *Alaria esculenta*, *Lithothamnion* sp. and frequent stunted *Corallina officinalis* L. Farther into shelter, *Fucus vesiculosus* f. *linearis* first appeared at about the upper limit of *Gigartina*, and gradually became dominant on the inner part of the reef where, as the whole littoral decreased in vertical extent, it soon entirely replaced *Fucus distichus anceps*—one of the best examples of this phenomenon seen anywhere. *Gigartina* also disappeared from the upper mid-littoral zone soon after the loss of *anceps*, as *linearis* came to dominate this level. Unfortunately, it was not possible to level accurately the zones of dominant species at this site, but uplift of the upper zones of algae was not nearly so marked as on some of the Caithness reefs, perhaps because of the oblique angle at which the prevailing swell hits the reef and runs along it rather than directly up it. The presence of a good high-level belt of *Porphyra* on the part of the reef most affected by spray from breaking waves was probably also a result of the relatively small amount of uplift of zones compared with some of the other Irish reefs described below; and, probably for the same reason, the *anceps* plants were rather larger than were found at some of the other Irish sites.

Donegal Point

Most of the littoral zone of this headland is precipitous and inaccessible, and *anceps* was found only at one very restricted site about half-way along the south-west flank (site 2 in Text-fig. 3). The reef was rather steep (*ca.* 20°), fully exposed to violent swell, and dominated mainly by *Chthamalus* (with some few stunted algae) on the middle and upper shore, and by *Alaria* on the lower shore. Small and frequent plants of *Fucus spiralis* f. *nana* formed a fairly well-defined belt below a relatively narrow belt of *Porphyra*. The mid-littoral zone was dominated mainly by *Chthamalus* and *Mytilus*, but some few stunted, narrow plants of *Fucus vesiculosus* f. *linearis* were also present, and occasional tufts of *Gigartina* lower down. Several small patches of *Fucus distichus anceps* occurred, situated mostly between the very open 'belts' of *nana* and *linearis*; the individual plants of *anceps* were very small, mostly vegetative, and conspicuously yellow in colour. Farther along this difficult reef (north-west, towards the point) *linearis* and *anceps* were soon absent from the flora, but *nana* persisted on to steeper and even more wave-beaten reefs.

Duggerna Rock, Kilkee (Text-fig. 3, site 3)

This type-locality for *anceps* is topographically one of the most anomalous, in the light of our recent knowledge of the distribution and ecology of this plant. The Duggerna Rock, situated at the southern entrance to Moore Bay, Kilkee, is a very extensive platform of intertidal rock, measuring approximately 550 m from east to west by about 500 m from north to south. Much of the inner part of this remarkable littoral plateau consists of relatively flat areas of broken rock (with deep pools, etc.) on which all of the fucoids of sheltered places occur, together with such species as

Bifurcaria rotunda (Huds.) Papenf. and *Himanthalia elongata* in deep, sheltered, mid-littoral pools. However, out towards the north-west extremity of the platform (about 320 m from the shore high-water line) the rocks become higher again over a quite small area and stick up as a small rock pinnacle which remains just above the surface at high tide, although waves usually wash over it. It was only on the steep seaward facing side of this 'offshore' elevation that *Fucus spiralis* f. *nana* and *F. distichus anceps* were found in typical narrow belts, although some few plants of *anceps* were found also on two narrow, exposed reefs immediately west of the elevation. Sometimes this particular offshore elevation is referred to as *the* Duggerna Rock and, judging by his description, this is undoubtedly the precise site at which W. H. Harvey first found *anceps* (see Carruthers, 1863; and Powell, 1957, for further references).

As already stated, however, the configuration of the shore at this site is somewhat different from that of most *anceps* sites in that, immediately to the west of the offshore elevation, lie two narrow reefs which slope gently *inshore*; these reefs are not very extensive and do not rise so high as the main offshore elevation so that they shelter from direct wave-crash only the lower parts of the Duggerna elevation. It was very interesting to find plants of *anceps* on the higher parts of both of these shallow inshore-facing reefs, in each case at a lower level than the *anceps* plants on Duggerna Rock itself.

Because of the unusual shore configuration, the zonation of dominants at this site was somewhat confused, but the salient features were as follows.

The offshore elevation (*Duggerna Rock*). The highest parts (flat) were covered with patches of *Chthamalus* and *Verrucaria* sp., and with frequent *Littorina saxatilis* (Olivi) and *L. neritoides* (Montagu). The western face of the elevation is steeply sloping or near vertical (for a vertical height of 2·7–3·1 m). The usual dominant species of such exposed Irish coasts occurred on this wall in a very open and mixed community, as follows: *Fucus spiralis* f. *nana* mostly in the uppermost 1·8 m (best developed on ledges) and *F. distichus anceps* in the lowermost 1·5 m, together with small plants of *F. vesiculosus* f. *linearis*, tufts of *Gigartina*, etc. The plants of *anceps* were rather small and had mostly ceased fruiting (17 July). Below the wall, on shallow ledges, *F. vesiculosus* f. *linearis* occurred in tufts, with barnacles, *Mytilus*, etc.

The two inshore-facing reefs beyond. The inner of the two reefs was about 18 m broad and, on the lower stretch of 12 m, was dominated principally by *Mytilus* and *Fucus vesiculosus* f. *linearis*, with frequent *Chthamalus*, *Gigartina*, etc., forming a dense closed community; on the higher part of the reef, however, about 6 m broad, these same species formed a much more open community (probably a direct result of severe wave-action) and here *Fucus distichus anceps* was found, either as isolated plants on small patches of otherwise bare rock, or else mixed with the other species in open communities.

The outer reef was about 30 m broad, and on the seaward side its uplifted western edge dipped quite steeply down into deep water; this western edge was dominated by *Alaria*. On the smooth inshore-facing surface of the reef the (lowermost) inner half was dominated by very crowded *Mytilus*, with scattered tufts of *Fucus vesiculosus* f. *linearis*, *Gigartina*, etc.; but throughout the higher half of the reef scattered plants of *Fucus distichus anceps* were again found, mixed with the above and other species of plants and animals in a rather open community.

Thus, on each of the two reefs, scattered plants of *anceps* occurred on the higher (least sheltered) parts only; it is of interest that the plants themselves were quite large (*ca.* 7–10 cm long) and that most were sterile, although some plants had precocious irregular areas of receptacular tissue some distance behind the apices; the deduced

age was 1 year—see p. 682). It is presumed that the relatively large size was a result of the plants growing at a relatively lower level on the shore than usual (less desiccation) and that they were able to do so because of the unusual configuration of the reefs at this otherwise very exposed site; however, since only very few fully fertile (2-year-old?) plants were found on the two outer reefs it may be assumed that conditions there are more hazardous (severe wave-action and intense competition from mid-littoral species) than subsp. *anceps* encounters at its more usual level.

It is of interest that on the outer reef one plant of *linearis* was found with several vegetative plants of *anceps* growing epiphytically on it; the two forms were readily distinguishable in the field by means of the midrib character (see p. 670). This is the only record of any form of *F. distichus* growing epiphytically on another large alga.

The remaining sites at which *anceps* was found in south-west Co. Clare are those numbered 4–8 in Text-fig. 3. Most of the intervening stretches of coast were either precipitous and inaccessible from land, or else were too sheltered for *anceps*.

Site 4 (Text-fig. 3)

This is a broad reef, several 100 m long, on a very exposed coast just to the west of Bridge of Ross (a natural arch of rock); the reef again faces north-west so that oceanic swell approaching mainly from the south-west tends to run along as well as slightly up the reef. At the more sheltered north-east head of the reef, the belts of some of the dominant plants and animals were again obviously uplifted relative to theoretical tide-levels, but there was much evidence that the high-level belts of algae were very adversely affected (stunted and desiccated) by summer air temperatures.

The reef sloped very evenly, at an angle estimated to be *ca.* 10°. The lower shore was dominated by an uplifted belt (*ca.* 7·5 m broad) of sparse *Alaria*, merging upwards into a very open belt (*ca.* 3 m broad) of mixed *Gigartina*, *Mytilus*, *Corallina officinalis*, *Patella aspera*, *Nemalion elminthoides* (Vell.) Batt., *Callithamnion arbuscula*, *Polysiphonia macrocarpa* Harv., small *Scytosiphon lomentaria* and (unusually for an *anceps* site) frequent small plants of *Laurencia pinnatifida* (Huds.) Lamour., with *Chthamalus* largely confined to small pits and cracks in the otherwise very smooth surface of the rock. *Fucus distichus anceps* occurred in the zone next above (up to *ca.* 7·5 m wide), mixing with the above-named species and some few plants of *F. vesiculosus* f. *linearis* below, and with *F. spiralis* f. *nana* above; the maximum width of the *nana* belt was *ca.* 3·5 m. Both fucoid belts were very open. The plants of *anceps* appeared to comprise two distinct year-groups: (i) larger plants, mostly in the centre of the belt, which were in a late fruiting stage (2 years old?) and covered with brown epiphytes; (ii) younger vegetative plants (1 year old?) mainly above and below the belt of older plants, and with few or no epiphytes. The older plants particularly were very dried out on a warm day (18 July) and the epiphytes borne on the arched fronds had stuck to the rock in many instances. Above the two fucoid belts occurred a belt (*ca.* 7·5 m broad) of sparse and stunted *Porphyra* with *Chthamalus* (and some *Pygmaea pumila* (Huds.) Kuntze and *Blidingia minima*), while *Chthamalus* continued farther upshore for approximately 11 m, but strictly confined to crevices and altogether very inconspicuous. On the open rock in the upper part of the *Chthamalus* belt, patches of dried-out *Bangia fuscopurpurea* (Dillw.) Lyngb. and Myxophyceae indicated that earlier in the year algae had flourished at much higher levels on the open reef than they could in summer. *Littorina saxatilis* and *L. neritoides* continued in crevices very much higher upshore than *Chthamalus*. The theoretical range of spring tides in this area is about 4·3 m and from very approximate estimations it seems that most of the *anceps* belt probably occurred below the theoretical level of M.H.W.S. Unfortunately, *Balanus balanoides* was extremely scarce and no estimate could be made of its 'general upper

limit' to assist comparison of the levels occupied by *anceps* in Ireland and Scotland. However, there is little doubt that *anceps* generally occupies a somewhat lower zone (relative to both theoretical and effective mean high water levels) in south-west Co. Clare than it does in Scotland.

Toward the more exposed and wave-beaten south-west end of this same reef, the zones of dominant species were uplifted to a greater extent and first *anceps* and then *nana* were lost from the flora.

Fucus distichus anceps occurred also on the next reef immediately to the north.

Site 5 (Text-fig. 3)

Here very good belts of *anceps* and *nana* were found on a rather steeper reef (estimated slope 15–20°), with the same associated dominant species above and below. At this site *anceps* again occurred in two distinct forms, apparent year-groups, the larger having mostly ceased fruiting and occurring mainly in the lower half of the *anceps* belt.

Site 6 (east of site 5)

Here the littoral area is for the most part very steep (30–40°), but with flat ledges of rock at intervals; *anceps* was very well developed, especially on the ledges, and occurred in a zone at least 1·5 m in vertical extent (directly measurable at this site). Plants of the two apparent year-groups (see p. 682) were again present in about equal numbers, and at this site both young and old plants occurred throughout the 1·5 m range. In addition, many crowded groups of *anceps* sporelings occurred on *Chthamalus* and on rock in the *anceps* belt. This reef was examined during a heavy rain-storm, and it was noted that some *anceps* plants were growing in a depression completely submerged by a temporary strong stream of fresh water. Some specimens of *Balanus balanoides* were noted among the frequent *Chthamalus* in the *anceps* zone. It was again observed that *nana* persisted farther than *anceps* along the steeper and more wave-beaten part of this shore.

Site 7 (Text-fig. 3)

This site is extremely difficult of access, with a steep descent to a very exposed littoral zone. The reef is small in area, mostly steep in the lower littoral and affected by violent swell; however, the upper littoral area flattens out to a shallow slope and, at this level, on the more exposed part of the reef, good belts of *Fucus spiralis* f. *nana* and *Gigartina* (below) were developed. *Fucus distichus anceps* occurred below the *nana* only on a slightly more sheltered part of this restricted high-level platform; the plants were small and some were still in a late fertile stage.

Goleen Bay (Text-fig. 3, site 8)

F. distichus anceps was found in quantity on the outer reefs of the rocky promontory at the northern entrance to the bay. The reefs at this site slope very steeply (20–30°) down into deep water, but they mostly face due north so that swell from the south-west again tends to run along them rather than directly upshore. The characteristic zonation of dominant species on the more exposed rock faces was as follows: *Chthamalus* on the upper shore; then *Chthamalus*/*Porphyra umbilicalis*; *Fucus spiralis* f. *nana*; *F. distichus anceps*; *Gigartina*, etc.; *Alaria*. The site was apparently too exposed for *Fucus vesiculosus* f. *linearis*. Again, *nana* was more tolerant than *anceps* of increasing exposure. The *anceps* formed an almost closed community and occurred in three

distinct colour shades: (i) light yellow—young, first-year vegetative plants; (ii) russet brown to orange—old plants, just ceasing to fruit; (iii) dark brown—old plants densely covered with epiphytic *Elachista fucicola* (Vell.) Aresch. and *Spongonema tomentosum* (Huds.) Kütz. Both young and old plants occurred throughout the *anceps* belt, and in general the plants of both age-groups were smaller towards the top of the belt. Epiphytes were most dense on the lowermost old plants. A large number of *anceps* sporelings were again observed, on *Chthamalus* and on rock, in the *anceps* belt.

The inner part of Goleen Bay is very sheltered and the shore consists of mixed boulders and reefs, covered with all the usual fucoids of sheltered Irish shores. Since *anceps* occurred in unusual abundance at the entrance to the narrow bay it was considered that, if sporelings of Irish *anceps* were able to develop into larger plants (approaching subsp. *edentatus* in form) under sheltered conditions, the inner part of Goleen Bay would be one of the most likely places to find such plants. No plants of *F. distichus* were found in the inner parts of the bay, however. Further, no intermediate forms between *anceps* and *edentatus* were found anywhere in Ireland.

At Baltard Bay (see Text-fig. 3) the shore configuration is very similar to some of the least steep Caithness reefs, and such reefs are extremely rare in the west of Ireland. The angle of slope was estimated as probably not more than 5° and the reef extends as an almost unbroken sheet of smooth Millstone Grit, from the base of low cliffs well above effective high-water level right down into deep water. The reef faces west and oceanic swell, running in along the southern flank of Baltard Bay, sweeps directly upshore. As in Caithness, these conditions result in a considerable uplift of the belts of dominant species, but the shallow reef is so extensive that the upper shore is not subjected to anything like the severity of swell and wave action experienced on the lower shore. Thus *F. vesiculosus* f. *linearis* was found to be well developed in the upper mid-littoral zone (mostly small, narrow plants), with *F. spiralis* f. *nana* frequent above it; subsp. *anceps*, however, was absent. The principal differences at this site, compared with sites of similar configuration in Caithness, were seen on the upper shore: *Chthamalus* was now the dominant barnacle and extended upshore (usually confined to cracks and hollows in the rock) for a considerable height above theoretical mean high-water level; and the high-level belts of *Porphyra* (above *nana*) and Myxophyceae were not nearly so well developed in summer (although *Porphyra umbilicalis* was abundant in the effective mid-littoral zone on such Irish shores).

FRUITING RECORDS

Among the records and collections of subsp. *anceps* reported above, fertile plants have been found in all of the months from April to August. Only sterile plants were collected at Kilkee in 'September 1897' (by E. George); and J. Sinclair likewise found only sterile plants at Hole o'Rowe, Orkney, on 16 October 1938.

The only plants collected in the month of April (island of Lewis-Harris, *W. J. Gibson*, 1909—see p. 667) were fully mature, so it may be supposed that receptacles start to develop at least as early as January and probably a little earlier.[1] However, even though it is not known when fruiting starts, it is certain

[1] Börgesen (1902) reports that in the Faeröes fertile specimens of *Fucus distichus* were found from April to August; specimens gathered in October and November were sterile; in December a few specimens were found bearing young receptacles. However, Börgesen does not state which form of the species was examined in December.

that it largely ceases during August at all sites. There is a suggestion that the peak of fruiting is reached some few weeks earlier near the southern limits of distribution (the Kilkee district) than in the Scottish localities.

POSSIBLE LONGEVITY

The observations on populations of *anceps* in south-west Co. Clare in July 1953 strongly suggest that there this plant has typically a 2- to 3-year life-span. Thus, at several sites, it was obvious that two distinct populations occurred intermixed: (i) relatively large, fully mature plants, frequently with all the apices fertile (or else with old receptacles dying back), and bearing many mature brown epiphytes (principally *Elachista fucicola* and *Spongonema tomentosum*); and (ii) shorter, vegetative plants, usually quite sterile, or else with only one or two (precocious) receptacles (often just part of a frond some way back from the apex), and with few or no epiphytes. Usually populations (i) and (ii) were quite intermixed, but occasionally, on reefs of even slope, belts of (ii)-type population occurred principally above and below a crowded main belt of (i)-type population. At several sites, crowded groups of really small sporelings were found in the *anceps* belt; length of sporelings (0·5–)4–10 (–13) mm, with one or two dichotomies and with prominent cryptostomata. It is thought that these small sporelings were probably not more than a few months old, population (ii) 1 year old, and population (i) 2 years old. After fruiting, the receptacles of the presumed 2-year-old plants die back and, since often no vegetative leaders are left to continue growth, it seems that the whole of such a plant usually dies back and is removed from the rock by wave-action during the third winter of its life. Indeed, vestiges of holdfast and stipe were seen at several sites in Ireland. However, some of the mature (i)-type Irish plants examined did show a few remaining vegetative leaders that could continue growth into a third year if the plants are able to survive the storms of a third winter; these leaders are usually lateral branches issuing from quite low down on the stipe.

At the Scottish sites, sterile (1-year-old) plants were again distinctive at all sites, but the fertile plants (probably at least 2 years old) commonly bore quite a number of vegetative leaders (again issuing mainly from the proximal rather than the distal parts of the plants) and it is probably more usual for plants to survive for at least 3 years, especially on many of the Caithness reefs where conditions are not quite so rigorous as at some of the other Scottish sites.

DISCUSSION

Fucus distichus subsp. *anceps* thus shows a very discontinuous distribution in Britain and Ireland, being confined to some few isolated and usually very limited stretches of exposed coast in the north and west. The various centres of distribution are mostly geographically isolated from each other by con-

siderable distances, and locally the species is ecologically confined to very exposed reefs, that are often difficult of access.

At all the *anceps* sites described above, all or most of the littoral area of the shore slopes evenly and more or less steeply (5–40°) down into deep water, usually without any major offshore protection, and with the 5 and 10 fathom (9 and 18 m) isobaths usually close inshore. All of the sites are also subjected to constant and frequently violent oceanic swell, as well as severe wave-action, which sweep a long way up shores of this configuration and result in a marked upward extension of the littoral zone as a whole. The conditions of life for species growing in the upper littoral at such sites are obviously more rigorous than on more sheltered shores for, although frequently inundated during rough weather, and wetted by spray from breaking waves and swell even more often, there will be periods of relatively calm weather when the uplifted high-level species must suffer severe desiccation, especially in the warmer summer months, unless frequent rain or mist mitigates these conditions. In general, the desiccation will be a good deal more severe at the warmer southern (Irish) sites than at the cooler northern (Scottish) sites. Fucoids are only able to survive on such wave-beaten shores at the higher levels, where they develop into narrow dwarf forms such as *F. spiralis* f. *nana* and *F. distichus anceps*, and it is interesting that in Ireland the former with the more southerly over-all distribution tolerates rather more rigorous exposure conditions than the latter 'northern' species; whereas at the Scottish localities *anceps* persists farther into exposure than *nana*. It is very difficult to make comparisons of levels occupied by the same dominant species on shores such as these (with differing tidal ranges, aspect, angle of slope, etc.), but there were some indications that the two belts of high-level fucoids occur at relatively rather lower levels at some of the Irish sites than they do at the Scottish sites, and this could be a result of more severe desiccation at the Irish sites. Indeed, it seems that the eventual southern limit of *F. distichus anceps* is probably determined by increasingly severe desiccation at the high level occupied, retreat downshore being limited by the more severe wave-action and intense competition from other plant and animal species in the zone below.

This type of smooth shore configuration is very rare, and most of the exposed rocky shores of Britain and Ireland are very much more broken up. This usually means that much of the force of swell and wave-action is dissipated either on off-shore reefs or islands or, more often, in the lower littoral, with the result that the over-all height of the littoral zone is not raised to anything like the same extent; indeed, the upper shore is often comparatively sheltered from wave-action under these conditions, as is best indicated by the species that usually grow there (e.g. *Pelvetia canaliculata*). On such broken or flatter coasts, with intermediate exposure conditions prevailing at least in the mid- and upper littoral zones, *Fucus vesiculosus* f. *linearis* commonly

dominates the mid-littoral in Britain, with a zone of *F. spiralis* (or *F. spiralis* f. *nana*) above it.

Ecologically then *F. distichus anceps* appears to be confined to exposed sites (with extended littoral zone) largely as a result of competition from more successful forms of *F. vesiculosus* and *F. spiralis* on coasts of intermediate exposure; and intermediate forms of *F. distichus* (between subsp. *anceps* and subsp. *edentatus*) are largely absent from British coasts of intermediate exposure (except for a few instances in Caithness) probably for the same reason. It is very interesting that farther north, nearer to one of the centres of distribution of *F. distichus* (e.g. in the Faeröes, Iceland and northern Norway), intermediate forms of the species are commonly found on coasts of intermediate exposure and, although a form of *F. vesiculosus* without vesicles occurs commonly in these places, it is apparently restricted to more sheltered sites than in Britain (see Börgesen, 1902, p. 478; 1905, p. 720 *et seq.*).

Additional records of *F. distichus anceps* may be expected from certain restricted stretches of very exposed coast that have a similar configuration and ecology to that described above for the various sites known to date. However, in view of the over-all distribution, it is considered most unlikely that the form will be found anywhere else on the *mainland* of Britain other than on the north coast of Scotland. Additional records will probably come only from exposed coasts in the following areas: the Shetland and Orkney Islands, the Outer Hebrides (and possibly Tiree and Islay), and the north and west coasts (only) of Ireland. Even within these areas, however, the number of possible sites physically, and hence ecologically, suitable for *F. distichus anceps* are remarkably few as can be seen from large-scale maps and charts. Indeed, several of the Irish sites for *F. distichus anceps* were predicted from a study of fairly large-scale maps (1 in. to 1 mile, with contours, gives sufficient detail).

FUCUS DISTICHUS L. EMEND. POWELL, SUBSP. *EDENTATUS* (DE LA PYL.) POWELL (Pl. II, fig. 2)

DISTRIBUTION

In Britain, *F. distichus* subsp. *edentatus* has been found at the following three localities only: Lerwick and Scalloway, Shetland Islands, and North Haven, Fair Isle (Text-fig. 1).

In reporting the presence of the species at Lerwick in 1902, Börgesen (1903, p. 304) stated that 'it grew here at about low-water mark on the quay itself, as well as on stones opposite to it; but in spite of a very close search I did not succeed in finding it anywhere else, neither to the south-east of Lerwick, nor in the sound near Bressay, nor [at] Burra Voe, nor on Muckle Holm' (Yell Sound).

According to the printed label attached to specimens of *edentatus* distributed by E. M. Holmes as '*Fucus inflatus* Vahl' (*Alg. Brit. Rar. Exsicc.*,

Fasc. XII, No. 288), another collection of plants from Lerwick harbour was made in 'June 1908' by 'W. A. Russell'.

In June–July 1952, *edentatus* was found to be still abundant in the harbour at Lerwick and was found also at the following two new localities—in the shelter of the small harbour at Scalloway, a small fishing town not far from Lerwick, and in the sheltered North Haven on Fair Isle, which is the usual harbour for the island. The Fair Isle record represents a new southern limit for this form of the species on the British side of the North Sea and a preliminary notice of the record (under the name *F. inflatus* f. *edentatus*) was given in Burrows *et al.* (1954).

ECOLOGY

Lerwick, Shetland

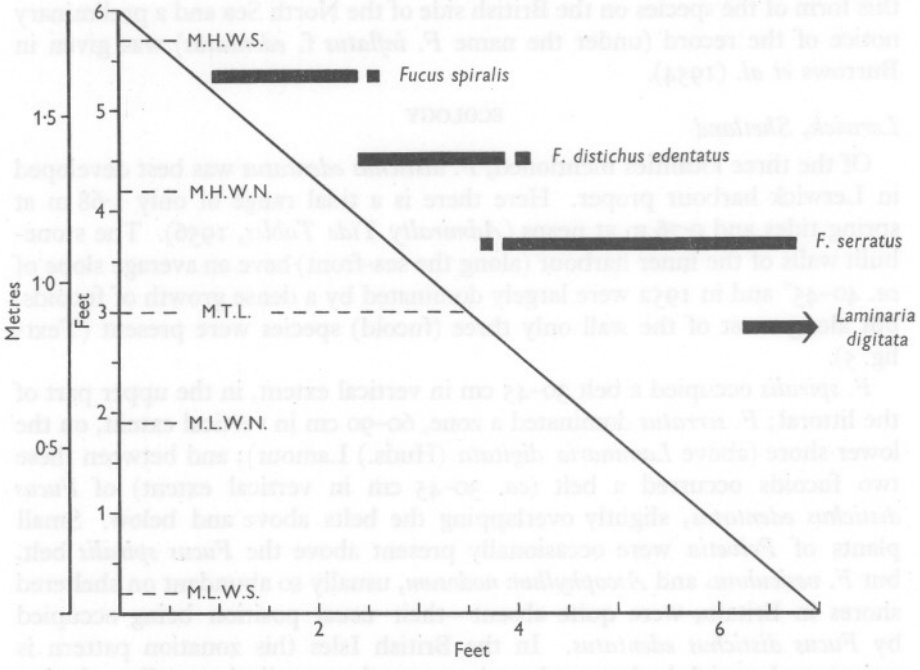
Of the three localities mentioned, *F. distichus edentatus* was best developed in Lerwick harbour proper. Here there is a tidal range of only 1·68 m at spring tides and 0·76 m at neaps (*Admiralty Tide Tables*, 1956). The stone-built walls of the inner harbour (along the sea-front) have an average slope of *ca.* 40–45° and in 1952 were largely dominated by a dense growth of fucoids, but along most of the wall only three (fucoid) species were present (Text-fig. 5).

F. spiralis occupied a belt 30–45 cm in vertical extent, in the upper part of the littoral; *F. serratus* dominated a zone, 60–90 cm in vertical extent, on the lower shore (above *Laminaria digitata* (Huds.) Lamour); and between these two fucoids occurred a belt (*ca.* 30–45 cm in vertical extent) of *Fucus distichus edentatus*, slightly overlapping the belts above and below. Small plants of *Pelvetia* were occasionally present above the *Fucus spiralis* belt, but *F. vesiculosus* and *Ascophyllum nodosum*, usually so abundant on sheltered shores in Britain, were quite absent—their usual position being occupied by *Fucus distichus edentatus*. In the British Isles this zonation pattern is unique to Lerwick harbour, where it occurred on vertical as well as sloping walls. Tracing the fucoids south-eastwards beyond the built-up walls of the harbour proper, it was found first that, on a more open (but still comparatively sheltered) and gently sloping shore (of natural reefs, boulders and sand), near Queen's Hotel (Leag beach), *edentatus* occurred down to lower levels and the individual plants were then larger; again *F. spiralis* occurred on the upper shore and *F. serratus* (here with very deeply incised serrations) on the lower shore, and no other fucoids were present. Continuing south-eastwards along the shore, however, *F. vesiculosus* quite soon appeared in the mid-littoral zone and, as it increased in amount, so the *F. distichus edentatus* decreased until, within a few hundred metres of Lerwick harbour, it disappeared from the flora. (*Pelvetia* appeared just before *Fucus vesiculosus*, and some plants of *Ascophyllum* were found with the first *Fucus vesiculosus*).

On the Leag shore especially, plants of *edentatus* frequently had irregular inflations in the distal parts of the fronds, and sometimes grew in shallow

pools. *F. serratus* also frequently had inflated apices at this site (observed on a rather warm day).

These observations at Lerwick could suggest that *F. distichus edentatus* may compete with *F. vesiculosus* and *Ascophyllum* for the available space in parts of the *outer* harbour area, but on the *inner* harbour wall the complete replacement of the other two species by *edentatus* is altogether unusual, and



Text-fig. 5. Diagram to show zonation of the dominant algae on the wall of the inner harbour at Lerwick, June 1952, and the approximate relation of the algal belts to the mean tidal levels there (mean levels derived from *The Admiralty Tide Tables*).

is almost certainly not entirely (and perhaps not at all) the result of competition. There is very considerable pollution in Lerwick harbour caused particularly by effluent pouring directly into the harbour from the fish factories that line the quays, and it would seem that *edentatus* is more tolerant of this pollution than is either *Fucus vesiculosus* or *Ascophyllum*. It is interesting that Lund (1949*a*, *b*) also has noted that *Fucus distichus edentatus* in Copenhagen harbour shows greater tolerance of polluted water than does *F. vesiculosus* or *F. serratus*; the individual plants of *edentatus* were also smaller at such polluted localities (Copenhagen) than at less polluted places nearby.

Scalloway, Shetland

During a brief visit to Scalloway on 3 July 1952, patches of rather small plants of *edentatus* were found in the sheltered harbour. The plants occurred on a gently sloping shore composed of boulders, shingle and sand, at the western head of the bay between the two piers. The tidal range is small (only 1·13 m at springs), and it is probable that these waters were again somewhat polluted. The fucoids present in open communities on this rather unstable shore were: *F. spiralis* forming a belt on the upper shore; small amounts of both *F. distichus edentatus* and *F. vesiculosus* intermixed in the middle part of the littoral; and plentiful *F. serratus* on the lower shore. The small plants of *edentatus* had almost ceased fruiting, and many plants had irregular inflations. It was most unusual (for Britain) to find that nearly all of the plants of *F. serratus* had inflated apices.

North Haven, Fair Isle

In the sheltered North Haven on Fair Isle (a small and predominantly sandy bay), *edentatus* was again not very abundant compared with Lerwick, although it was found on rocks or boulders at both the east and west sides of the bay, on the boat-slip at the centre of the bay and on the stone landing jetty in the south-east corner of the bay. The tidal range is 1·74 m at springs, and the Haven is not polluted. On the west side of the Haven the rock face above the sandy beach is very steep or vertical; here *F. spiralis* occurred in the uppermost 30–45 cm of the *Balanus balanoides* belt, and occasional plants of *Fucus distichus edentatus* were found below the *F. spiralis* belt and farther down to about M.T.L.; the lower plants of *edentatus* were larger than those growing higher up; no other fucoids occurred on this steep face, the lower levels being occupied by *Gigartina stellata*, *Acrosiphonia centralis* and *Enteromorpha* spp.

The boat-slip in the centre of the bay is made of concrete and iron and runs down the sandy beach into deep water. The cement was well covered with *Balanus balanoides*; *Pelvetia* and *Ascophyllum* were absent; on the inshore end of the sides of the slip occurred a belt of *Fucus spiralis* (30–45 cm vertical extent) and below this a belt of *edentatus* (30–38 cm vertical); farther out on the slip and at a lower level, *edentatus* occurred mixed with *F. vesiculosus* and occasional *F. serratus*, with an undergrowth of *Gigartina*, *Lomentaria articulata* (Huds.) Lyngb., etc.

In the south-east corner of the bay the nearly vertical sides of the stone-built landing jetty showed the following zonation of fucoids: a narrow belt of *Fucus spiralis* above, then a belt of *F. vesiculosus* but with a small amount of intermixed *Ascophyllum*, and finally some plants of *Fucus distichus edentatus* on the lower part of the wall.

On the shore nearby (just a few metres to the west of the jetty) the zonation

of the dominant algae was worked out in detail and is recorded in Burrows *et al.* (1954, see especially Figs. 4, 5). The shore here sloped very gently; the upper part consisted of a broken rocky reef and the lower part of rounded boulders and rock outcrops embedded in sand. *F. spiralis* formed a good belt (38–45 cm vertical extent) on the reef; *F. vesiculosus* and some *Ascophyllum* dominated the mid-littoral rock and boulders (0·9–1·2 m vertical extent), with associated *Gigartina*, *Cladophora rupestris* (L.) Kütz, *Enteromorpha* spp., *Acrosiphonia centralis*, etc.; while *Fucus distichus edentatus* (large plants) occurred only on boulders on the lower shore, together with *F. vesiculosus* and some *F. serratus*.

Just beyond the jetty, the eastern shore of the Haven (rock reefs and boulders) is very broken, and here only one small group of plants of *edentatus* was present, on the lower shore.

Thus *edentatus* appeared to be fairly well-established in the North Haven: in the most sheltered corner (near the landing jetty) frequent *F. vesiculosus* and some *Ascophyllum* dominated a zone below *Fucus spiralis*, and *edentatus* was confined to more open communities on boulders embedded in sand on the lower shore; but, at the rather more exposed (also steep) sites in the bay, *edentatus* appeared to be more successful than *F. vesiculosus* in colonizing the zone immediately below *F. spiralis*.

FRUITING RECORDS

The plants collected at Lerwick by F. Börgesen in 1902,[1] and by W. A. Russell in June 1908, were both fertile; otherwise records are limited to the 1952 observations when, during the period 24 June–3 July, fully fertile plants were noted at Lerwick, Scalloway and North Haven; at Scalloway, however, most of the receptacles were old and the fruiting period appeared to be nearing an end.

DISCUSSION

These three records of *F. distichus edentatus* represent the southern limit of this form of the species on the British side of the North Sea; the southern limit on the eastern shores of the North Sea is in Copenhagen harbour (Lund, 1949*a*,*b*). In the Faeröe Islands (about 250 miles to the north-west) and in Norway (a similar distance to the east) the plant is plentiful, and it has very probably been introduced accidentally to the three Shetland harbours by the fishing vessels which ply between them, and the Faeröes, and Norway.

There are several ways in which this could happen: pieces of (fertile) *edentatus* could be scraped from a jetty wall by the hull of a fishing vessel (perhaps itself roughened with attached barnacles) and be carried about to some other

[1] In his paper Börgesen (1903, p. 300) states that he visited Lerwick 14–16 July [1902]; a fully mature specimen of subsp. *edentatus* in Herb. Kew, however, is labelled by Börgesen 'Lerwick, 16. 6. 1902'.

harbour where the pieces could readily be scraped off against another quay. The chances of subsequent establishment would be increased by the fact that the species is hermaphrodite. Alternatively, as Hylmö (1933) suggests (with reference to the recent spread of the plant on the west coast of Sweden), it could be taken onto fishing vessels, growing on the shells of *Mytilus edulis* (used for bait), and later be jettisoned with the empty shells perhaps in another harbour. Introduction by fishing vessels seems a more likely possibility than introduction by floating plants, although the terminal parts of fertile plants (with swollen receptacles, and often with irregular inflations in the thallus) probably could float and be carried for considerable distances by surface currents.

It is fairly safe to assume that *Fucus distichus edentatus* has been present in Lerwick harbour for the past 55 years at least. However, we cannot judge from Börgesen's limited observations whether or not the species has increased in quantity in this time; he may not have seen those parts of the inner harbour wall where the species now forms a definite belt between *F. spiralis* and *F. serratus*.

The size and vigour of the British specimens indicate that such physical conditions of the environment as sea and air temperatures do not directly determine the present southern limits of *edentatus*. Perhaps rather the limits to further spread (very locally) are imposed principally by increasingly severe competition from species that are more successful locally. If this is a correct interpretation of the observations, it would be an excellent illustration of Gause's (1934) contention that two species with similar ecology cannot live together in the same place. On a broader scale in northern Britain, the further spread of *edentatus* southwards (to other sheltered sites, where for one reason or another conditions are not favourable for *F. vesiculosus*) is doubtless limited to a large extent by sea-barriers.

If *edentatus* were to spread further in Britain, and if fishing boats are indeed the principal means of dispersion, it might be supposed that the plant would appear next in harbours (especially those that are more or less polluted) in the south of Shetland, in the Orkney Islands (e.g. Kirkwall and Stromness), or even in harbours in north-east Scotland such as at Thurso and Wick. I have looked for the species but not found it in the following likely places. (1) Grutness Voe (south end of Shetland Mainland), 1952. (2) Kirkwall harbour (Orkney), 1952, a brief examination of the vertical harbour wall showed very few fucoids present at all, and much oily pollution. (3) Stromness harbour (Orkney), 1952; a rather more careful search here showed, very interestingly, that *F. vesiculosus* and *Ascophyllum* were absent from the harbour area; on parts of the harbour wall (tidal range 3·08 m at springs) a wide belt of *Fucus spiralis* above merged into a wide belt of *F. serratus* below, but very often there was a 'gap' between the two belts occupied in part by *Balanus balanoides* but quite devoid of fucoids. Stromness harbour appeared to be polluted, and

is a likely place for *Fucus distichus edentatus* to become established if ever it were introduced, there being a suitable vacant 'ecological niche'. (4) The harbour at Scrabster (near Thurso), 1951.

There is no evidence to suggest that *edentatus* is actively extending its range southwards in Britain at the present time.

TAXONOMIC CONSIDERATIONS

The distribution and ecology of forms of *F. distichus* in Britain and Ireland, described above, is a good illustration of the fact that, towards the southern limits of distribution, the species is represented by populations of only one or two of the best adapted forms, confined to restricted habitats and often geographically isolated. It may well be that such ecological restriction and geographical isolation (particularly of subsp. *anceps* in Ireland) could result in the gradual evolution of genetically distinct ecotypes or even species.

It is probably safe to assume that *anceps* has been present in Ireland since 1863 at least, and it is highly possible that it may even be a survivor there from a time when the seas around Britain were much colder, but able to exist now only under the extraordinarily narrow range of habitat conditions described in the present paper. It is a well-known phenomenon that species or subspecies that are represented by a single ecotype confined to a limited area frequently exhibit exceptionally small 'ecological amplitude' (i.e. the range of habitat variation that a plant can tolerate; see Daubenmire, 1947) compared with others which, by means of genetic diversification, are represented in a variety of habitats. The apparent genetic impoverishment of these entities may arise by either of two courses of events: (i) catastrophes destroy most of the population and the remnants are *depleted species* or *relicts*, with only limited genetical possibilities for morphological variation; or (ii) an ecotype of small ecological amplitude may result from a very limited crossing of an effective geographical barrier. The population descending from such a single introduction can have no greater genetic heterogeneity than that possessed by the individuals that immigrated (subsequent mutations excluded). Certainly *anceps* shows very limited ecological amplitude in Ireland, but rather more in Caithness. Wherever it occurs in Britain and Ireland, however, *anceps* seems more likely to be a relict form, rather than an introduction of recent centuries. That it may be actively extending its range southwards at the present time is considered very unlikely.

The *edentatus* in Shetland and Fair Isle harbours, on the other hand, has more probably been introduced to those places in comparatively recent times, but certainly before 1902 in Lerwick harbour.

ACKNOWLEDGEMENTS

This paper brings together information from many sources, including field observations made during several surveys of parts of the coasts of north Scotland and west Ireland, and I wish to record my thanks to all the colleagues who participated in the various expeditions—Dr E. M. Burrows, Dr E. Conway, Dr J. R. Lewis, Dr S. M. Lodge, Dr M. de Valéra (Galway), and my wife, Grace Powell—for help of various kinds and for permission to include here some of the observations made on the surveys; these colleagues, however, are not responsible for the views here expressed.

I wish to thank also: Dr Burrows and Dr Lewis for the photographs shown as Pl. II, fig. 2, and Pl. I, fig. 1, respectively; Dr Mary Parke (Plymouth) and Dr A. P. Orr (Millport) for helpful criticism of the typescript; Dr Burrows and Prof. L. A. Harvey (Exeter) for material of *F. vesiculosus* f. *linearis* from Lundy; and Miss C. I. Dickinson (Kew) for help in tracing herbarium specimens.

Finally the author gratefully acknowledges grants received from the Browne Fund of the Royal Society toward expenses incurred in the surveys of the north coast of Scotland and parts of the west coast of Ireland.

SUMMARY

The distribution and ecology of subspp. *anceps* and *edentatus* of *F. distichus* L. emend. Powell (1957) in Britain and Ireland is described in detail, based on recent ecological surveys and critical examination of all past records.

F. distichus anceps is a small form confined to certain very exposed coasts in the north and west of Scotland and Ireland, where it reaches the southern limit of its geographical range. This plant may be a relict form in Britain, existing now only under an extraordinarily narrow range of rigorous habitat conditions; it is not thought to be actively extending its range southwards at the present time. The ecology of subsp. *anceps* is considered principally in relation to that of other reduced fucoids found on exposed British shores, viz. *F. spiralis* f. *nana* and *F. vesiculosus* f. *linearis*; all three forms are illustrated by photographs and means of distinguishing them are described. The life-span of subsp. *anceps* is thought to be 2 to 3 years at some Irish sites, but may be longer at some of the Scottish sites.

F. distichus edentatus is a large, sheltered-water form, and has been found only in the harbours of Lerwick and Scalloway (Shetland Islands) and North Haven (Fair Isle), which mark the southern limits of this subspecies on the British side of the North Sea. It is best developed in Lerwick harbour where it forms a belt between *F. spiralis* and *F. serratus* and appears to be very tolerant of water polluted by effluent from fish factories. *F. distichus edentatus* has possibly been introduced to these three harbours within recent centuries,

perhaps by fishing vessels; it is not thought to be actively extending its range southwards in Britain.

The facts presented show that, at the southern limits of its distribution in Britain, *F. distichus* is represented by populations of only one or two of the best adapted forms, confined to restricted habitats and often geographically isolated. It may be that such restriction and isolation (particularly of subsp. *anceps* in Ireland) could result in the gradual evolution of genetically distinct ecotypes or even species.

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EXPLANATION OF PLATES

PLATE I

Fucus distichus L. emend. Powell, subsp. *anceps* (Harv. et Ward ex Carruthers) Powell

Fig. 1. Photograph of part of a belt of plants growing on an exposed reef near Lower Dounreay, Caithness, Scotland (site 4 in Text-fig. 2), July 1951, showing characteristic arching of the fronds. (Photograph J. R. Lewis.)

Fig. 2. Photograph of a typical mature Caithness plant (preserved in formalin/seawater, but not pressed), collected just west of Sandside Head, Caithness (site 2 in Text-fig. 2), July 1951, *H. T. Powell* (MILL). Greatest length of plant 17·4 cm; most of the apices are fertile; plant probably *ca.* 2 years old. The scale is 15 cm long.

PLATE II

Fig. 1. *Fucus distichus* L. emend. Powell, subsp. *anceps*. Photograph of a living mature plant from a reef just east of Brims Ness, Caithness (site 9 in Text-fig. 2), June 1956, *Mrs Grace Powell* (MILL). Greatest length of plant 23·7 cm; receptacles up to 5·7 cm long and up to 6 mm broad; some of the branches have been cut off. This is the longest plant of subsp. *anceps* found so far in Britain and it was growing on a reef slightly sheltered from direct wave-crash; all of the apices were fertile. In certain respects the plant is intermediate in form between subsp. *anceps* and subsp. *edentatus* (see p. 672).

Fig. 2. *F. distichus* L. emend. Powell, subsp. *edentatus* (De la Pyl.) Powell. Photograph of a mature plant growing on a fairly sheltered shore at Leag, just to the south of Lerwick harbour, Shetland Islands, 3 July 1952. Some plants of *F. spiralis* are present in top right background; the barnacles are *Balanus balanoides*. (Photograph E. M. Burrows.)

PLATE III

Fig. 1. *Fucus distichus* subsp. *anceps*. Same plant as in Pl. I, fig. 2, with some of the branches cut off, spread out and photographed under conditions similar to those for the lower illustration. Note that in the distal branches the midribs are scarcely distinct from the alae.

Fig. 2. *F. vesiculosus* L., f. *linearis* (Huds.) Powell. Photograph of a very reduced plant (preserved in formalin/seawater, but not pressed), from very exposed coast at Jenny's Cove, Lundy, Bristol Channel, *L. A. Harvey* (MILL). April 1949, with young receptacles. Greatest length of plant 14·4 cm. Some of the branches have been cut off. Note the very distinct midribs in the distal branches, and the absence of vesicles (see p. 670).

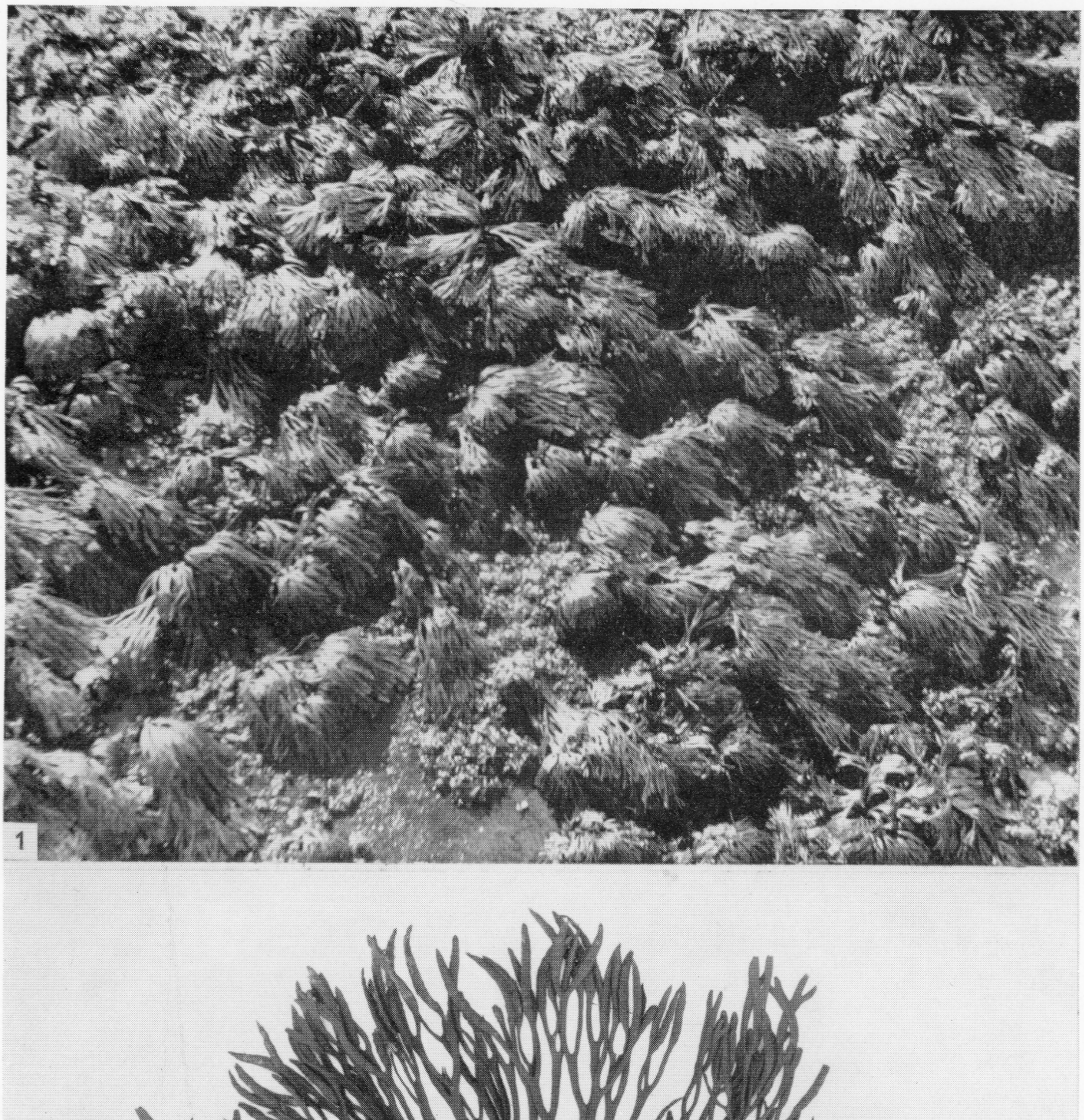
The scales show cm and mm.

PLATE IV

Fig. 1. *Fucus vesiculosus* f. *linearis*. Photograph of a very reduced plant (preserved in formalin/seawater, but not pressed) from exposed coast at Jenny's Cove, Lundy, Bristol Channel, August 1950, *L. A. Harvey* (MILL). Greatest length of plant 15·0 cm. Note the long, narrow receptacles, most of which are mature, the prominent midribs and the absence of vesicles (see p. 670). Some of the branches have been cut off.

Fig. 2. *F. spiralis* L., f. *nana* (Stackh.) Batt. Photograph of several plants (preserved but not pressed) from exposed reefs near Lower Dounreay, Caithness (site 4 in Text-fig. 2), July 1951, *H. T. Powell* (MILL) (see p. 671). Greatest length of right-hand plant 12·9 cm.; most of its apices are fertile.

The scales show cm and mm.



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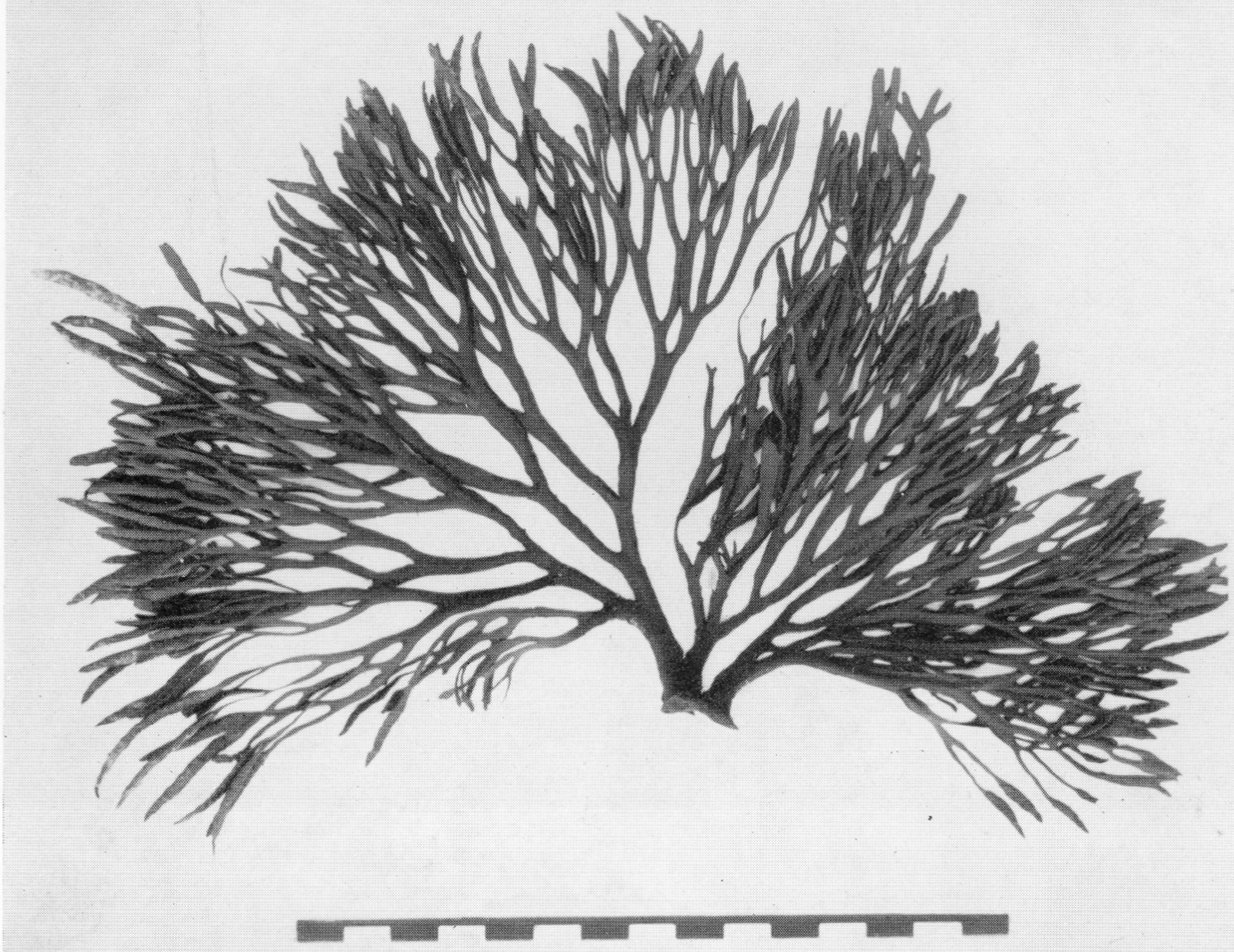
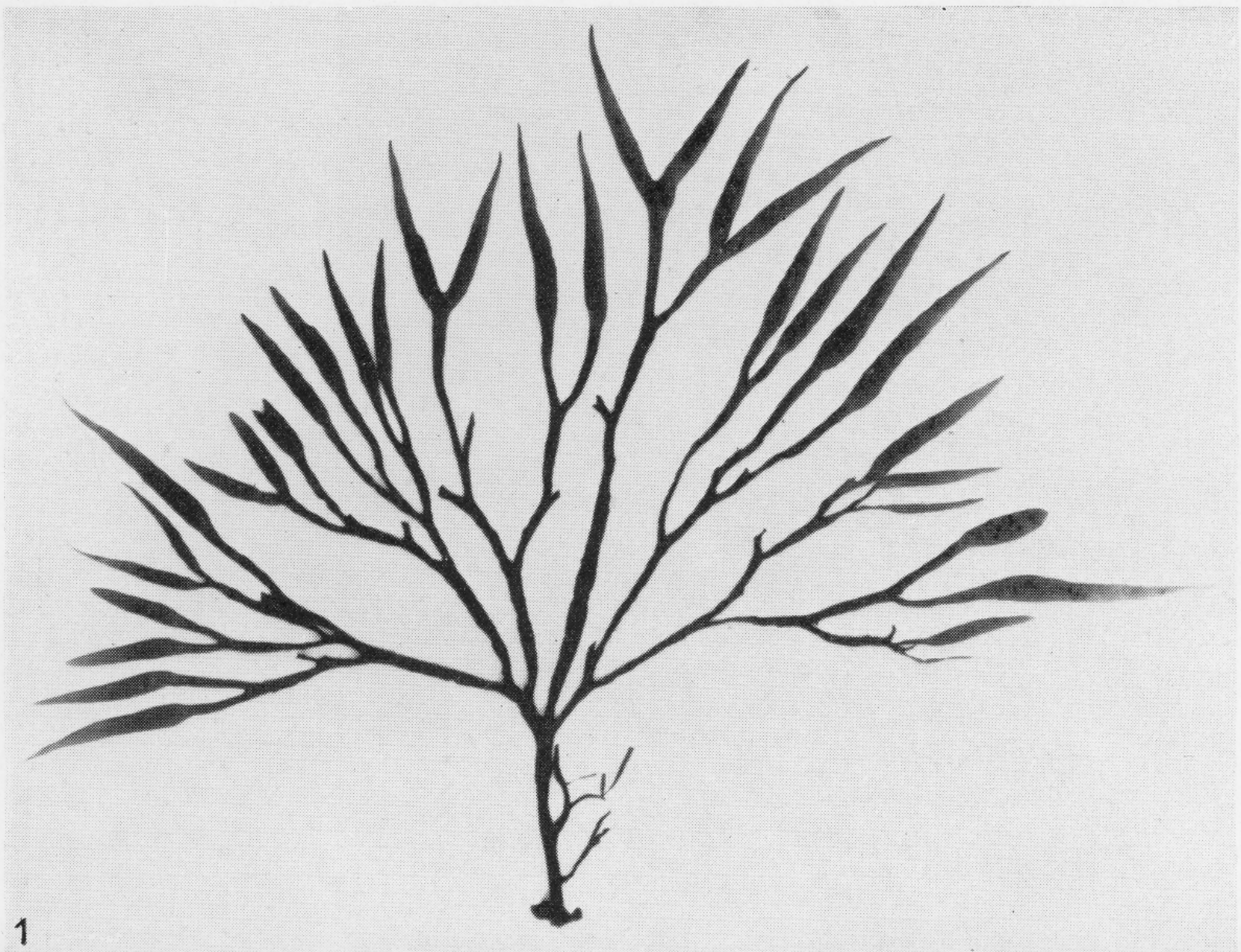


2

(*Facing p.* 694)



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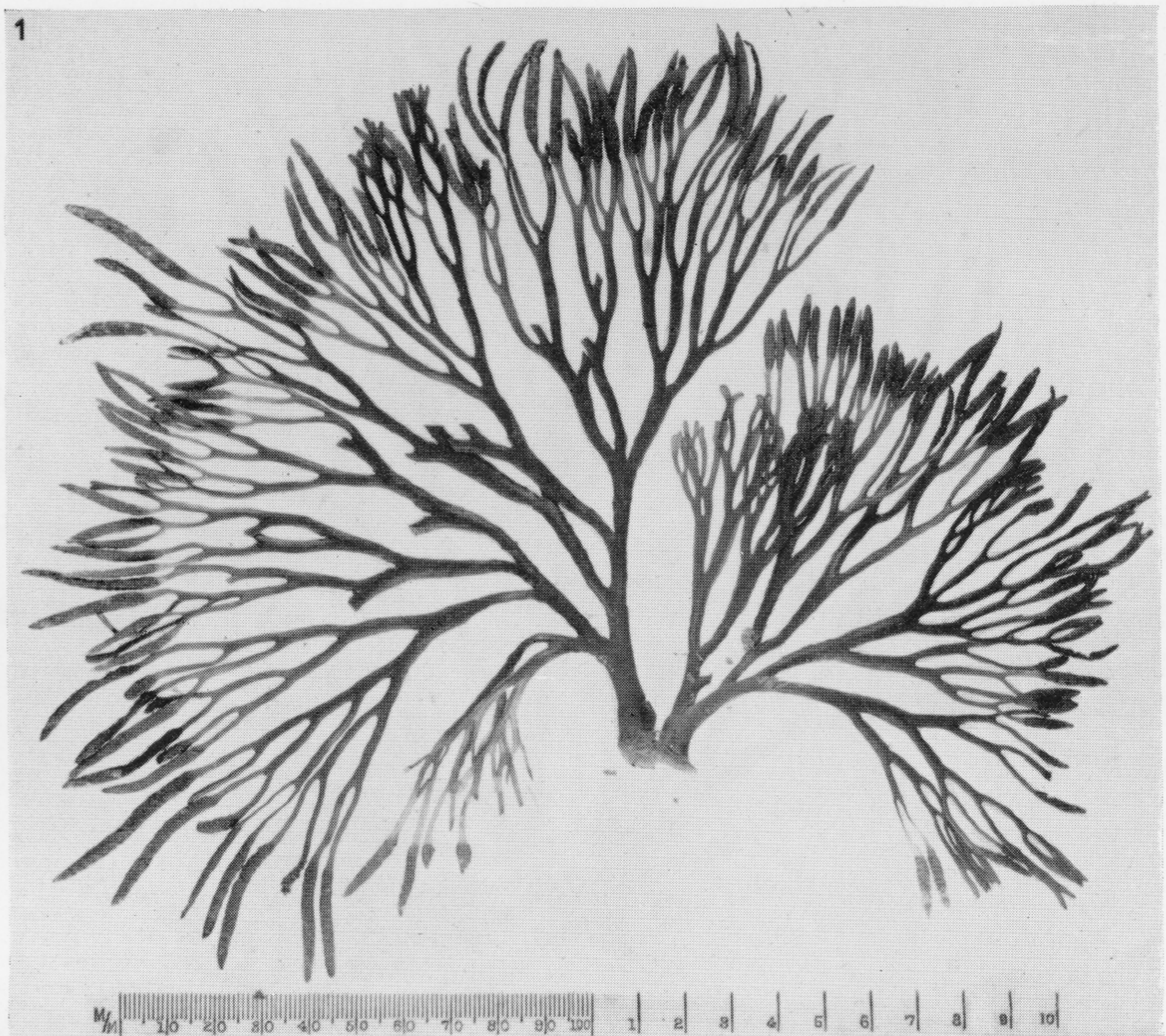
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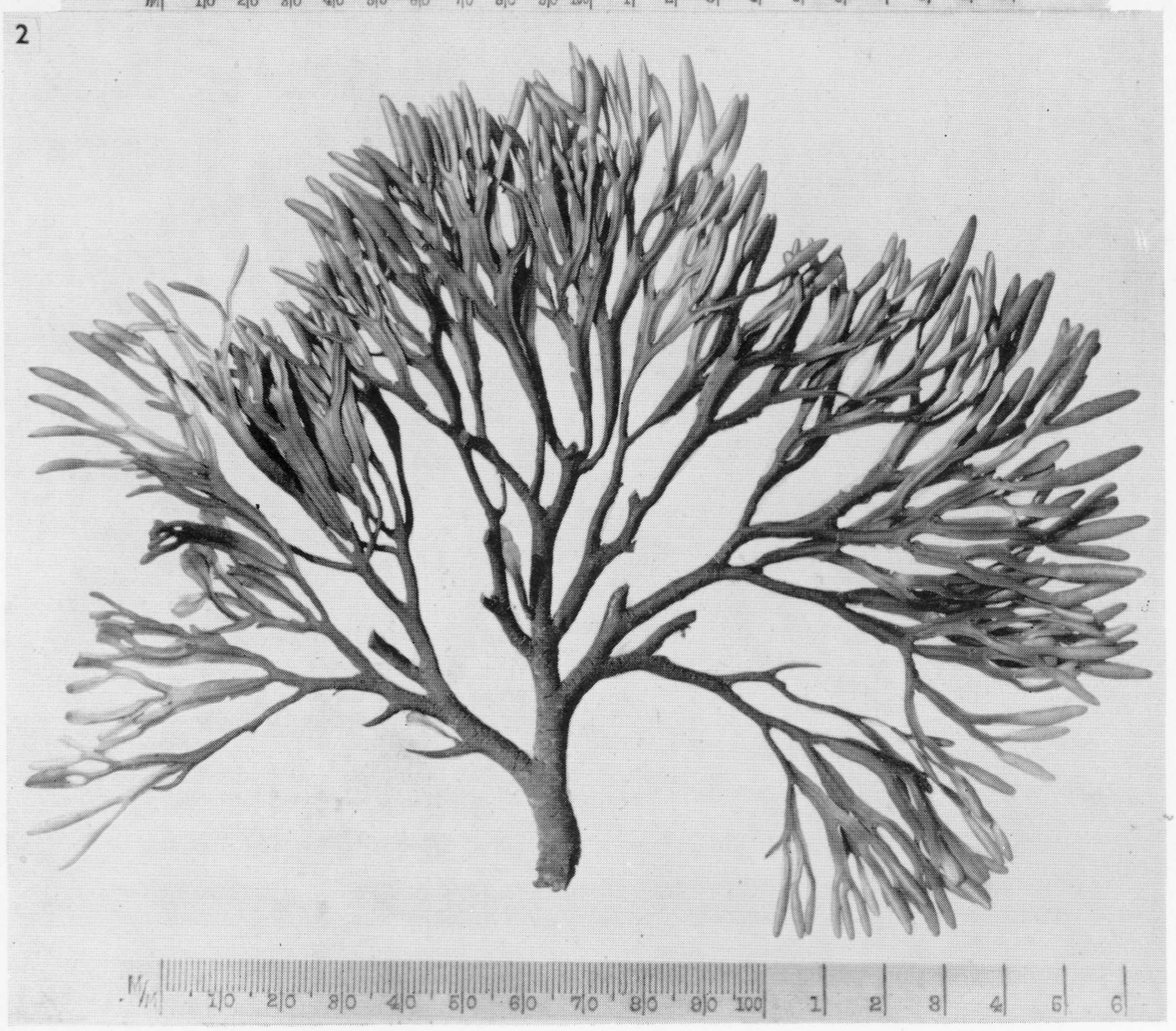
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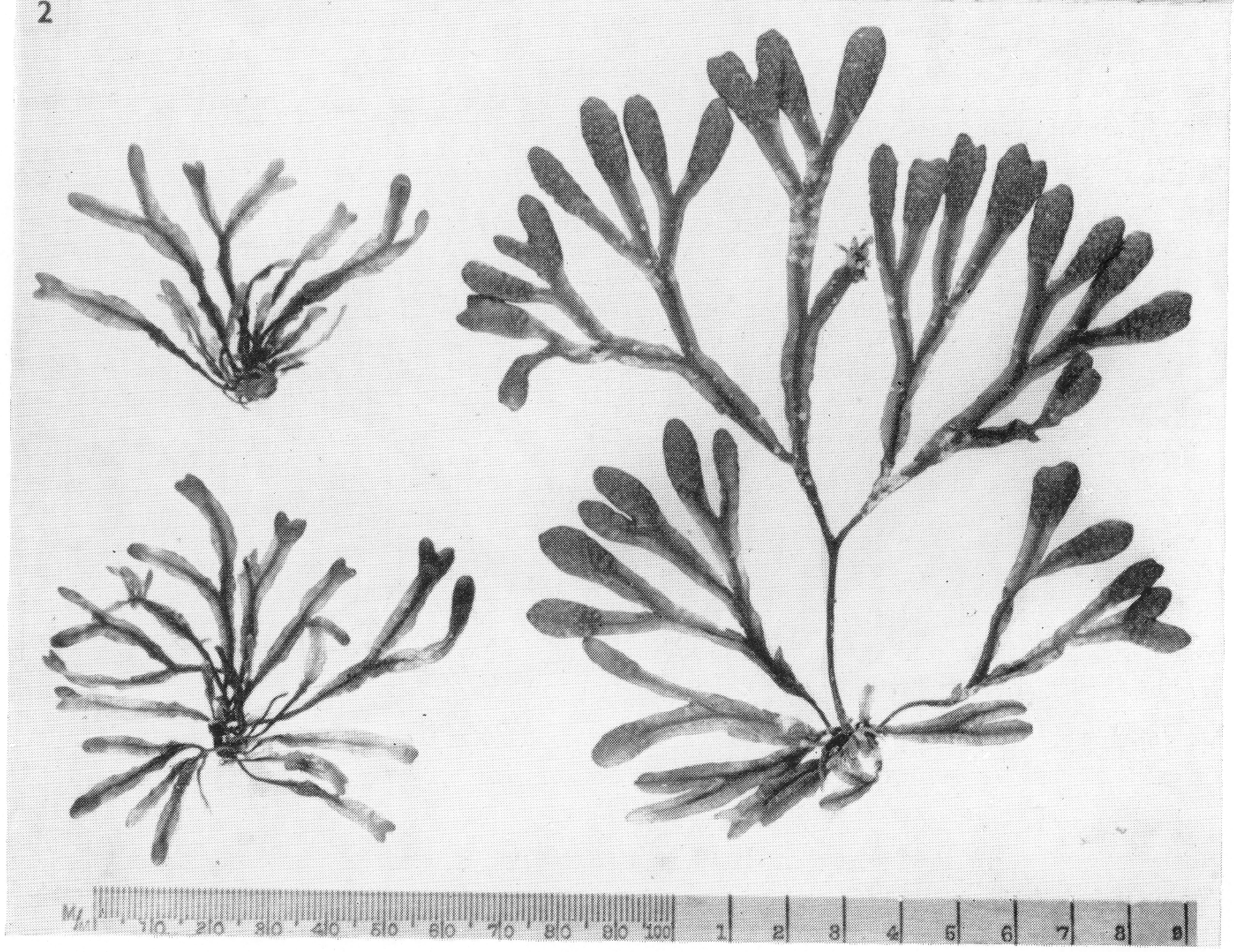
2



ABSTRACTS OF MEMOIRS

RECORDING WORK DONE AT THE PLYMOUTH LABORATORY

RED BLOOD-CELL ANTIGENS IN SOME LOWER VERTEBRATES

By DOREEN E. ASHHURST

J. exp. Biol. 1956, Vol. 33, pp. 249–55

The main aim of the work described in this paper was to discover if blood groups could be found in Amphibia and fish using human blood grouping techniques. No evidence for blood groups could be found in the whiting, pouting, plaice or frog by cross-matching the red cells and serum of animals of the same species. Some frogs were injected with the red cells of other frogs but no antibodies to red cells could be detected in the injected frogs. The experiments suggest that, in these species, all the animals used had the same antigens on their red cells.

The red cells of frogs, toads, tree-frogs and newts were tested against human ABO sera. All the sera (anti-G(A), anti-G(B), anti-G(A+B) and AB serum) reacted with the red cells of each species, but with the Anuran red cells, the reactions with anti-G(B) and anti-G(A+B) were much stronger. The weak reaction is caused by species antibodies present in all human sera, but the strong reaction was shown to be due also to the presence of a B-antigen on the Anuran red-cells. In frogs the B-antigen is identical with the human B-antigen. D.E.A.

TOXIC MARINE FLAGELLATES; THEIR OCCURRENCE AND PHYSIOLOGICAL EFFECTS ON ANIMALS

By DOROTHY BALLANTINE and B. C. ABBOTT

J. gen. Microbiol. 1957, Vol. 16, pp. 274–81

The distribution of toxic water blooms in the sea and brackish water is discussed and illustrated by a map. This distribution picture is not complete but gives indications of the cosmopolitan nature of the phenomenon. The causative organisms have also been listed as far as possible, and a brief discussion of the causes and economic importance of red tides follows.

The latter half of the paper is devoted to a discussion of the physiological effects of these toxins, with particular emphasis on the toxin from *Gymnodinium veneficum*. The effect of this toxin is compared with the action of the toxin causing paralytic shellfish poisoning.

This paper is one of a series in a symposium on plankton, held by the Society for General Microbiology, in September 1956, at Exeter. D.B.

THE DIRECT ACTION OF ANTERIOR PITUITARY EXTRACTS ON THE INITIATION OF LACTATION IN THE RABBIT

By D. B. CARLISLE

Physiol. Comparata et Oecologia, 1957, Vol. 4, pp. 295–312

Experiments are described which demonstrate that a crude pituitary extract, which has a systemic effect in initiating lactation in the primed male rabbit, does not possess any direct, local action. From such an extract it is possible to prepare a purified hormone which is directly, locally lactogenically active. Some of the implications are discussed. D.B.C.

LARVAE OF THE BRITISH SPECIES OF *DIOGENES*, *PAGURUS*, *ANAPAGURUS* AND *LITHODES* (CRUSTACEA, DECAPODA)

By J. D. MACDONALD, R. B. PIKE and D. I. WILLIAMSON

Proc. zool. Soc. Lond., 1957, Vol. 128, pp. 209–57

Larvae, obtained both from laboratory hatchings and from plankton, are described for the species *Diogenes pugilator* (Roux), *Pagurus bernhardus* (L.), *P. pubescens* Krøyer, *P. prideauxi* Leach, *P. cuanensis* Thompson, *Anapagurus laevis* (Thompson), *A. hyndmanni* (Thompson), *A. chiroacanthus* (Lilljeborg) and *Lithodes maia* (L.), and a single larva obtained from plankton from off Plymouth attributed to *Pagurus sculptimanus* Lucas. Keys to these larvae are given.

A consideration of all the known larvae of hermit crabs and stone crabs shows that they fall into two main divisions, corresponding to the Coenobitidae plus Diogeninae on the one hand and the Lithodidae plus Pagurinae on the other: a division which can also be made from the disposition of the third maxillipeds of the adults. It is suggested that the classification generally accepted fails to reflect the phylogeny of the various groups, and a revised classification is proposed in which each of the two divisions indicated by the larvae forms a superfamily of the Anomura.

It is also shown that the larvae of the species of *Pagurus* fall into two distinct groups; when further species have been investigated the splitting of the genus might be justified. D.I.W.

BOOK REVIEW

ALLGEMEINE MEERESKUNDE: EINE EINFÜHRUNG IN DIE OZEANOGRAPHIE

By G. DIETRICH

With a chapter by K. KALLE

Published by Gebrüder Borntraeger, Berlin, 1957; Price: DM. 56. Pp. viii+492 (including 223 text-figures), 30 text-plates and 7 loose folding plates.

It is fifteen years since Sverdrup, Johnson and Fleming's '*The Oceans*' appeared. The time is now ripe for another standard text-book of general oceanography. Dietrich has met the need with a book which combines the German gift for accurate detail with clear and concise presentation of broad issues. He has used a direct prose style free from the grammatical tangles which may make the German language so difficult for those who have not mastered it.

His colleague, Kurt Kalle, has contributed a chapter of sixty pages on the geochemistry, biochemistry and productivity of sea water. This is the only chapter into which biological matters enter. The remaining 400 pages are devoted to physical oceanography, all branches of which are covered more than adequately. Where all is so good it is not easy to select one section for special mention. Mathematics is used when necessary but no biologist need fear that he will be overwhelmed by formulation of which he has neither need nor interest. An English translation of this excellent book with such a distinctive approach ought to sell well.

L. H. N. COOPER

MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

Report of the Council for 1956–57

The Council have to report with regret the death of Mr B. Storrow, an Associate Member of the Association since 1930.

The Council and Officers

During the year Major E. G. Christie-Miller resigned from the office of Honorary Treasurer to the Association, which he has held since 1941. The Council wish to record their thanks to Major Christie-Miller and their appreciation of his devoted services to the Association for so long a period.

Mr Harrison S. Edwards has been elected Honorary Treasurer, and it is a source of much gratification to the Council that the office continues to be held by a Governor representing the Fishmongers' Company.

Four ordinary meetings of the Council were held during the year, three in the rooms of the Royal Society and one at Plymouth. At these the average attendance was seventeen. The Association is indebted to the Council of the Royal Society for the use of its rooms.

The Plymouth Laboratory

The excavation of the new sea-water reservoirs which began in October 1955 has proved a harder task than originally anticipated. The drilling of the rock was not completed until the end of October 1956.

The final construction of the reservoirs was, however, completed by 31 March 1957, and the building of new outside circulation tanks is well in hand.

The walls of one of the old sea-water reservoirs, which had been leaking, have been relined with a waterproof coating.

Aquarium

The aquarium has been open throughout the year and has been well attended. No major structural alterations have been made.

Research Ships

The three research vessels, *Sarsia*, *Sula* and *Gammarus*, have been in regular operation apart from routine surveys.

Plymouth Marine Fauna

During the year the new edition of the *Plymouth Marine Fauna* has been in the hands of the printers and it is anticipated that it will soon be ready for publication.

The Council wish to record their thanks to members of the Plymouth laboratory staff and others who have contributed to this new fauna list. The editing of the manuscripts and correction of the proofs have been an exacting and time-consuming work, and the Council wish specially to thank Dr D. P. Wilson on whom this burden has fallen and whose skill and knowledge have been given so willingly, and Mr G. M. Spooner for the help given from his wide faunistic experience.

Staff

Dr J. S. Alexandrowicz retired from the staff of the Plymouth laboratory on 31 March 1957. The Council wish to place on record their appreciation of the distinguished researches made by Dr Alexandrowicz, and the valuable help he has given to the Association.

Dr E. J. Denton joined the staff of the Plymouth laboratory as Principal Scientific Officer on 1 April 1956.

Dr A. J. Southward joined the staff of the Plymouth laboratory as Scientific Officer on 1 October 1956 in a special supernumerary post.

Mr E. I. Butler joined the staff of the Plymouth laboratory on 1 October 1956 in the grade of Experimental Officer.

Mr F. A. J. Armstrong has been promoted to the grade of Senior Scientific Officer as from 2 April 1956.

Dr D. P. Wilson visited a number of marine biological and other laboratories in the United States in April–May 1956 after attending the Symposium on Marine Biology at the Scripps Institute of Oceanography, La Jolla.

Dr B. C. Abbott attended a colloquium on Marine Biology held under the auspices of the International Union for Biological Sciences at the marine biological laboratory at Roscoff in June 1956.

Dr D. B. Carlisle spent three weeks in April 1956 at Lund University and the Kristineberg Marine Zoological Station.

Dr B. C. Abbott, Dr E. J. Denton and Dr T. I. Shaw attended the International Congress of Physiology in Brussels in August 1956.

Mr G. R. Forster attended the meeting of the International Council for the Exploration of the Sea in Copenhagen in October 1956.

Dr B. C. Abbott has been elected a Fellow of the Institute of Physics.

Mr W. H. Searle was awarded the British Empire Medal in the New Year's Honours for 1957.

Occupation of Tables

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

E. Adams, Plymouth (Library).
Dr Daphne Atkins, Plymouth (Ciliary mechanisms of brachiopods).
T. B. Bagenal, Millport (Spawning of plaice).
Miss J. A. Bailey, London (General).
Mlle R. Barreau, Bordeaux (Algae).
Prof. E. J. W. Barrington, Nottingham (Endocrinology of tunicates).
Miss G. Beeson, Oxford (General).
P. E. Benstead, Southampton (Chemistry of sea water).
E. J. Binyon, London (Permeability of tube feet in *Asterias*).
G. T. Boalch, London (*Ectocarpus*).
Q. Bone, Oxford (Primitive chordate nervous systems).
A. D. Boney, Plymouth (Red algae).
Miss P. E. Brockman, Plymouth (Library).
K. H. Bultitude, Birmingham (Sensory physiology of elasmobranchs).
Dr P. C. Caldwell, Beit Memorial Fellow (Biochemistry of muscle and nerve).
Mrs P. C. Caldwell, Plymouth (*Spartina*).
J. W. Coles, London (Nematodes associated with seaweeds).
K. Copeland, London (Electronic equipment).
Mrs R. M. Cornell, Liskeard (Library).
Dr E. D. S. Corner, International Paints Research Fellow (Effects of toxic substances on marine organisms).
C. A. Cosway, Torquay (Library).
Miss W. A. M. Courtney, London (Ecology of cirratulids).
Dr D. J. Crisp, Anglesey (Feeding of cirripedes).
Dr Phyllis G. Croft, London (Humane killing of lobsters).
Prof. Sears Crowell, Indiana (Morphogenesis and growth of hydroids).
Dr R. Phillips Dales, London (Feeding rates in sabellids and serpulids).
E. W. Dawson, Cambridge (Physiology of lamellibranch foot).
R. D. Deshpande, Reading (Physiology of Trochidae).
Miss E. J. Dimelow, Reading (Functional morphology of *Antedon*).
J. T. Dunbar, Kingsbridge (Library).
D. Etherington, London (Library).
Mrs D. Etherington, London (*Ectocarpus*).
Surg.-Lt. R. J. Fallon, R.N., Plymouth (Library).
Dr Maria Felinska, Oundle (Ciliates).
Dr L. R. Fisher, Reading (Vitamin A in zooplankton).
E. Ford, Millport (Library).
Cdr R. H. C. F. Frampton, R.N. (Rtd.), Plymouth (Library).
R. F. H. Freeman, London (Activity cycles in *Scrobicularia*).
Dr Vera Fretter, Reading (Prosobranchs).
Dr D. N. Ganguly, Calcutta (General).
Dr J. B. Gilpin-Brown, Bristol (Nervous system of *Nereis*).
Dr Sylvia J. Gilpin-Brown, Bristol (Behaviour of littoral gastropods).
Dr M. Ginsburg, Bristol (Teleostean neurohypophysis).
Dr D. R. Glasson, Plymouth (Library).
Prof. A. Graham, Reading (Prosobranchs).
P. Gray, Plymouth (Library).

E. R. HANSEN, Plymouth (Library).
Dr E. JEAN HANSON, London (Histology of molluscan muscles).
Prof. A. C. HARDY, F.R.S., Oxford (Drawings of marine animals).
M. G. HARDY, Reading (Nervous system of ctenophores).
Dr A. E. HARPER, Cambridge (Glucose-6-phosphatase in *Lophius*).
F. A. B. HAWES, Poole (Settlement of *Tubularia*).
Dr R. H. HEDLEY, London (Foraminifera).
B. T. HEPPER, Conway (Lobsters).
Prof. A. V. HILL, F.R.S., London (Heat production in nerve).
J. V. HOWARTH, London (Heat production in nerve).
Dr G. M. HUGHES, Cambridge (Respiratory movements of *Scyllium*).
O. D. HUNT, Newton Ferrers (Library).
W. G. INGLIS, London (Osmo-regulation and locomotion in nematodes).
Dr C. H. JELLARD, Plymouth (Library).
Mrs J. JELLARD, Plymouth (Library).
Miss P. M. JENKIN, Bristol (Library).
Dr MARGARET W. JEPPS, Cambridge (Foraminifera).
W. E. JONES, Anglesey (Algae).
Miss E. A. KAY, Hawaii (Cypraeidae).
Dr G. Y. KENNEDY, Sheffield (Marine pyrrol pigments).
Dr R. D. KEYNES, Cambridge (Nerve physiology in *Loligo*).
M. C. KINGWELL, South Brent (Library).
Dr J. A. KITCHING, Bristol (Library).
Sir FRANCIS KNOWLES, Bt., Marlborough (Colour change in crustaceans).
Miss A. KUKU, London (Axial organs and tube feet in *Echinus*).
Miss B. I. LADE, London (General).
Dr MARIE V. LEBOUR, Plymouth (Decapod crustaceans).
K. LEDERIS, Bristol (Teleostean neurohypophysis).
Dr J. LLEWELLYN, Birmingham (Trematode ectoparasites of fishes).
A. R. LONGHURST, Freetown (Bottom sampling methods and library).
Prof. O. E. LOWENSTEIN, F.R.S., Birmingham (Sensory physiology of elasmobranchs).
Dr J. LOWY, Belfast (Physiology and histology of muscle).
Dr G. A. C. LYNCH, Plymouth (Library).
Miss C. I. MACFARLANE, Canada (Brown algae).
Dr ANNA MALQUORI, Naples (*Sepia*).
Prof. IRENE MANTON, Leeds (Marine flagellates).
E. R. MARCH, Plymouth (Library).
A. L. MARTIN, London (Feeding and digestion in amphipods).
R. B. MAYNE, Plymouth (Library).
P. B. MEURLING, Lund (Development of blood vessels in hypophysis region of *Scyllium*).
Prof. N. MILLOTT, London (Light reaction in echinoderms).
Miss F. M. MOLLOY, London (Digestion in mysids).
Prof. W. F. H. M. MOMMAERTS, Los Angeles (Heat production in nerve).
Dr J. E. MORTON, London (Ecology and physiology of mollusca).
Dr R. W. MURRAY, Birmingham (Sensory physiology of *Raia*).
Prof. LILY NEWTON, Aberystwyth (Algae).
Dr E. R. NOBLE, Santa Barbara (Protozoan parasites of fishes).
Dr C. E. O'HEOCHA, Galway (Library).
Dr C. F. A. PANTIN, F.R.S., Cambridge (Neuromuscular physiology of *Metridium*).
A. H. PAPWORTH, Ashford, Mddx. (Plankton).
Prof. B. PEYER, Zurich (Dentition of fishes).
Miss J. M. PLUMTREE, Nottingham (Endocrinology of tunicates).

Dr W. T. W. POTTS, Birmingham (Ion exchange in lamellibranchs).
P. REEVE, London (General).
Dr A. REVHEIM, Bergen (Mackerel).
Miss B. RICKARD, Plymouth (Library).
Dr F. H. RIGLER, Toronto (Ion exchange in *Bryopsis*).
Prof. P. ROA MORALES, Venezuela (Chemistry of sea water).
Dr ELAINE A. ROBSON, Cambridge (Neuromuscular physiology of *Metridium*).
Y. S. R. K. SARMA, London (Green algae).
Miss R. S. M. SAVAGE, London (Axial organs and tube feet in *Echinus*).
G. SHELTON, Cambridge (Respiratory movements of *Scyllium*).
J. P. SINHA, London (Green algae).
D. S. SMITH, Cambridge (*Clunio marinus*).
Miss M. M. SOARES, Southampton (Cirripede larvae).
B. W. SPARROW, Newton Ferrers (Library).
Dr A. J. SOUTHWARD, D.S.I.R. (Distribution and breeding of barnacles).
Dr Eve C. SOUTHWARD, Plymouth (Polychaetes).
Miss F. A. STANBURY, Plymouth (*Cladophora*).
U. STEFANSSON, Iceland (Oceanography).
Prof. W. STEPHENSON, Brisbane (General).
D. H. STEVEN, Cambridge (Library).
O. SUDDABY, Plymouth (Library).
R. V. TAIT, London (Plankton).
Dr MARTA VANNUCCI, Sao Paulo (Plankton).
H. WALLACE, Oxford (Ascidians).
Miss M. A. WALKER, London (Visual pigments of fishes).
P. R. WALNE, Conway (Library).
G. E. WALSTER, Plymouth (Library).
Dr T. WEIS-FOGH, Cambridge (Methylene blue staining of nerves).
R. L. WELCOMME, London (Library).
Dr MARY WHITEAR, London (Histology of fish skin and sensory organs in crustaceans).
R. J. WOOD, London (General).
M. YOSHIDA, London (Light reactions in echinoderms and coelenterates).

Among the many scientists who have visited Plymouth during the year to see the general work of the laboratory and to discuss problems with members of the scientific staff, the following have come from overseas: Prof. B. Steinbach (U.S.A.), Dr Gertrud Pleskot (Austria), D. W. LeMare (Penang), Prof. M. Stangenberg (Poland), H. W. Kakyomya (Uganda), Prof. R. P. Forster (U.S.A.), G. Küchler (Holland), Dr R. Buchsbaum (U.S.A.), R. W. Foster (U.S.A.), Prof. W. R. Boss (U.S.A.), Dr G. Filteau (Canada), Prof. C. L. Prosser (U.S.A.), Prof. A. H. Whiteley (U.S.A.), Prof. C. G. Miller (U.S.A.), Miss I. Bennett (Australia), D. L. Worf (U.S.A.), G. H. P. de Bruin (Ceylon), Mr and Mrs S. A. Wainwright (U.S.A.), Prof. K. Suriwata (Japan), J. Kikkawa (Japan), Dr P. E. Thompson (U.S.A.), Dr B. Halstead (U.S.A.), M. R. Ranade (India).

The Easter Vacation Courses were conducted by Mr G. M. Spooner and Mr P. G. Corbin, and were attended by forty students from the following Universities: Oxford, Cambridge, Glasgow, Aberdeen, Edinburgh, London,

Durham, Sheffield, Southampton, Exeter, Chelsea Polytechnic and Regent Street Polytechnic.

Also during the Easter Vacation Mr R. J. Jones and Dr C. T. Prime brought a party of ten boys from Whitgift School and Mr J. R. Packham brought seven boys from Varndean School, Brighton.

Scientific Work of the Plymouth Laboratory Staff

Sea Water and Plankton

Dr L. H. N. Cooper has completed the first stage of his study of the causes underlying long-term fluctuations in productivity of the English Channel. A group of hypotheses has been erected which imply that the deep Atlantic provides the connecting link between fluctuations in Arctic climate and productivity of the shelf waters of Western Europe.

During 1956 precise observations have been made in deep waters off La Chapelle Bank, which is within the range of Decca navigation. Accurate knowledge of depth was ensured by using four unprotected reversing thermometers on a hoist, and oxygen analyses were made in triplicate after randomizing.

The working up of the analyses is not yet completed, but the following deductions may be drawn. (*a*) The muds of the continental slope and abyssal ocean bed are sources of biological oxygen demand; this results in a curtain of partly deoxygenated water blanketing the slope and having no relation with density. (*b*) This curtain seems to be moving with the continental slope on its right, and has vertical and horizontal oscillatory displacements caused by internal waves; these displacements may be large—for example observations three days apart showed changes in oxygen content of up to 1·0 ml./l. (*c*) Strips of this deoxygenated curtain of water may be torn off and form isolated elongated cores surrounded by the well-oxygenated oceanic water. (*d*) The deoxygenated water may have acquired biologically active substances resulting from organisms living in the slope mud and their metabolic products, which may affect the nature and composition of the plankton. (*e*) These investigations and deductions support the direct observations made in a bathyscaphe by Prof. F. Bernard of the University of Algiers who observed strata of almost azoic water lying between layers in which many animals were seen.

This work done in 1956 has strengthened the ideas resulting from the work in earlier years and pointed to new lines. The value to fishery research of a knowledge of the transport of energy across the depths of the ocean and its effects on the distribution of water masses on the continental slope and its adjacent areas does not need stressing.

A paper by Dr Cooper on the use of carbon-14 for assessing the age of oceanic waters has been published in Vol. 35, No. 2, of the *Journal*.

Mr F. A. J. Armstrong has continued monthly cruises to station E 1 and the analyses for phosphate, total phosphorus and silicate. The results for 1955 are being prepared for publication. During the summer of 1956 there have been some rather rapid fluctuations in the silicon content of offshore water. At the same time the salinity of the water has been higher than 35·4‰, which is unusual.

Analyses for iron by the new digestion method have been done regularly at E 1 and five 'L' stations. The results, which now cover nearly two years, show a marked seasonal variation, more iron being found in the winter months. This is thought to be due to greater turbulence and land drainage at this time of year. A few more analyses of deep water have been done, and a method of storing samples without change for a short time has been found.

Some trials of an indophenol method have shown that it can be used for routine determinations of ammonia in sea water after low-pressure distillation. The method will be used for analysis of water from E 1, where it seems that phosphate has not in recent years been the limiting nutrient for phytoplankton growth.

Further analyses of sea water for aluminium by the improved method have shown that the quantities present are too small for sufficiently precise measurement, and a more sensitive method must be found.

The prototype absorptiometer designed by Mr Armstrong has had further tests at sea, and he is now constructing an instrument for regular use, either in the laboratory or aboard ship. A method of checking zeros is incorporated, which simplifies correction for drift caused by battery voltage changes.

Dr D. B. Carlisle and Dr B. C. Abbott have continued their investigations on the uptake of niobium and vanadium by certain ascidians, and the presence of these substances in the sea. Mr L. G. Hummerstone has improved the colorimetric techniques for niobium analysis and has estimated the niobium content of sea water. In collaboration with Dr T. I. Shaw, these investigations have been extended to include a study of the adsorption of radio-active niobium and caesium upon various surfaces under varying conditions of ionic strength. The experiments have shown that whereas sodium and niobium compete for adsorption sites, sodium cannot discharge caesium from most surfaces.

Dr H. W. Harvey has followed the rate at which the cellular carbon increases in cultures of *Phaeodactylum tricornutum* during exponential growth in bright and in dim light, and also the effect of periods of darkness on the subsequent rate of growth. The change in cellular carbon was assessed from the decrease in total carbon dioxide in the medium, which was calculated from the increase in hydrogen-ion concentration.

The experiments are indicating that when growing with ample nutrients and in sufficient light to allow maximum rate of growth, the exponential rate

depends upon the chlorophyll content of the cells. That is, the rate of chlorophyll production limits the rate of carbon assimilation when 'light saturated'. In turn the rate of chlorophyll production appears to be the resultant of the rate of (light independent) synthesis minus its rate of photochemical breakdown.

When a 'light saturated' culture growing at a regular, and reproducible, rate was kept dark for twelve hours its chlorophyll and other pigments increased; then when transferred to the same light intensity its cellular carbon increased at an enhanced rate for twelve hours or more, thereafter falling to the regular rate for that temperature and light intensity. Likewise, if a culture growing exponentially in dim light, the cells then being richer in chlorophyll than when growing in bright light, was transferred to 'light saturation', then the increase in cellular carbon proceeded more rapidly for a time than the regular rate for that light intensity and temperature.

The second paper by Dr Mary Parke, in collaboration with Prof. Irene Manton and Mr B. Clarke, of Leeds University, on new members of the Chrysophyceae has been published in Vol. 35, No. 2, of the *Journal*. The study of a further group of these new forms, maintained in culture at Plymouth, should be completed soon. In addition to showing a different type of surface scale covering, these new forms also differ from any previously described in the behaviour of the haptonema (the retractile filiform appendage used for the temporary anchorage of the cell); attachment can occur right along its whole length—not just at the swollen distal end—suggesting that the haptonema in these forms may be ribbon-shaped. Prof. Manton is continuing to collaborate with Dr Parke in the electron microscopy.

The collection of unialgal cultures of marine phytoplankton organisms has had to be maintained throughout the year by Dr Parke and Miss Ballantine owing to the illness of Miss I. Adams. Large numbers of cultures, at least two a week, have been distributed for research purposes to institutions in this country and abroad, in addition to the large volumes of cultures that have been prepared for use by scientists working in the laboratory.

'Corrections and Additions, 1953–1955' to 'A Preliminary Check-List of British Marine Algae' (1953, Vol. 32 of the *Journal*) has been compiled by Dr Parke and published in *Phycological Bulletin*, No. 4, pp. 23–31, May 1956.

Miss D. Ballantine's descriptions of the two new species of *Gymnodinium* (*G. veneficum*, which is toxic to fish and other animals, and *G. vitiligo*) have now been published in Vol. 35, No. 3, of the *Journal*, and she is continuing her work on dinoflagellates.

In February 1956 she visited the East African Colonial Fisheries Laboratory in Zanzibar and was there for one month, during which time she collected numerous tow-net samples of phytoplankton and is still examining these for dinoflagellates. Some work was also attempted on living plankton there, but as there was no means of temperature control, this was almost impossible.

The work of Dr B. C. Abbott and Miss Ballantine on the toxin from *Gymnodinium veneficum* was published in Vol. 36, No. 1, of the *Journal*. This covers the action of the dinoflagellate culture on various animals; the extraction and partial concentration of the poison and study of its action on isolated preparations of hearts, nerves, muscles and frog skin. It has been demonstrated that the poison acts on the nervous system, and depolarizes excitable tissues, probably by interfering with the sodium exchange mechanism. Comparable experiments have been made using a Canadian extract (from shellfish which have become poisonous after eating certain flagellates), which is responsible for paralytic shellfish poisoning in man. This poison is different from that of *Gymnodinium veneficum*. It is hoped to carry out further experiments using the shellfish toxin to ascertain its mode of action and also to carry further the purification of the *Gymnodinium* toxin.

The study of flagellate toxins has practical value since they cause mass mortality of fish in the sea and under cultivated conditions.

Dr E. D. S. Corner, International Paints Research Fellow, in collaboration with Mr B. W. Sparrow (International Paints Research Laboratory, Newton Ferrers), has completed a preliminary investigation of the modes of action of copper and mercury as poisons to certain planktonic crustaceans, and the results of this study have been published in Vol. 35, No. 3, of the *Journal*.

In the course of more recent work determinations have been made of the toxicities of an homologous series of alkylmercuric halides to larvae of *Artemia salina*, nauplii of the barnacle *Elminius modestus* and adults of the copepod *Acartia clausi*. The ethyl ether:sea water partition coefficients of the same series have also been measured. It has been found that although toxicities to both *Artemia* and *Elminius* increase logarithmically as the series is ascended, much larger differences between toxicities are observed when *Artemia* is used than when the compounds are tested with *Elminius*. In addition, a close correlation has been found between the toxicities of organomercurials to *Artemia* and their partition coefficients, a finding consistent with the view that an important factor influencing the toxicities of these compounds to this animal is lipoid solubility. Further experiments are at present being carried out in order to examine the importance of chemical interaction with proteins as a further factor influencing the toxicities of organomercurials, and preliminary studies have been concerned with the relative abilities of these compounds to inhibit urease.

A continuation of this research may lead to an understanding of some of the factors governing the limitation of different species of plankton animals to certain types of water, e.g. oceanic and coastal.

Mr F. S. Russell has continued his observations on deep-sea medusae collected on the cruises of R.V. *Sarsia*. Descriptions of the two species of Scyphomedusae *Nausithoë atlantica* and *N. globifera* have been published in Vol. 35, No. 2, of the *Journal*. Two new species of anthomedusae, *Amphinema*

krampi and *Merga reesi*, and one new leptomedusa, *Tiaropsidium atlanticum*, have also been described in Vol. 35, Nos. 2 and 3, of the *Journal*.

The 1956 catches of the 2 m stramin ring-trawl showed no departure from the prevailing low level of macroplankton production and *Sagitta setosa* continued as the dominant chaetognath: Mr P. G. Corbin examined the catches.

In co-authorship with his wife, Dr D. P. Wilson has published in Vol. 35, No. 2, of the *Journal* an account of the strandings of *Ianthina janthina* (L.) which took place mainly along the north coasts of Cornwall and Devon in August 1954 during a sustained period of strong westerly winds. Letters to *The Times* and other newspapers obtained the co-operation of members of the public in forwarding reports and specimens from a wide area. These have enabled the extent of the strandings to be plotted and the writing of an account which is unique in the literature of this relatively little-known mollusc, of which no stranding of comparable magnitude appears to have taken place on English coasts for fifty years. Measurements of all the undamaged shells obtained showed that while there is considerable variation in the width of shells of the same height, the width becomes proportionately less with age. From this it is practically certain that small wide shells previously described as separate species (e.g. *I. planispirata* Adams & Reeve) are young specimens of *I. janthina* (L.). These observations confirm and extend the conclusions, based on other evidence, of the Danish author Laursen. Some living snails in excellent condition were also obtained and these enabled observations to be made on float building, reproduction, and some other aspects of the activities of the living animal.

Macro-Flora and Fauna

The reorganization of the herbarium of marine algae has now been completed by Dr Parke and Miss Ballantine and a number of additions have been made to it during the year.

Following his work with the larvae Dr Wilson has made some preliminary observations on the burrowing of adult *Ophelia bicornis* into sands of different types. These experiments can only be regarded as exploratory, intended primarily to lead to a satisfactory technique, and have not reached a stage where it is possible to discuss results.

In readiness for his attendance at the Symposium on 'Perspectives in Marine Biology' arranged by the Scripps Institution of Oceanography and held at La Jolla, California, in March 1956, Dr Wilson spent some time during the preceding months preparing his contribution. This took the form of a paper, entitled 'Some Problems in Larval Ecology Related to the Localized Distribution of Bottom Animals', in which were reviewed several aspects of larval development and settlement about which more knowledge is desirable, as for instance the necessity for paying more attention to the micro-biology of bottom soils in relation to the distribution of the larger species. The paper was well

received, and it is understood that it will eventually be published along with other contributions to the Symposium.

In collaboration with Dr J. E. Morton of Queen Mary College, London, and Mr A. D. Boney of the Plymouth Technical College, Dr Corner has made a study of the respiration, rate of filtering and resistance to desiccation of the intertidal bivalve mollusc, *Lasaea rubra*, an animal which may be particularly useful in providing a regular supply of material for future toxicity studies. It is hoped that details of recent work concerning aspects of the ecology of this animal will shortly be published. Preliminary studies of the respiration of the hydroid *Tubularia* have shown that this important fouling organism may also serve as suitable material for toxicity experiments.

Mr G. M. Spooner has continued his work on three of the temperate-zone species of clunionine marine gnats. The early stages of *Thalassomyia frauenfeldi*, not hitherto studied in this country, are being compared with the two existing published accounts on material from the Adriatic and Black Sea respectively. There are differences in both the larval mouthparts and the adult male genitalia which contrast the British population with that of the other two areas, and suggest a subspecific distinction. The larvae live in *Enteromorpha* from H.W.S. to below mid-tide; they are now known to be abundant on the concrete blocks protecting the outer face of the Plymouth Breakwater and to occur even on the Eddystone Rock.

The growth of the larvae of marine chironomids occurs in a few instars with a large jump in size at each moult. Measurements of the head capsule of a collection of larvae of *Cricotopus* (one of the two orthocladine genera with marine species) showed that the instars are absolutely separate in size, the ratio between the dimensions of successive stages being about 1·6.

Study of the occurrence of the commensal polynoid *Harmothoë lunulata* has continued. Specimens have now been obtained in *Phascolosoma elongatum* burrows, and these appear to be indistinguishable in pattern from those of larger size found with *Amphitrite johnstoni*. There is evidence for the existence of at least three independent *lunulata* populations on the Devon and Cornwall coast which seem to have the status of 'host races', familiar among some insects.

Further local collections have been examined of amphipods and isopods for faunistic information. Attention has been given to the amphipod *Isaea elmhirsti*, a little-known epizoic species that lives on the lobster (*Homarus gammarus*), lurking at the bases of the thoracic limbs. Hitherto unrecorded from southern Britain, it proves far from common, but up to five have been found on one lobster. The undescribed adult male is evidently less numerous than the female, but two examples have now been obtained for description.

Study has begun of the Amphipoda from deep water stations in collections made by R.V. *Sarsia*. The species and their relative numbers are being systematically recorded, with an eye for possible links between the distribution of certain forms and that of water masses.

Mr N. A. Holme has continued his work on bottom-living animals, and in July 1956 made a successful bottom-sampling cruise off the south-west coast of Ireland. The continental shelf is here fairly narrow and it was possible to work a line of stations from the shallow water of Dingle Bay out almost to the 100-fathom line. These quantitative samples are of considerable interest since the sea conditions off this coast would only very rarely enable such work to be done.

Mr G. R. Forster has continued work on the fauna of sublittoral rocks. A further twenty-five dives have been made during the summer. Some variations in the sessile fauna in relation to depth and degree of exposure to wave action have been found. For instance, various species of erect bryozoans usually replace ascidians and sponges as the most abundant group when a particular level of shelter is reached. But one of the commonest species, the little madreporarian anemone *Corynactis viridis*, with attractive pink, green, orange and brown colour patterns, is found both in sheltered and exposed conditions and also over the whole depth range so far studied.

New records of sponges include: *Stelletta lactea*, *Stryphnus ponderosus*, *Microciona strepsitoxa* and *Antho involvens*; these together with notes on other rare species have been included in the new fauna list.

The spotted goby referred to in last year's report has been found to be fairly generally distributed in rocky areas near Plymouth and not restricted to the one place from which specimens were taken last year. A waterproofed robot camera, with a flash bulb holder, capable of taking under-water pictures at any distance between 8 inches and 5 feet, has been tested.

Dr A. J. Southward has continued his studies on the distribution, breeding and physiology of barnacles and other intertidal animals. The routine observations at Plymouth and other places in south-west England have shown no marked changes in the barnacle populations during the year, whereas the northern species *Balanus balanoides* had increased in abundance in previous years. The paper on the distribution of intertidal animals and plants along the Channel, prepared in collaboration with Dr D. J. Crisp of Bangor, has been completed after a visit to the Channel Islands.

Dr Southward has finished the study of the breeding of the lugworms *Arenicola ecaudata* and *A. branchialis*, undertaken in collaboration with Dr Eve C. Southward. The former species breeds nearly all the year, ceasing only during the two coldest months, whereas the southern species *A. branchialis* ripens during the summer and spawns mainly from October to December.

During a cruise of R.V. *Sarsia* to the continental slope in the vicinity of 48° 30′ N., 10° W., Dr Southward and Mr Forster dredged up many specimens of the deep-sea barnacle *Hexelasma hirsutum* Hoek from 600 to 700 fathoms. The behaviour of this barnacle in the laboratory suggests that its occurrence may indicate the presence of deep-sea water currents, and further work is being carried out in collaboration with Dr Cooper.

Observations on the Lucernariidae have been continued by Mr P. G. Corbin. Perfect conditions resulted in an exceptionally low spring tide on one occasion in August, making it possible to collect over a large area of the shallow channel dividing Looe Island from the mainland shore: this part is not usually accessible even on a good low spring tide. In the channel, *Halyclistus* was common as on the *Zostera* beds higher up the shore, but in addition *Lucernaria campanulata* was numerous, whereas usually only two or three specimens occur on the *Zostera*. This finding was useful confirmation of the hitherto rather slowly accumulating evidence that this species is distributed from low springs downwards into the sublittoral zone and is not so successful intertidally as *Haliclystus*.

Since H. W. Chang recorded *Callionymus reticulatus* in British waters, there has been some difficulty in separating the 'off-season' males and the females of this species from small *C. lyra* of the same size: the third species, *C. maculatus*, is readily distinguished. Mr Corbin has observed that living specimens of *lyra* and *reticulatus* can be recognized by characteristic differences of their tail markings, of the patterns of spots along the side of the body and of the melanophores on the under-side: these differences hold good for specimens down to 3·0 cm long.

Dr G. A. Steven's work has been badly curtailed and interrupted by serious illness. Nevertheless, he has been able to work up data compiled on otter trawl fish surveys by Dr R. S. Clark and Mr E. Ford in 1919 and the early 1920's (1920, 1921, 1922) and comparative data collected by himself, Mr A. D. Mattacola, and Captain C. A. Hoodless in the early 1950's (1950, 1951, 1952). The area concerned is roughly bounded by a line drawn in a wide sweep from Stoke Point to the Eddystone Lighthouse and thence to Polperro. It appears that on the whole the fish fauna has remained remarkably constant, the 1920's being, if anything, slightly more productive than the 1950's. A few species, previously plentiful, have now, however, all but disappeared from the area. These are *Capros aper*, *Molva molva*, *Squalus acanthias* and *Trigla gurnardus*. Five species have markedly increased in numbers—*Cepola rubescens*, *Merluccius merluccius*, *Mullus surmuletus*, *Pagellus centrodontus* and *Trachurus trachurus*.

Apart from these early data by Clark and Ford, no accurate records of demersal fish fauna in the vicinity of Plymouth have subsequently been kept. Since 1953, therefore, Dr Steven, assisted by Mr A. D. Mattacola and Capt. W. J. Creese, has been recording the catches taken as nearly as possible at weekly intervals in an hour's haul at international station L 4, which is located about mid-way between Rame Head and Eddystone Lighthouse. Already these data are providing interesting and useful information on the rise and decline of year-classes in certain fishes and on the variations in times of appearance and disappearance of migratory species.

During his mackerel investigations Dr Steven has found that best fishing by commercial fishing vessels never occurs in the area of maximal spawning

activity. Early in April 1955 (in association with Mr L. B. Pradhan of India) a five-day visit was made to the spawning grounds in the Celtic Sea during which an echo-sounding survey of the area was made in addition to plankton sampling for the collection of eggs and larval stages. Mackerel may evade capture during maximal spawning activity, either because they do not 'swim' when spawning or because they are too deep to be taken in drift nets. Conclusive evidence in support of either hypothesis was not obtained; and a second visit to the area in April 1956 could not be undertaken because of illness. It is hoped to continue the investigation at some future date.

Physiology of Marine Organisms

Much information is available on the life and habits of organisms in the sea and on the chemical and physical factors of their environment. But in order to understand how the organisms react to their environment it is necessary to know much more of their physiology. This is the largest lacuna in the science of marine biology and a wide range of physiological problems are now being investigated at Plymouth.

It is well known that certain brown sea weeds concentrate iodine in their tissues. Dr T. I. Shaw is investigating the mechanism involved and the function of the iodine in *Laminaria digitata*, using the radioactive isotope. The liberation of elementary iodine from iodide outside the weed has been demonstrated, and evidence has been adduced to show that it is this elementary iodine, or a related oxidation state, which is involved in the uptake of the radioactive element. Compounds inhibiting iodine uptake in the weed are known to block the iodine uptake in thyroid tissue.

Further study has indicated that the accumulation of iodine in the weed is closely associated with the oxidative metabolism of carbohydrates, and it has been found that approximately one to two iodine atoms are taken up for each hexose molecule broken down. It has also been found that the respiration rate during the uptake of iodine is very rapid, approaching that found in mammalian tissues at 38° C.

Dr D. B. Carlisle has continued work on the endocrinology of crustaceans, particularly on colour change and on sexual endocrinology. On the former aspect he has continued in collaboration with Mme M. Dupont-Raabe of the Sorbonne, Paris, and with Sir Francis Knowles of Marlborough. A preliminary account of some of the results of this collaboration has appeared in *C. R. Acad. Sci., Paris*, where it is shown that one at least of the colour change hormones of *Leander* contains peptide linkages essential to its function. A visit to Sweden to work in collaboration with Dr R. Fänge and Dr E. Östlund led to further information being obtained on the chemistry of colour change hormones. A recent advance in this field has been the isolation and characterization of yet another chromactivating hormone precursor from the

X organ-sinus gland complex. Like the previously isolated precursors it is not destroyed by boiling and is more stable than most hormones.

Work on the physiology of growth and breeding of prawns is proceeding. The ovarian inhibiting hormone is now the subject of chemical investigation by Prof. Sir Alexander Todd of Cambridge and by Dr R. K. Callow of the National Institute for Medical Research, Mill Hill, both of whom are collaborating with Dr Carlisle. Preliminary results suggest that the hormone may be a steroid. Injection of various known steroids into prawns has been without effect on the ovaries, but this series of experiments is far from complete, since many more steroids remain to be tried. Dr Carlisle has found no evidence for the existence of a testis inhibiting hormone in prawns, despite an intensive search. The only operation which has led to inhibition of testicular function has been to block the vasa deferentia with plasticine plugs. While he was in Sweden, Dr Carlisle took the opportunity of investigating the endocrine basis of sex reversal in the red prawn *Pandalus borealis*. This he found to be essentially similar to that in *Lysmata seticaudata*, but he was able to carry his observations further. It seems evident that sex reversal is controlled primarily by the action of the X organ-sinus gland complex in secreting the ovarian inhibiting hormone, which appears to be the only hormone concerned. This hormone, or rather the cessation of its secretion, is responsible for the control of the onset of sex reversal. The actual assumption of the female form seems to take place at the moult following the attainment of a minimum ovarian size. The degeneration of the testis which follows sex reversal is probably to be attributed to the blocking of the opening of the vasa deferentia which takes place when the animal develops a female shell with the genital openings on the third rather than the fifth thoracic segment.

The moulting process in *Ligia oceanica* is apparently under the same type of control as in the Natantia, according to evidence presented by Dr Carlisle in Vol. 35, No. 3, of the *Journal*. The interval between the two halves of the moult, however, appeared to be outside this control, and no trace was found of any mechanism which might regulate it. He has investigated further the differences in moulting and its regulation in populations of prawns from different localities, and has been examining in the field the moulting and biology of *Maia squinado*. In this species moulting takes place only during a short period of the year, when moulting animals congregate in heaps, apparently for protection. Underwater observations of such a heap have proved fruitful of information.

Dr Carlisle has identified one of the heart-beat regulating hormones (reported by Alexandrowicz & Carlisle in 1953 in the *Journal*) as an *ortho*-dihydroxy indole alkylamine, probably 5,6-dihydroxy tryptamine. A preliminary account has appeared in the *Biochemical Journal*.

Dr J. S. Alexandrowicz has continued his study on the innervation of the heart of the prawn *Leander serratus*. The general arrangement of nerve elements

follows a pattern similar to that of other crustaceans. The local system is made up of nine ganglion cells which are all alike. This fact strengthens the contention that in other decapods these cells, although occurring in two sizes, are basically of the same sort. It has also been found that in *Leander* nine arteries, two more than in other decapods, arise from the heart. Each of these vessels has valves supplied by a special set of nerve fibres.

The observations on the histological structure of muscle tissue in crustaceans has led to the following conclusions: (*a*) that the muscles are not composed of units like the muscle fibres of vertebrates, but consist of bundles of myofibrils anastomosing with each other; (*b*) that in the thorax and the abdomen two sorts of muscle tissue with fine and coarse cross-striation are present: the former makes up the bulk of the muscle system which consists of bundles which are usually twisted, whereas the latter forms certain weak muscle units with bundles lying parallel and never twisted.

Dr Alexandrowicz has also studied the innervation of the heart of some molluscs. In the lamellibranchs, *Pinna fragilis* and *Pecten maximus*, it has been found that the two nerves reaching the heart at its anterior part run through the ventricle anastomosing with each other and giving off branches supplying the whole muscular wall; they do not seem to pass to the auricles which are supplied by separate nerve fibres. No ganglion cells have been found in the heart wall.

In *Sepia officinalis* the heart nerve arising from the commissure of the visceral nerves has been found to penetrate the heart wall and appear on its inner surface as a wide trunk the branches of which ramify abundantly and spread over the whole muscular network of the heart. As in lamellibranchs, neither in the ventricle nor in the auricles could ganglion cells be found. From the course of the nerve fibres it would appear that the cell bodies of a good part of the neurons supplying the heart are situated in the branchial ganglion from which some of the cell axons pass directly to the auricles, whereas those of the ventricle run up to the visceral commissure to curve here and enter into the heart nerve. Other fibres of the latter come straight from the central nervous system.

In collaboration with Dr Mary Whitear of University College London Dr Alexandrowicz has investigated nervous organs in the legs of decapod crustaceans. Groups of cells of several types, some containing more than 100 cells in a row, have been observed at the leg joints. Their special features and arrangement in various segments have been determined in several species. A muscle receptor of hitherto unknown type presumably controlling the position of the coxopodite in relation to the thorax has been found in the five appendages in *Homarus*, *Palinurus* and *Eupagurus*, but only in the chela of the crabs, *Maia*, *Cancer*, *Carcinus* and *Portunus*. It consists of a thin muscle attached proximally to a rod-like processus of the endophragmal skeleton and inserting distally into the coxopodite. It has a complicated innervation

composed of fibres of various sorts, most of them ending on a dense entanglement.

It has also been found that on the chitinous apodemes projecting into some of the leg muscles nerve cells are present. It is conjectured that they may be elements of the sensory apparatus of the moulting process.

Apart from his work with Miss Ballantine on flagellate toxins, Dr B. C. Abbott has continued his research on the comparative physiology of invertebrate muscle, especially on the lamellibranch molluscs. This work has been done in collaboration with Dr J. Lowy of Queen's University, Belfast. The results of research on the adductor muscle of *Pinna* have recently been published in Vol. 35, No. 2, of the *Journal*, where the mechanical properties of the muscle at rest and during activity are reported. Two papers have been written on the mechanical properties of smooth muscles, one dealing with the general properties of resting lamellibranch muscle and the other with tension changes following stretch of resting muscle (stress relaxation); one of these papers has been published in the *Proceedings of the Royal Society*. The results of experiments on active smooth lamellibranch muscle are being worked up: it is probable that the long sustained closure of the two valves in the mussel and other bivalves is due to tetanic activation and very slow relaxation, rather than to a catch mechanism.

Research has also been carried out on the opacity changes in squid muscle. When at rest the animal, as in a great number of planktonic organisms, is transparent. Striking changes in transparency accompany muscular activity, there being an early increase in transparency followed by a large increase in opacity.

Dr B. C. Abbott has collaborated with Prof. A. V. Hill and Mr J. V. Howarth of University College London on a basic investigation of heat production in isolated crab nerve.

The measurements of heat production during repetitive stimulation at room temperature indicated that an initial rapid outburst of heat was followed by an absorption of heat (so-called negative heat). The rapidity of the changes limited the precision of time analysis of the events; but it was possible to record the heat changes at 0° C following a single impulse in the nerve. The results confirmed the earlier results, showing an initial rapid positive phase followed by a longer lasting negative phase of heat. During such measurements the nerves have to conduct for several centimetres, and the wide range of propagation velocities complicates the time relationships. Records of the action potentials have been made in order to study the total times involved and the range of velocities; and also to ensure that the majority of the fibres are conducting.

In attempts to indicate the origin of the heat production it has been necessary to investigate the ionic exchanges occurring during nervous activity at 0° C. This is done using radioactive potassium which enables the fluxes to be measured: these experiments are still proceeding.

The light produced by fish-photophores is intermittent, and much remains obscure about the method of regulation. Utilizing material of a hardy luminescent species, *Porichthys*, which he collected while in California in 1954, Dr J. A. C. Nicol has investigated the possibility of nervous control. Histological studies have revealed that the photogenic tissue receives nerve fibres, and electrical stimulation of the nervous system (spinal cord) has been used to evoke the response. The pattern of innervation suggested that the light organs are supplied by the sympathetic system. An account of this work has been accepted for publication in the *Quarterly Journal of Microscopical Science*. An unusual bloom of *Noctiluca* in 1955 provided abundant material for physiological studies. Recordings were made of the luminescent flashes of single cells, and the effect of varying conditions of stimulation on the excitability of the cell studied. Cells luminesce only when stimulated (electrically and mechanically), when they give off brief flashes, some 0·1 sec. in duration. With repeated stimulation the light becomes weaker, but gradually recovers after a rest period. Several shocks produce a brighter response, owing to build up of some favouring agent. This work is to be continued when further material is available.

In collaboration with Dr G. Y. Kennedy of the Cancer Research Unit, Sheffield, Dr Nicol has been investigating the green pigments of *Chaetopterus*. These pigments are a mixture of phaeophorbides, localized in apparently symbiotic inclusions in the gut wall. An account of this work will soon be ready for publication.

Dr E. J. Denton has begun investigations on vision in marine fishes, both coastal and deep sea. Using an apparatus designed to make measurements of spectral absorption on very small areas of retina, he has worked on the photosensitive pigments found in the retinae of fish. In collaboration with Miss M. A. Walker of the Institute of Ophthalmology, London, the retinal rods of *Conger vulgaris* were shown to contain neither the rose-coloured 'visual purple' found in most coastal fish nor the purple-coloured 'visual violet' found in fresh water fish, but a golden coloured pigment. Dr Denton and Mr F. J. Warren adapted the apparatus for use at sea, and aboard R.V. *Sarsia* demonstrated similar golden coloured pigments in the retinae of four deep sea fish caught in the Bay of Biscay. The kindness of the Director of the National Institute of Oceanography enabled this result to be confirmed and extended aboard R.R.S. *Discovery II* to include in all fifteen species of deep sea fish. Alone amongst the oceanic fish studied, the surface fish *Saurus scombresox* was found to have a retina containing visual purple.

These golden coloured pigments, to which the names visual golds or chrysopsins have been given, have their maxima of absorption close to the maximum transmission of oceanic waters. The densities of photosensitive pigments found in the retinae of deep sea fish are very high; in some over 90% of light of wave-length 480 mμ is absorbed for one passage through the retina.

This figure may be compared with the corresponding figure of about 20% given for man by Dr W. A. H. Rushton. This is an adaptation to enable them to make most use of the feeble light found in the deep ocean.

The 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.

The Library has again been much used by visiting members of the Association.

The actual movement of the contents of the library, necessitated by the completion of the new extension and the re-classification of all material, was begun in May 1956. The Council wish to record their appreciation of the skill and devotion of the librarian, Miss L. M. Serpell, in completing the reorganization without interference to the normal use of the library.

Published Memoirs

Volume 35, No. 2, of the *Journal* was published in June 1956, Volume 35, No. 3, in October 1956 and Volume 36, No. 1, in February 1957.

The following papers, the outcome of work done at the Plymouth laboratory, have been published elsewhere than in the *Journal* of the Association:

Abbott, B. C. & Lowy, J., 1955. Heat production in a smooth muscle. Proc. physiol. Soc., 23–24 September 1955. *J. Physiol.*, Vol. 130, 25P.

Abbott, B. C. & Lowy, J., 1956. A new muscle preparation for the study of optical changes during contraction. *Nature, Lond.*, Vol. 177, pp. 788–9.

Abbott, B. C. & Lowy, J., 1956. Resting tension in snail muscle. *Nature, Lond.*, Vol. 178, pp. 147–8.

Abbott, B. C. & Lowy, J., 1956. Early tension changes during contraction of certain invertebrate muscles. Proc. physiol. Soc., 2 June 1956. *J. Physiol.*, Vol. 133, 8–9P.

Abbott, B. C. & Lowy, J., 1957. Stress relaxation in muscle. *Proc. Roy. Soc.* B, Vol. 146, pp. 281–8.

Ashhurst, Doreen E., 1956. Red blood-cell antigens in some lower vertebrates. *J. exp. Biol.*, Vol. 33, pp. 249–55.

Atkins, D., 1956. Ciliary feeding mechanisms of brachiopods. *Nature, Lond.*, Vol. 177, pp. 706–7.

Atkins, W. R. G. & Jenkins, Pamela G., 1956. Factors affecting the vernal phytoplankton outburst in the English Channel. *Nature, Lond.*, Vol. 177, pp. 1218–19.

Ballantine, D. & Abbott, B. C., 1957. Toxic marine flagellates; their occurrence and physiological effects on animals. *J. gen. Microbiol.*, Vol. 16, pp. 274–81.

CARLISLE, D. B., 1956. An indole-alkylamine regulating heart-beat in Crustacea. Proc. biochem. Soc., 25 May 1956. *Biochem. J.*, Vol. 63, 32P.

CARLISLE, D. B., 1957. The direct action of anterior pituitary extracts on the initiation of lactation in the rabbit. *Physiol. Comp. Oecol.*, Vol. 4, pp. 295–312.

CLARK, R. B., 1956. The eyes and the photonegative behaviour of *Nephtys* (Annelida, Polychaeta). *J. exp. Biol.*, Vol. 33, pp. 461–77.

COOPER, L. N. H., 1955. Deep water movements in the North Atlantic as a link between climatic changes around Iceland and biological productivity of the English Channel and Celtic Sea. *J. Mar. Res.*, Vol. 14, pp. 347–62.

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DENTON, E. J., 1956. On the vision of the conger eel. Proc. physiol. Soc., 20–21 July 1956. *J. Physiol.*, Vol. 133, 56–7P.

DENTON, E. J. & WARREN, F. J., 1956. Visual pigments of deep-sea fish. *Nature, Lond.*, Vol. 178, p. 1059.

HEDLEY, R. H., 1956. Studies of serpulid tube formation. II. The calcium-secreting glands in the peristomium of *Spirorbis*, *Hydroides*, and *Serpula*. *Quart. J. micr. Sci.*, Vol. 97, pp. 421–7.

HOBSON, G. E. & REES, K. R., 1957. The annelid phosphokinases. *Biochem. J.*, Vol. 65, pp. 305–7.

HORRIDGE, ADRIAN, 1956. The nervous system of Ephyra larva of *Aurellia aurita*. *Quart. J. micr. Sci.*, Vol. 97, pp. 59–74.

JACKMAN, L. A. J., 1957. *Marine Aquaria*, 137 pp. London: Cassell and Co. Ltd.

JONES, W. C., 1956. Colloidal properties of the mesogloea in species of *Leucosolenia*. *Quart. J. Micr. Sci.*, Vol. 97, pp. 269–85.

KEYNES, R. D. & LEWIS, P. R., 1956. The intracellular calcium contents of some invertebrate nerves. *J. Physiol.*, Vol. 134, pp. 399–407.

KNOWLES, FRANCIS G. W. & CARLISLE, DAVID B., 1956. Endocrine control in the Crustacea. *Biol. Rev.*, Vol. 31, pp. 396–473.

LESTON, D., 1956. Systematics of the marine-bug. *Nature, Lond.*, Vol. 176, pp. 427–8.

MILLOTT, N. & YOSHIDA, M., 1956. Reactions to shading in the sea urchin, *Psammechinus miliaris* (Gmelin). *Nature, Lond.*, Vol. 178, p. 1300.

MURRAY, R. W., 1957. Evidence for a mechanoreceptive function of the ampullae of Lorenzini. *Nature, Lond.*, Vol. 179, pp. 106–7.

OLDFIELD, E., 1955. Observations on the anatomy and mode of life of *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius). *Proc. malac. Soc. Lond.*, Vol. 31, pp. 226–49.

ROSS, D. M., 1957. Quick and slow contractions in the isolated sphincter of the sea anemone, *Calliactis parasitica*. *J. exp. Biol.*, Vol. 34, pp. 11–28.

RUSSELL, F. S., 1956. Hydromedusae: Order: Anthomedusae. Families: Rathkeidae and Bougainvilliidae. (Zooplankton, Sheet **51**.) (1953.) Hydromedusae: Families: Pandeidae and Tiarannidae. (Zooplankton, Sheet **54**.) (1955.) *Fich. Ident. Zoopl.*, nos. 50–60.

SMITH, J. E., 1957. The nervous anatomy of the body segments of nereid polychaetes. *Phil. Trans.*, B, Vol. 240, pp. 135–6.

SOUTHWARD, A. J., 1956. The population balance between limpets and seaweeds on wave-beaten rocky shores. *Ann. Rep. for* 1955 (*no.* 68) *Mar. Biol. Stn Port Erin*, pp. 20–9.

WALKER, MARY ANN, 1956. Homogeneity tests on visual pigment solutions from two sea fish. Proc. physiol. Soc., 20–21 July 1956. *J. Physiol.*, Vol. 133, 56P.

WELSH, J. H., 1955. On the nature and action of coelenterate toxins. *Pap. Mar. Biol. and Oceanogr., Deep-Sea Research*, suppl. to Vol. 3, pp. 287–97.

Membership of the Association

The total number of members on 31 March 1957 was 900, being 39 more than on 31 March 1956; of these the number of life members was 109 and of annual members 791. The number of associate members is four.

During the year Mr E. H. E. Havelock, C.B., C.B.E., Dr A. G. Huntsman and Dr A. C. Redfield have been elected Honorary Members.

Finance

General Fund. The thanks of the Council are again due to the Development Commissioners for their continued support of the general work of the laboratory.

Private Income The Council gratefully acknowledge the following generous grants received during the year:

From the Fishmongers' Company (£400), The Royal Society (£100) British Association (£50), Physiological Society (£50), 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*.), Southampton (£31. 10*s*.), Reading (£10. 10*s*.), Nottingham (£10. 10*s*.), Hull (£10. 10*s*.), Exeter (£10. 10*s*.), Leicester (£10. 10*s*.), the Imperial College of Science and Technology (£10), Gonville and Caius College, Cambridge (£5), and the Zoological Society of London (£10. 10*s*.).

President, Vice-Presidents, Officers and Council

The following is the list of those proposed by the Council for election for the year 1957–58:

President

Prof. A. V. Hill, C.H., O.B.E., Sc.D., LL.D., F.R.S.

Vice-Presidents

The Earl of Iveagh, K.G., C.B., C.M.G.
Sir Nicholas E. Waterhouse, K.B.E.
Col. Sir Edward T. Peel, K.B.E., D.S.O., M.C.
Vice-Admiral Sir John A. Edgell, K.B.E., C.B., F.R.S.
Sir Edward J. Salisbury, Kt., C.B.E., D.Sc., F.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 Earl of Verulam
Prof. Sir James Gray, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S.

Council

To retire in 1958

Miss Vera Fretter, D.Sc.
N. A. Mackintosh, C.B.E., D.Sc.
G. E. Newell, Ph.D.
Prof. Lily Newton, D.Sc.
R. S. Wimpenny, O.B.E.

To retire in 1959

G. E. R. Deacon, C.B.E., D.Sc., F.R.S.
M. N. Hill, Ph.D.
O. D. Hunt
Prof. R. J. Pumphrey, Sc.D., F.R.S.
Prof. G. P. Wells, Sc.D., F.R.S.

To retire in 1960

Prof. E. Baldwin, Ph.D.
C. H. Mortimer, Dr.phil., D.Sc.
C. F. A. Pantin, Sc.D., F.R.S.
Prof. J. E. Smith, Sc.D.
H. G. Vevers, M.B.E., D.Phil.

Hon. Treasurer

Harrison S. Edwards, Westhumble Lacey, Near Dorking, Surrey

Secretary

F. S. Russell, C.B.E., D.S.C., D.F.C., F.R.S.
The Laboratory, Citadel Hill, Plymouth

The following Governors are also members of the Council:

R. G. R. Wall (Ministry of Agriculture, Fisheries and Food)
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)
S. Smith, Ph.D. (Cambridge University)
Edward Hindle, Sc.D., F.R.S. (British Association)
N. B. Marshall (Zoological Society)
Prof. Sir James Gray, Kt., C.B.E., M.C., Sc.D., LL.D., F.R.S. (Royal Society)

BALANCE SHEET 1956–57

THE MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM

BALANCE SHEET

31 MARCH 1957

	£	£
CAPITAL RESERVE ACCOUNT:		
As at 31 March 1956	174,827	
Add: Expenditure on fixed assets recovered	1,257	
		176,084
SURPLUS ACCOUNT:		
As at 31 March 1956	8,856	
Add: Composition Fees fund transferred	1,089	
	9,945	
Less: Excess of expenditure over income for the year	3,163	
		6,782
		182,866
BALANCES ON SPECIAL FUNDS (see annexed statement)		6,902
CURRENT LIABILITIES:		
Sundry creditors and accrued expenses	4,055	
Subscriptions received in advance	46	
		4,101
		£193,869

Note: Capital commitments outstanding amount to £10,400 (1956 £10,193) of which £9,300 will be recoverable under Development Fund grants.

JOHN E. HARRIS
N. B. MARSHALL } *Members of the Council*

	Cost, etc.	Depreciation	£
FIXED ASSETS:			
Boats and equipment:			
At cost:			
R.V. 'Sarsia'	137,761	—	137,761
At valuation as estimated by the Director at 31 March 1957:			
M.F.V. 'Sula'	12,500	—	12,500
R.L. 'Gammarus'	200	—	200
Laboratory apparatus, equipment and machinery:			
At cost *less* depreciation	14,637	2,668	11,969
Library at valuation by Mr Ridgill Trout in January 1941 plus additions as valued by the Director	22,300	—	22,300
	187,398	2,668	
			184,730
INVESTMENTS:			
General Fund (including Composition Fees) at book amount (Market value £1,277; last year £1,219)			1,609
E. T. Browne Bequest Funds at cost (Market value £3,346; last year £3,180)			4,497
			6,106
Less: Provision for diminution in value of investments			1,483
			4,623
CURRENT ASSETS:			
Stocks on hand as valued by the Director			1,700
Sundry debtors			982
Prepayments			276
Balances at bank and cash in hand			1,558
			4,516
			£193,869

AUDITORS' REPORT 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 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 31 March 1957 and of its excess of expenditure over income for the year ended on that date.

We have obtained all the information and explanations which we considered necessary. In our opinion the Association has kept proper books and the said accounts which are in agreement with them and with the said information and explanations, give in the prescribed manner the information required by the Companies Act 1948.

Norwich Union House
2 St Andrew's Cross
Plymouth
24 May 1957

PRICE WATERHOUSE & Co.
Chartered Accountants

INCOME AND EXPENDITURE ACCOUNT

FOR THE YEAR ENDED 31 MARCH 1957

	£	£
SALARIES, NATIONAL INSURANCE AND SUPERANNUATION SCHEME CONTRIBUTIONS		35,084
LABORATORY AND BOATS' CREWS' WAGES, NATIONAL INSURANCE, SUPERANNUATION SCHEME CONTRIBUTIONS AND EMPLOYERS' LIABILITY INSURANCE		29,202
UPKEEP OF LIBRARY		709
SCIENTIFIC PUBLICATIONS, *less* SALES		2,015
UPKEEP OF LABORATORIES:		
Buildings and machinery	910	
Electricity, gas, coal and water	1,254	
Chemicals and apparatus	1,965	
Depreciation of Laboratory apparatus, equipment and machinery (no depreciation is provided on the other fixed assets)	1,330	
Rents and insurance	219	
Travelling expenses	792	
Audit fee	126	
Stationery, postage, telephone and sundries	1,433	
Specimens	196	
Collecting expenses and upkeep of truck	359	
		8,584
MAINTENANCE OF BOATS:		
Petrol, oil, paraffin, etc.	1,866	
Maintenance and repairs	6,371	
Insurances	2,303	
Hire of Decca Navigator—R.V. 'Sarsia'	395	
		10,935
ENTERTAINMENT EXPENSES		39
		£86,568

	£	£
GRANTS AND TABLE RENTS:		
Ministry of Agriculture, Fisheries and Food Grant from Development Fund	74,172	
Fishmongers' Company	400	
Miscellaneous (including Royal Society £100, British Association £50, Physiological Society £50, Cornwall Sea Fisheries Committee £10, Universities of London £210, Cambridge £125, Oxford £100, Bristol £50, Birmingham £31. 10*s*., Leeds £20, Southampton £31. 10*s*., Durham £10. 10*s*., Exeter £10. 10*s*., Leicester £10. 10*s*., Manchester £10. 10*s*., Nottingham £10. 10*s*., Hull £10. 10*s*., Reading £10. 10*s*., and Sheffield £10. 10*s*., Imperial College, £10, Zoological Society of London £10. 10*s*., Ministry of Works £104, Imperial Chemical Industries Ltd. £52. 10*s*., International Paints Ltd. £52. 10*s*., Gonville and Caius College, Cambridge £5)	1,209	
		75,781
SUBSCRIPTIONS (excluding those received in advance)		802
SALES:		
Specimens	2,901	
Fish	1,015	
	£	
Nets, gear and hydrographical apparatus	850	
Less: Cost of materials	636	
	214	
		4,130
SUNDRY PUBLICATIONS		2
INCOME FROM INVESTMENTS		53
INTEREST ON BANK DEPOSITS, *less* CHARGES		171
AQUARIUM:		
Admission Fees	2,561	
Sale of guides	54	
	2,615	
Less: Maintenance, printing and advertising	149	
		2,466
BALANCE being excess of expenditure over income for the year		3,163
		£86,568

MOVEMENTS ON SPECIAL FUNDS DURING THE YEAR TO 31 MARCH 1957

	Aquarium Sinking Fund	Composition Fees	E. T. Browne Bequest			A. R. T. Momber Bequest	Rockefeller Foundation Fund	Library Extension and Dogfish House	'Plymouth Marine Fauna' Fund	Reservoir and Sea Water Tanks	Research Funds*	TOTAL
			Library	Special Apparatus	Scientific Publications							
	£	£	£	£	£	£	£	£	£	£	£	£
BALANCE AT 31 MARCH 1956 (after providing £1,487 for diminution in value of investments)	386	1,030	1,012	2,114	325	1,124	(9)	1,353	(3)	—	190	7,522
Add: Income during year												
Grants	—	—	—	—	—	—	2,672	2,425	—	3,335	2,515	10,947
Income from investments	—	—	40	84	17	—	—	—	—	—	—	141
Bank deposit interest	13	—	—	—	—	39	—	—	—	—	—	52
Other income	32	48	—	—	121	—	—	—	—	—	—	201
Transfers between Special Funds	—	—	—	—	—	(1,163)	—	—	—	1,163	—	—
Decrease in provision for diminution in value of investments	—	11	12	24	1	—	—	—	—	—	—	48
	431	1,089	1,064	2,222	464	—	2,663	3,778	(3)	4,498	2,705	18,911
Deduct: Expenditure during year	—	—	13	170	—	—	2,394	2,591	—	3,335	2,417	10,920
Transfer to General Fund	—	1,089	—	—	—	—	—	—	—	—	—	1,089
BALANCE AT 31 MARCH 1957	£431	—	£1,051	£2,052	£464	—	£269	£1,187	£(3)	£1,163	£288	£6,902

* Including International Paints Ltd. Research Fellowship.

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, and, since that date, a new library and further laboratory accommodation have been added.

The Association is maintained by subscriptions and donations from private members, universities, scientific societies and other public bodies; 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. 27 (p. 761) and Vol. 31 (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.

TERMS OF MEMBERSHIP

		£	s.	d.
Annual Members	per annum	1	1	0
Life Members	Composition fee	15	15	0
Founders		100	0	0
Governors		500	0	0

Members of the Association have the following rights and privileges: they elect annually the Officers and Council; they receive the Journal of the Association free by post; they are admitted to view the laboratory at Plymouth, and may introduce friends with them; they have the first claim to rent a place in the laboratory for research, with use of tanks, boats, etc.; they have the privilege of occupying a table for one week in each year free of charge; and they have access to the books in the library at Plymouth.

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

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